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ABSTRACT

The decision to process an incoming stimulus attentively - and to trigger a follow-up cascade of high-level processes - is strategic for the human brain as it becomes transiently unavailable to subsequent stimulus processing. In this study, we set to identify brain networks that carry out such evaluations. We therefore assessed the time-course of neural responses with intracerebral EEG in human patients during an attentional reading task, contrasting to-be-attended vs. to-be-ignored items. We measured High-Frequency Activity [50–150 Hz] as a proxy of population-level spiking activity and we identified a crucial component of a Gate-Keeping Mechanism bilateral in the mid-Ventro-Lateral Prefrontal Cortex (VLPFC), at the interplay of the Ventral and Dorsal Attention Networks, that selectively reacts before domain specialized cortical regions that engage in full stimulus analysis according to task demands.

1. Introduction

Attentive processing of an incoming stimulus is characterized by a cascade of high-level processes which make the prefrontal cortex transiently unavailable to subsequent events (Raymond et al., 1992). It is therefore crucial that attention networks include a 'gate-keeper' that quickly evaluates the behavioral relevance of events capturing attention and most often leave them at the doorstep, to save resources for later, more important and relevant, events. This 'gate-keeper' (GK) performing late attentional selection has yet to be "caught in the act" in the human brain, because of the difficulty to record its fast reaction with high anatomical precision.

The protection of cognitive resources is partially mediated by early attentional filtering mechanisms that make sensory systems more responsive to certain items, defined by physical features or ecological characteristics (i.e. red objects, or faces, Desimone and Duncan, 1995; Eimer, 2014; Eimer and Kiss, 2007). However, considerable evidence demonstrate vulnerabilities of such filter: irrelevant stimuli can capture attention in a bottom-up fashion because of their salient physical features (Theeuwes, 2010; Theeuwes and Godijn, 2001; Yantis, 1996), their subjective utility (Donohue et al., 2016) or their similarity to task-relevant items (a phenomenon called contingent involuntary orienting; Bacon and Egeth, 1994; Eimer and Kiss, 2007; Folk et al., 1994; Gibson and Kelsey, 1998; Lamy et al., 2004). EEG studies have shown

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that this capture occurs quickly, within 250 ms (Sawaki and Luck, 2010), suggesting a critical time window around that latency for a second filter that would reject such false-positives, with a strict application of task-rules.

In non-human primates, rules governing stimulus-response mapping during tasks can be decoded from neural activity in several regions of the lateral prefrontal cortex (LPFC) (Sigala et al., 2008; Wallis et al., 2001; White and Wise, 1999). In humans, fMRI Multi-Variate Pattern Analysis has shown that activity in the same regions can be used to discriminate between different task-rules when participants switch between tasks (Woolgar et al., 2016). Further, recent recordings in non-human primates have shown that neurons in the posterior portion of the principal sulcus, in the LPFC, process all incoming stimuli within 200 ms and differentially according to task-rules, as expected from a 'gate-keeper' (Stokes et al., 2013). The LPFC thus appears as a plausible candidate in Humans to hold the necessary information to discriminate between task-relevant and irrelevant items and act as a 'gate-keeper'. However, any evidence that the Human LFPC would react only to task-relevant items, or later than 300 ms would immediately rule out that scenario, because the former would indicate that filtering has already taken place, and the latter would indicate that the LPFC reacts too late to prevent full processing of distractors. Our objective was therefore two-fold: test whether the Human LPFC reacts to all incoming stimuli with similar latency to monkeys' observations, within 250–300 ms; and if so, identify precisely which regions of the LPFC activate first within that time-range.

Although simple in principle, such study had not been conducted so far, probably because it requires extensive, distributed and yet local electrophysiological recordings of the Human PFC with both millisecond and millimetric precision, in a task contrasting stimuli that should elicit a full cognitive response vs stimulus that should be ignored (relevant vs irrelevant items). This is a very strong constraint, but it can be achieved with intracranial EEG in epilepsy patients during their pre-surgical exploration, provided that a large population of patients be recorded in a single task with the desired characteristics, because intracranial electrodes sample only a very limited part of the PFC in each patient, and vary in position across individuals. We had the opportunity to access and analyze such a rare dataset and found that across more than 2000 FC (including PFC, motor and premotor cortex) sites in 85 patients, all sites with the specific characteristics of a 'gate-keeper' lied in the Ventral-LPFC, in a region anatomically consistent with localizations found in non-human primates. Within our spatial sampling, the Inferior Frontal Sulcus (IFS) was the first region of the PFC to process all incoming stimuli with a timing that was a) ideal to prevent extensive cognitive processing of irrelevant stimuli capturing attention, between 200 and 250 ms (e.g., Jung et al., 2008) and b) explained the phenomenon of contingent involuntary orienting. We propose that this region harbors a crucial component of the proposed Gate-Keeper mechanism, ideally located to harmonize the conflicting influences of the ventral and dorsal attentional networks, and immediately adjacent to regions involved in the inhibition of automatic responses to task-irrelevant stimuli (e.g., Miller and Cohen, 2001).

2. Material and methods

2.1. Participants

Intracranial EEG recordings were obtained in 85 neurosurgical patients with intractable epilepsy at the Epilepsy Department of Grenoble Neurological Hospital (Grenoble, France) and Epilepsy Department of Lyon Neurological Hospital (Lyon, France) between 2009 and 2015. Eleven to fifteen semi-rigid, multi-lead electrodes were stereotactically implanted in each patient (stereotactic EEG –SEEG-, Kahane et al., 2003). The SEEG electrodes had a diameter of 0.8 mm and, depending on the target structure, consisted of 10–15 contact leads 2 mm wide and 1.5 mm apart (i.e. 3.5 mm center-to-center, DIXI Medical Instruments). Cortical implant selection was entirely based on clinical purposes, with no reference to the present experimental protocol. Thus, it is an important source of inter-individual difference regarding overall cortical sampling. All electrodes showing traces of epileptiform activity were excluded from the present study (visual inspection by the clinical team). All participants were native French speakers and gave written informed consent; all experimental procedures were approved by the Institutional Review Board and by the National French Science Ethical Committee (CPP Sud-Est V 09-CHU-12).

2.2. Stimuli and tasks

In a task mixing (see Fig. 1), across trials, task-relevant and task-irrelevant stimuli, differentiated by a simple attribute (i.e. word colour), a "Gate Keeper" should respond to all stimuli, at a latency which should precede the specific processing of relevant items defined by task instructions (task-relevant items are first recognized as such, then processed). This main property was tested using an Attentive Reading task (see below for task description).

2.3. Tasks description

2.3.1. Attentive reading (AR)

This task was adapted from Nobre et al. (1998). In each experimental block, participants were presented with two intermixed stories, shown word by word at a rapid rate (one word every 700 ms shown for 200 ms). One of the stories was written in grey (on a black screen) and the other in white. Consecutive words with the same color formed a meaningful and simple short story in French. Participants were instructed to read the grey (low contrast) story to report it at the end of the block, while ignoring white (high contrast) words. Note that colors were chosen so that an early filter based on physical attributes only would be minimally efficient at filtering-out task-irrelevant items (they appear at the same location as task-relevant items and have higher contrast).

Each block comprised 400 words, with 200 grey words (task-relevant, attended stimuli: the targets) and 200 white words (task-irrelevant, to-be-ignored stimuli: the distractors). Color distribution within the 400 words was pseudo-randomized, so that participants could not predict whether the subsequent word was to be attended or not; (there were never more than three consecutive words of the same color). After the block, participants were asked questions about the attended text, which could not have been answered from general knowledge. Some words of the 'ignore' story were shuffled so that any participant attending that story also would have noticed that obvious problem. When asked ("did you notice anything wrong with the white story?"), none of the patients were able to report anything wrong. They were in fact puzzled by the inquiry ("but you told me to ignore the white story!").

Note that since all words were flashed foveally, and since participants could not guess the color of the upcoming word, all stimuli captured visual attention by design. Although an early filtering mechanism might in theory bias visual perception in favor of target words using their physical difference with distractors, this is unlikely since targets have a *lower luminosity* than distractors and to our knowledge, there is no known early filtering mechanism that can select out high-contrast stimuli. In fact, we observed in some patients (data not shown) that high-contrast distractors elicited initially a stronger response in the visual cortex than low-contrast targets, as expected from a comparison of their physical saliency.

Therefore, success in the task largely relies on the participant's ability to prevent extensive processing of distractors thanks to late filtering mechanism acting before the activation of the reading network and protecting verbal working memory. It is indeed essential that verbal working memory hold only the most recent words of the attended story, as one meaningful sentence rather than a meaningless string of unrelated words mixing both stories. Overall, the AR task is particularly well suited to identify a GK because it involves a late selection process between relevant and irrelevant stimuli.

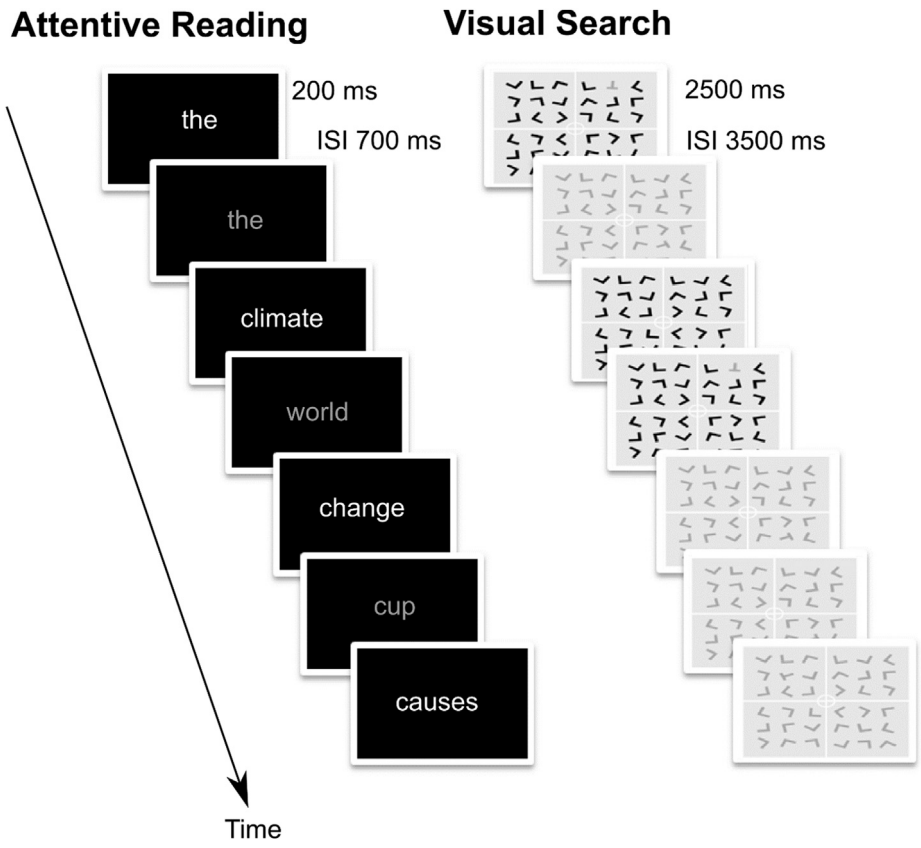

Fig. 1. The two behavioral tasks proposed in the study. The Attentive Reading task and the Visual Search task, see Methods section for details.

2.3.2. Visual search task (VS)

A majority of participants (five of the seven presented in the attentional task) also performed a visual search task as part of a standard battery used for pre-surgical functional brain mapping. We reasoned that the "Gate-Keeper" should also be a key player during visual search tasks, where a designated item must be detected in an array of distractors (Treisman and Gelade, 1980; see also Ossandón et al., 2011; Ossandón et al., 2012). Despite dissimilarities between the stimuli, Visual Search and Attentional Reading consistently asking the same question to the 'Gate-Keeper" ("*is this item relevant to the task?*"). The only difference is that in Visual Search, new items are presented to the visual system through visual/attentional scanning of the image, while they are delivered one by one on the computer screen during Attentional Reading. During Visual Search, we therefore expect the "Gate-Keeper" to be continuously active to keep a memory trace of the target stimulus, to discriminate between task-relevant and to-be-ignored items (Eimer, 2014; Olivers et al., 2011). The "Gate-Keeper" should therefore display an early response to all stimuli during Attentional Reading and a continuous activation throughout Visual Search.

The Visual Search task was an adaptation of a classical visual search test developed by Treisman and Gelade (1980). Each stimulus consisted of an array of 36 letters (6 × 6 square arrays with 35 Ls and one T randomly arranged). Participants were instructed to search as fast as possible for the "T" and press a response button as soon as they found it. Two main experimental conditions were contrasted: an *easy* search (pop out) and a *difficult* (sustained) search condition (see Ossandón et al., 2012). In the easy condition, the target was grey while all distracters were black. To dissociate correct from incorrect responses participants were required to indicate whether the target was located in the upper or lower half of the display by pressing one of two response buttons. In the difficult condition, both distractors and target were grey. The difficult and easy condition stimuli were presented randomly for a fixed duration of 3s and with an inter-stimulus interval of 1s. Each experiment consisted of 6 runs of 5 min recording.

Participants also performed additional tasks as part of a near-systematic neuropsychological evaluation, some of them brought important additional information for this manuscript and are described in the supplementary material section (a visual oddball task and a verbal categorization task, see Supplementary Fig. 1).

Experiments took place in patients' hospital rooms. Stimuli were presented to the participants on a 17-inch computer screen at 60 cm viewing distance and the average word subtended 2 degrees of visual angle. Cognitive task stimulation was delivered via the Presentation stimulus delivery software (Neurobehavioral systems Inc).

2.4. Intracranial recordings

Intracranial recordings were conducted using a video-SEEG monitoring system (Micromed), which allowed the simultaneous data recording from 128 depth-EEG electrode sites. The data were bandpass filtered online from 0.1 to 200 Hz and sampled at 512 Hz in all patients. At the time of acquisition, the data were recorded using a reference electrode located in white matter, and the signal in each recording site was subsequently re-referenced with respect to its closest site (bipolar derivations). This bipolar montage has a number of advantages over common referencing. It helps eliminate signal artifacts common to adjacent electrode contacts (such as the 50 Hz main artifact or distant physiological artifacts) and achieves a high local specificity by cancelling out effects of distant sources that spread equally to both adjacent sites through volume conduction. It might complicate functional connectivity analysis based on phase estimation (Arnulfo et al., 2015), but such analysis was not performed here. The spatial resolution achieved by the bipolar SEEG is on the order of 3 mm (Jerbi et al., 2009; Lachaux et al., 2003; Kahane et al., 2003). Both spatial resolution and spatial sampling achieved with SEEG differ slightly from that obtained with subdural grid electrocorticography (Jerbi et al., 2009).

2.5. Data analysis and statistical analysis

Time–frequency analysis, HFA power, and envelope computations.

The frequency band of interest, between 50 Hz and 150 Hz, was defined from preliminary time–frequency (TF) analysis of the SEEG data using wavelets (Tallon-Baudry et al., 1997), performed with in-house software package for electrophysiological signal analysis (ELAN) developed at INSERM U1028, Lyon, France (Aguera et al., 2011), and from previous studies by our group (Jerbi et al., 2009).

Raw data were transformed into High-Frequency Amplitude (HFA) time-series with the following procedure (Ossandón et al., 2011; Perrone-Bertolotti et al., 2012): step *1)* continuous SEEG signals were first bandpass-filtered in multiple successive 10 Hz wide frequency bands (e.g., 10 bands from [50–60 Hz] to [140–150 Hz]) using a zero phase shift no causal finite impulse filter with 0.5 Hz roll-off. *Step 2)* next, for each bandpass-filtered signal we computed the envelope using standard Hilbert transform (Le Van Quyen et al., 2001). The obtained envelope was down-sampled to a sampling rate of 64 Hz (i.e., once sample every 15.625 ms). *Step 3)* for each band this envelope signal (i.e., time-varying amplitude) was divided by its means across the entire recording session and multiplied by 100. This procedure yields instantaneous envelope values expressed in percentage (%) of the mean. *Step 4)* the envelope signals (expressed in %) computed for each consecutive frequency bands (the ten bands of 10 Hz intervals between 50 and 150 Hz) were averaged together to provide one single time series (High-Frequency Activity, HFA) across the entire session. By construction, the mean value of that time series across the recording session is equal to 100. Finally, the HFA time-series was epoched into data segments centred around each stimulus (in a window around the stimulus onset and in which the duration before and after the stimulus onset was adapted for each task), and then averaged together for each stimulus category. Note that computing the Hilbert envelopes in 10 Hz sub-bands and normalizing them individually before averaging over the broadband interval allows us to account for a bias toward the lower frequencies of the interval that would otherwise occur due to the 1/f drop-off in amplitude. The resulting signal is a measure of neural activity which has been shown to highly correlate with behavior at the single-trial level, and in real-time (Jerbi et al., 2009; Ossandón et al., 2012).

Statistical analyses were performed on high-frequency activity time series, HFA [50–150 Hz], computed as above. To test for significant increases or decreases compared to baseline activity, we used paired-sample Wilcoxon signed rank test, followed by false discovery rate (FDR) correction across all time samples (corrected p values). This allowed for quantitative definition of the onset time and duration of activation of specific recording sites. To compare the activity of paired conditions in each of the task we used the non-parametrical Kruskal–Wallis test followed by FDR correction across all time samples.

Finally, the anatomical display of all significant HFA modulations was obtained by pooling data from all participants and mapping them onto the standard Montreal Neurological Institute (MNI) single-subject brain based on the localization of each electrode. The precise anatomical location of the electrodes (and their MNI coordinates) were obtained by aligning the pre-implantation and the post-implantation (showing the electrodes in place) structural MRIs of each patient using the NUTMEG toolbox (Dalal et al., 2004) and IntrAnat (Deman et al., 2018), a specific toolbox interfacing with the BrainVisa software (IntrAnat Electrodes, GIN INSERM U1216, Grenoble, available on the WEB at https://f-tract.eu/index.php/softwares/).

3. Results

Our analysis focused on High-Frequency Activity [50–150 Hz] as a proxy of population-level spiking activity, to facilitate the functional and latency comparisons with non-human primate studies that combined single-unit and multi-unit activity into a mean spiking activity measure (Stokes et al., 2013).

In the Attentive Reading (AR) task, the main intervention of a "Gate-Keeper" would be to process all incoming words and authorize elaborate cognitive processing via the reading network for target words. And as shown in Fig. 2, HFA recorded in 85 patients revealed an extensive activation of the reading network for attended words only after 300 ms, but not before, including regions cardinal to working memory, semantic and phonological processing in the inferior frontal gyrus, the precentral gyrus and the left supramarginal gyrus. This defines a critical window of operation for the "Gate-Keeper" in the PFC, before 300 ms. Furthermore, we checked that none of the sites active before 250 ms in this paradigm (visible as red spots in Fig. 2) was language-specific: all of them were task-responsive during additional non-verbal tasks performed by the participants (the visual search task and also a visuo-spatial working memory task not presented in the present study).

Before that latency, we observed in seven patients a strong response in the lateral prefrontal cortex (LPFC) between 200 and 300 ms after both target and distractor words. Note that a less conservative analysis with no correction for multiple comparisons, and a threshold set at $p = 0.01$ detected the same sites. Those responses were the earliest significant HFA increases we observed in the prefrontal cortex (Wilcoxon comparison with prestimulus baseline, FDR correction), and all were spatially selective: the response quickly vanished when considering sites away from the sulcus on the same linear depth-electrode (see Supplementary Fig. 2). Quite remarkably, six of the seven sites were located in the same confined location of the Inferior Frontal Sulcus, in the extension of the ascending vertical branch of the lateral sulcus which separates the opercular and triangular parts of the inferior frontal gyrus (Donkelaar Ten et al., 2018), at the junction between the Ventro-Lateral Prefrontal Cortex and the Dorso-Lateral Prefrontal Cortex (4 sites in the left hemisphere in 4 patients, and 2 in the right hemisphere, in two patients) (see Fig. 3 and Supplementary Fig. 1 for detailed anatomical illustrations). The remaining site was slightly more anterior, in the triangular part of the inferior frontal gyrus and differed functionally from the other sites. The remaining site was slightly more anterior, in the triangular part of the inferior frontal gyrus and differed functionally from the other sites (see P1 in Fig. 3). Note also that early frontal responses were also observed more posteriorly, immediately anterior to the precentral sulcus, but in regions too remote functionally and anatomically from the monkey lunate sulcus to constitute a homologous region.

The response we observed peaked between 156 ms and 234 ms (Attended condition M = 204 ms, SD = 28 ms; Ignored condition M = 193 ls, SD = 16 ms) (see Fig. 3), with a variability across patients, and a response which was also stronger or equivalent for targets, similar to observations by Stokes et al. (2013) in macaque monkeys, but later. Yet, in all patients, the peak occurred before the first differentiation between responses to targets and distractors in language-related areas (such as the inferior frontal gyrus or the Supramarginalis Gyrus, see Fig. 4 for examples in 3 of 7 patients, in which we had the opportunity to record canonical language regions).

The function of the GK implies that it should evaluate any attended stimulus to decide whether it should be processed more extensively or not, based on ongoing task rules. One implication is that the "Gate-Keeper" should be active not only when stimuli are presented one by one, as in the Attentional Reading task, but also in a much more dynamic way, during the visual search, when attention and/or gaze moves through a visual display in search of the desired item (i.e., the target). Indeed, successful visual search requires a mechanism of continuous comparison between scrutinized items and the memory trace of the target, called attentional template (Eimer, 2014). This mechanism mirrors the action of the "Gate-Keeper" in the Attentional Reading, except that the flow of incoming stimuli is dictated by attention/oculomotor behaviour instead of an externally imposed timing. It follows that the sites identified with the Attentional Reading task should be continuously active in the Visual Search task. We could test that prediction in five patients, and as shown in Fig. 5 for some patients, the HFA of the sites identified above was each time continuously active during the total time of visual search, showing

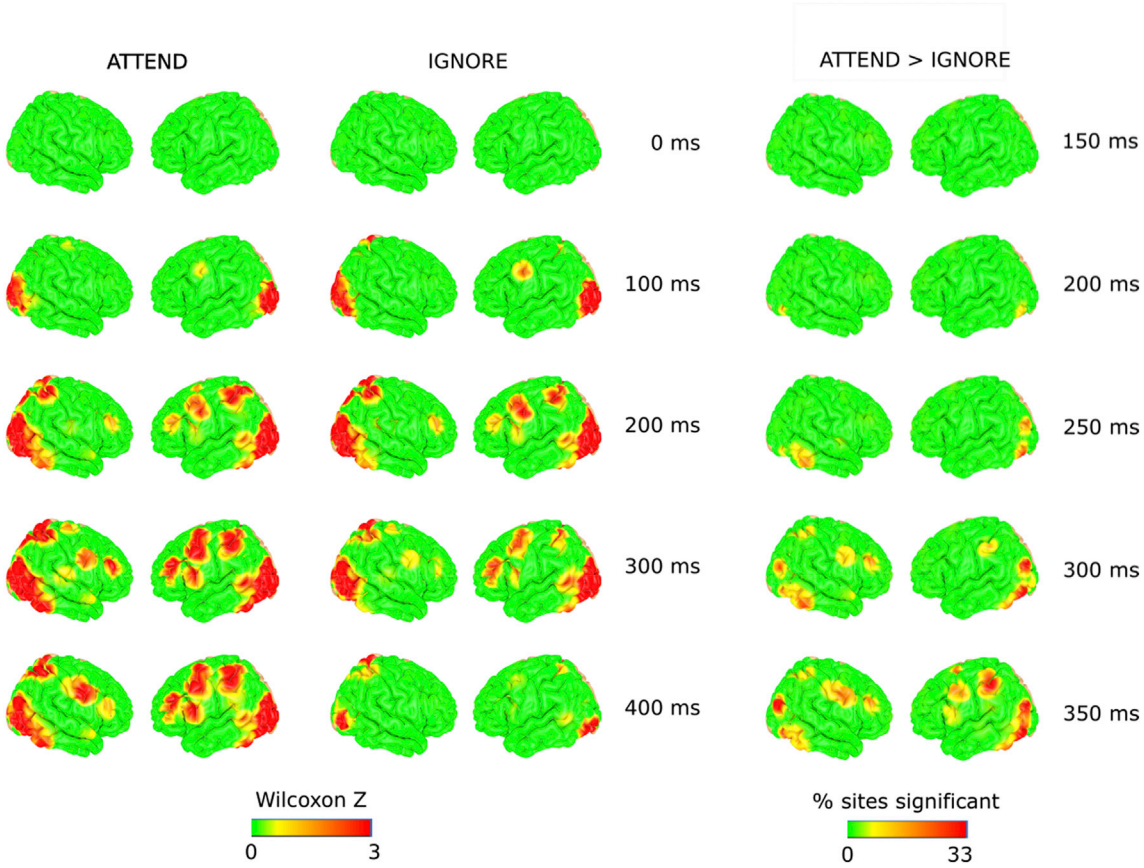

Fig. 2. Global cortical dynamics in response to Attend and Ignore condition (Attentive Reading task) for 85 patients, as revealed by High-Frequency Activity increase relative to baseline (HFA [50–150 Hz], energy decrease not shown). The cortical response diverges between the two conditions only after 300 ms (Attended > Ignore). After 300 ms HFA is higher for Attend than for Ignore words in the reading network including for instance in the left inferior frontal gyrus as well as in the posterior superior temporal cortex and the inferior parietal regions. See sup Fig. 3 for whole brain coverage.

also that the IFS response is not specific to verbal semantic stimuli.

Some of those patients performed additional cognitive tasks. We used this opportunity to test even further that our sites of interest were active as long as visual stimuli are processed attentively. This is a key feature of a GK mechanism, to extract information from an incoming stimulus until it decides that no more information is needed. In the VS task, our region of interest stopped its response slightly before the reaction time because the target had been found, and despite the fact that the stimulus was still displayed on screen: there was no need to extract any additional information. The supplementary section provides additional data consistent with this scenario; when asked to perform a visual, phonological or semantic categorization of written character strings, the response stopped again before the reaction time while participants still viewed the stimulus but didn't need to process it actively. Finally, we observed that the response can also be observed when a participant pays attention to a mental image (see Supplementary Movie), which means that our Region of Interest is involved in an active information exchange with visual areas characteristic of object-based attention: when it ceases to be active, attention is withdrawn from the object (stimulus), which is a key feature of a GK mechanism.

4. Discussion

Our daily environments are crowded with salient stimuli, which can deviate attention from the task at hand. We might notice many of them, but our attention is protected by a filtering mechanism, an attentional "Gate-Keeper", which quickly evaluates their behavioral relevance based on task-rules and leaves task-irrelevant events at the doorstep of cognition. Using direct intracranial EEG recordings, we "caught in the act" a single cortical region in the lateral prefrontal cortex (LPFC) with the desired functional and temporal characteristics of such a "Gate-Keeper": It reacts to incoming stimuli within 250 ms and lies precisely in the Inferior Frontal Sulcus (IFS), a subregion of the LPFC that was highlighted in a recent meta-analysis performed by Woolgar et al. (2016) summarizing regions where task-rules could be decoded in Humans from fMRI Multi-Variate Pattern Analysis (pIFS with $x = -40$, $y = 37$, $z = 27$ in Woolgar et al., 2016). Although we cannot claim that this region harbors the totality of the "Gate-Keeping mechanism", because it might also involve other cortical and subcortical regions not recorded in our study; we demonstrate that in Humans, as in macaque monkeys, that part of the LPFC reacts sufficiently fast to all incoming events to prevent full processing of task-irrelevant stimuli and save cognitive resources.

Since functional specialization can change drastically across a single sulcus, even in the human prefrontal cortex (e.g. Vidal et al., 2012 and Supplementary Fig. 1) one strength of the present study was to identify this putative "Gate-Keeper" anatomically in individual participants. This precision is characteristic of neurophysiological studies in non-human primates but not of human studies, which often rely on group analysis or even meta-analyses (e.g. Chein et al., 2011). Our individual data show that our target region lies, partly at least, deep in the IFS, next to the pars triangularis (BA 45) dorsally adjacent to BA 9/46. It is also observed in both hemispheres, which makes it robust to focal brain lesions.

The IFS constitutes the anterior part (Fedorenko et al., 2013; Duncan and Owen, 2000) of a global network showing increased, domain-general, activity with higher task-demand, the Multi-Demand (MD) or task-positive network (Amunts et al., 2010; Badre and Wagner, 2007; Badre and Wagner, 2007; Duncan, 2010; Fox et al., 2005; Miller and Cohen, 2001). IFS is anatomically connected with the Dorsal

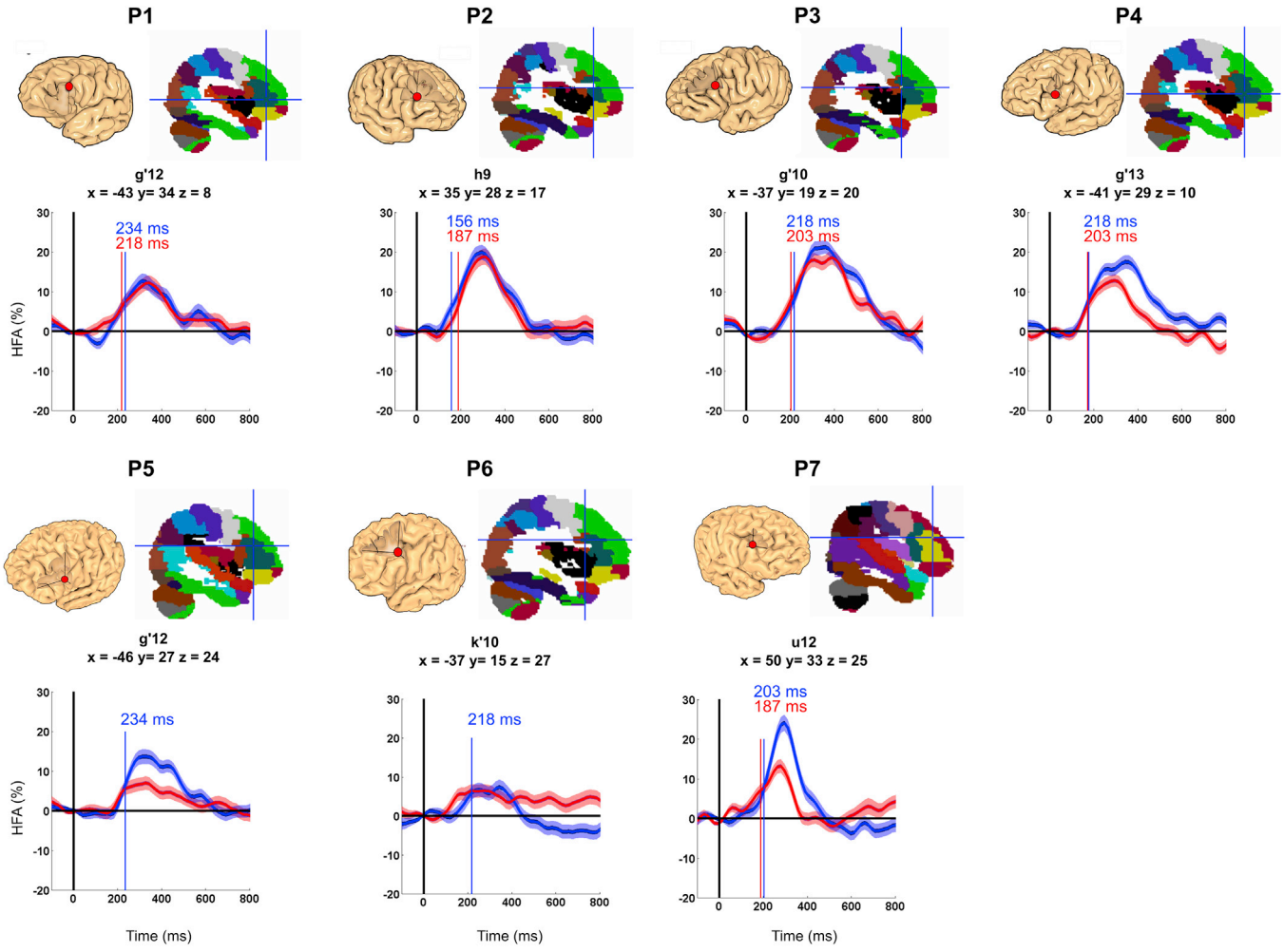

Fig. 3. Neural response to Attend (blue) and Ignore (red) word stimuli in cortical sites of interest in patients P1–P7 (HFA [50–150 Hz] ±SEM) during Attentive Reading task and individual anatomical location for each of presented cortical site. Anatomical location was presented in individual 3D plot and AAL template (electrode name and MNI coordinates of each of recorded cortical sites was also showed). Colored verticals lines and respective ms values indicate the first time samples in which HFA was significantly different from pre-stimulus baseline level ($p < .05$, Wilcoxon signed rank test, FDR corrected for multiple comparisons) for Attended (blue) and Ignored (red) condition.

and Ventral Attentional Networks (DAN and VAN) proposed by Corbetta and collaborators (Corbetta et al., 2008; Corbetta and Shulman, 2002). In their model, the DAN supports top-down, goal-directed, guidance of attention towards anticipated task-relevant stimuli and comprises the dorso-lateral Prefrontal Cortex; while the VAN extends in the Inferior and Middle Frontal Gyrus and acts as a 'circuit-breaker' which can reorient attention away from DAN priorities towards salient and *possibly*-relevant events (Corbetta and Shulman, 2002; Indovina and Macaluso, 2006; Yantis and Egeth, 1999). The "Gate-Keeper mechanism" is thus ideally located to integrate bottom-up (stimulus-driven features) and top-down (expectations related to the ongoing cognitive task) information from the VAN and DAN (Corbetta and Shulman, 2002) and determine the eventual impact of unexpected sensory events on the global brain dynamics.

Interestingly, comparative fMRI connectivity analysis in monkeys and humans have revealed an analogy between the LPFC and an area in the macaque brain in which the firing rates of prefrontal cells code for task rules (Mitchell et al., 2016). And indeed, Stokes et al. (2013) recorded a peak response around 150–200 ms, similar to our observations in the lateral region including BA8, 9/46 and 45, which also came after both targets and non-targets and that the authors associated with adaptive routing of processing trajectories (how to react to the stimulus), in line with our definition of a "Gate-Keeping mechanism". The response we recorded in the IFS is to our knowledge their closest equivalent in Humans and turns out to be later than in monkeys, as found in most sensory areas. This suggests that the whole cognitive cycle is shortened in species with faster behavioural dynamics.

Several models of cognitive architecture have proposed that interaction with the external world repeats short cycles of perception, understanding and action selection ("cognitive cycles"; Madl et al., 2011). In most models, the cycle breaks down into two successive components: one for perception/cognition and one for decision/action, with a temporal delimitation around 200 ms (with some variations across models, Anderson et al., 2004; Card et al., 1986). This is when an efficient "Gate-Keeper" should act to save cognitive resources for task-relevant items, while processing all salient stimuli (potential threats should not remain unnoticed).

The latency of the IFS activation is therefore ideal for such a role: at 250 ms, the reaction is too late to prevent the capture of attention by salient events, but early enough to prevent further high-level processing. Indeed, EEG studies of attention capture suggest that salient stimuli can deviate spatial attention within 250 ms, with a characteristic Event-Related Potential called N2pc (Sawaki and Luck, 2010). The IFS response occurs by the end of that process, but precedes the active processing of relevant items according to task instructions, such as phonological/semantic processing in specialized temporo-frontal language

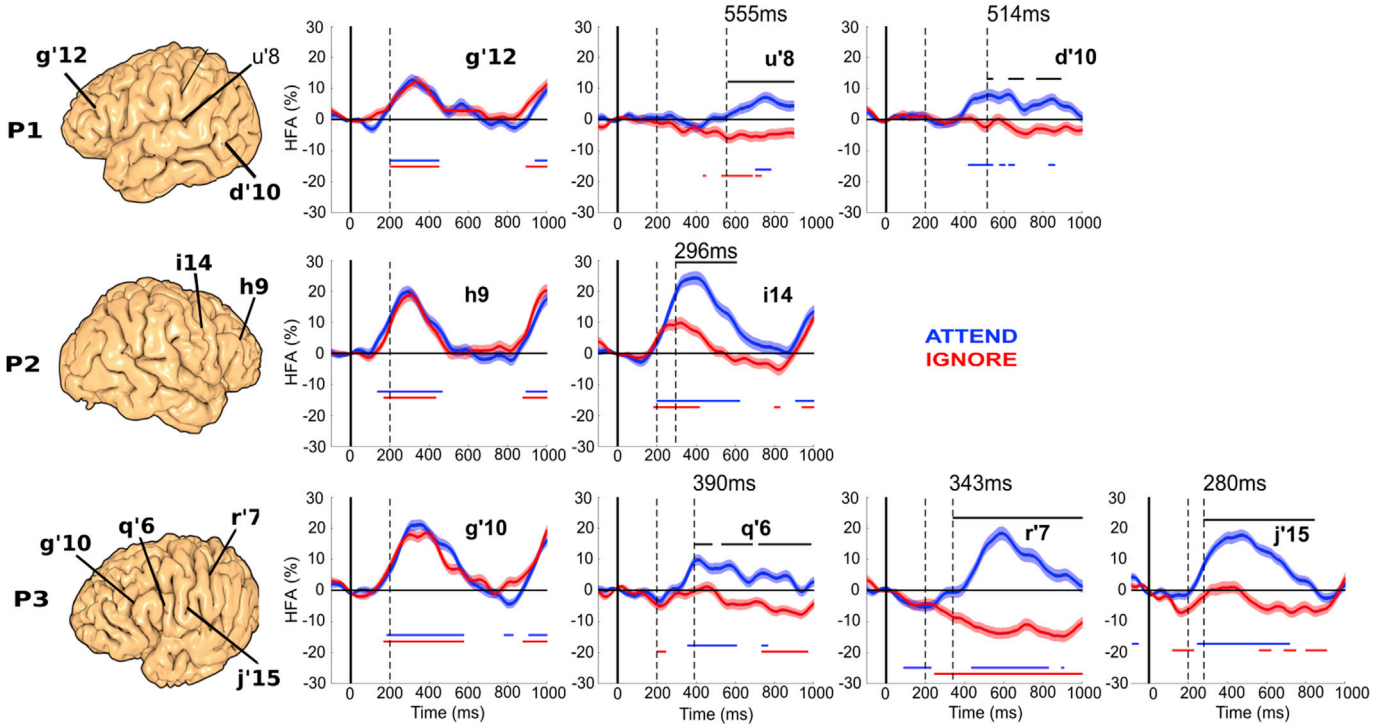

Fig. 4. Effect of task-relevance in the reading network during the Attentive Reading task for patients P1–P3, as measured by HFA [50–150 Hz]. (Average HFA (±SEM) across trials for the Attend (blue) and Ignore (red) conditions. Horizontal colored lines indicate time samples when HFA was significantly different from baseline ($p < .05$, Wilcoxon signed rank test, FDR corrected for multiple comparisons); horizontal black lines above the curves indicate time samples at which HFA was significantly different between Attentive and Ignore condition ($p < .05$, Kruskal–Wallis, FDR corrected for multiple comparisons) and vertical dotted line represent the first 200 ms and the first time sample at which a significant differences between Attend and Ignore conditions were observed (including the numeric value of the first significant time sample post-stimulus presentation).

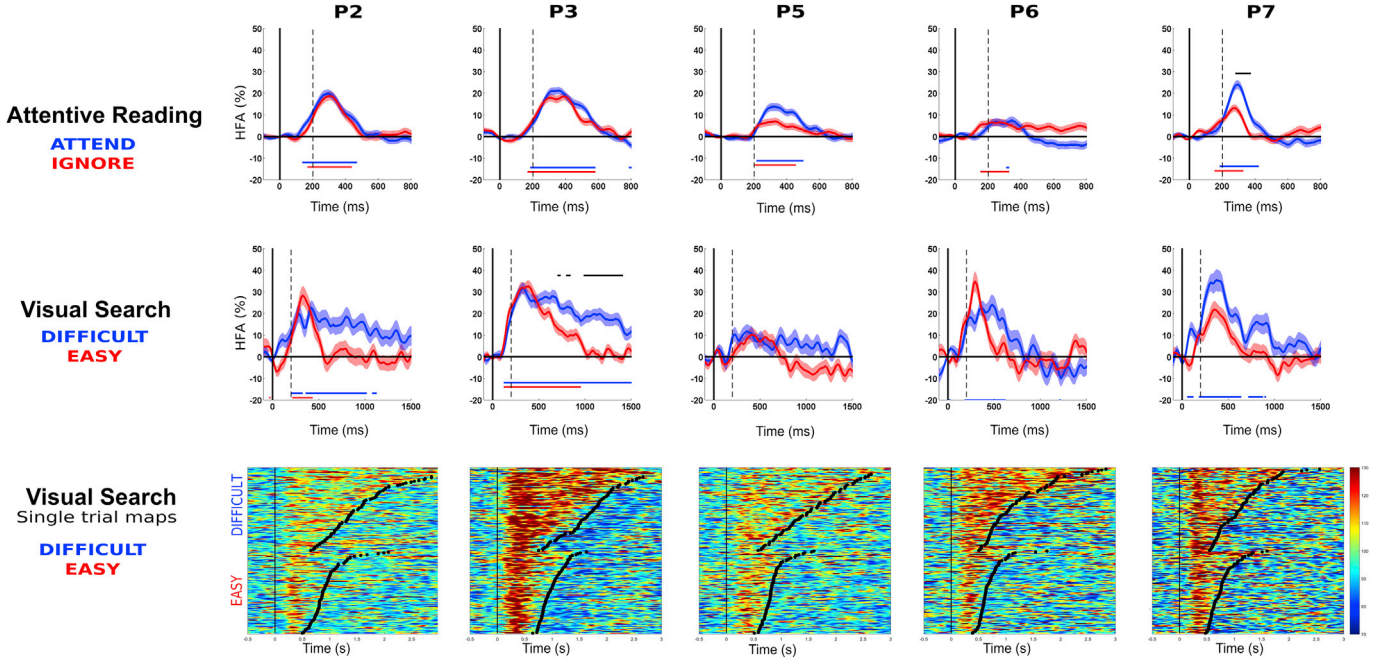

Fig. 5. Neural responses (HFA [50–150 Hz]) in the regions of interest for five patients (P2, P3, P5, P6 and P7) recorded in the Attentive Reading and Visual Search tasks. HFA variations induced by the tasks are shown for the Attentive Reading (Attend and Ignore conditions, blue and red respectively), Visual Search (Difficult and Easy conditions, blue and red respectively). The vertical dotted line represents 200 ms post-stimulus presentation and horizontal colored lines indicate time samples when HFA amplitude was significantly different from average baseline amplitude ($p < .05$, Wilcoxon signed rank test, FDR corrected for multiple comparisons); horizontal black lines above the amplitude curves indicate time samples at which HFA was significantly different between experimental conditions ($p < .05$, Kruskal–Wallis, FDR corrected for multiple comparisons). For the Visual Search task, single-trial HFA plots for the same electrode are displayed below, (Difficult and Easy search conditions) with trials ordered vertically according to RTs (fastest to slowest target detection). Black line depicts RT (i.e., latency of button press indicating target detection for each trial. Time t0 corresponds to Visual Search array onset).

areas in our reading task (see also Jung et al., 2008, and Fig. 3). This second processing stage would extend well beyond the mere capture of attention, and would correspond to what might be called a *captivation* of attention, that is, a chain of motor or purely cognitive processes triggered by the stimulus, that can keep a whole cognitive network busy until processing is complete.

This two-stage interpretation of the cognitive cycle, where stimuli can first capture attention - during the perception phase - then captivate it – during the action phase - is reminiscent of the early/late selection models of attention. Both types of selection are known to co-exist, and our results suggest a critical border around 250 ms, at which latency the IFS on the LPFC would harbor a late selection mechanism for stimuli that passed earlier filters using simple discriminating features. The "Gate-Keeper" would react sufficiently early to block high-level analysis of distracting stimuli, but late enough so that a first stage of sensory analysis, within the first 200 ms, recognize and signal stimuli which are ecologically-relevant and should not be systematically ignored (such as faces, animals or a mother's baby cry; VanRullen and Thorpe, 2001).

This scenario is congruent with the Rythmic Theory of Attention, recently proposed by Fiebelkorn and Kastner (2019). The theory suggests that visual attention involves a rhythmic alternation between two phases: a first phase devoted to an active sensory analysis of the attended object, and a second phase suitable for shifts towards new objects if no additional information needs to be extracted from the current target. This theory is obviously of direct interest to the present study, as it requires that a decision be made periodically (to shift or to stay), which is a key feature of a gatekeeping mechanism. In the context of a task, we could even predict from the theory that an early "visual response" should be observed in regions with an access to task-set information at latencies similar to the ones we report, since the authors propose that the process repeats itself every theta cycle.

Finally, our results are in line with observations from Stokes at al. (2013) that single neurons responding to target and non-target stimuli in the homologous macaque brain area, did not stay continuously active in between. They proposed that task-rules were not stored in the spiking activity of neurons, but through a mechanism of short-term synaptic plasticity. Indeed, we also found that neural responses in the "Gate-Keeper" were transient, with a rapid return to baseline level after stimulus offset. We found sustained activity of the "Gate-Keeper", but only in the Visual Search task, which might be explained by the fact that the Visual Search task requires participants to continuously compare stimuli that receive attention with a template held in memory and defining their target, what has been called an "attentional template", or "search template" during Visual Search task, that is the representation of search goals in working memory (Duncan and Humphreys, 1989; Eimer, 2014; Olivers et al., 2011; Wolfe, 1994). Such sustained activation during the VS task would then suggest that what is stored in the Gate-Keeper is similar to an "attentional template".

What is still missing is the formal demonstration that the IFS stores the definition of task-rules and attention-templates in Humans. The main strength of our study – a dataset of 85 patients – came with two limitations: the task had to be short and with few conditions to fit systematically in the tight clinical schedule, and patients were implanted with standard macro-electrodes recording local field potentials rather than micro-electrodes recording single/multi-unit activity. This prevented further analysis to test whether task-rules could be decoded from the IFS, as shown by Stokes et al. (2013) in monkeys.

What appears robust is that the posterior part of the IFS, in the VLPFC, remains active as long as a visual object (or a mental image) is processed attentively. The termination of the response to an incoming stimulus corresponds to the moment that the stimulus is no longer attended and thus filtered out, indicative of a Gate-Keeping mechanism. That region might even play a role in conscious perception, since recently, a visual response in the homologous area of the LPFC in monkeys has been correlated with the ability to detect visual stimuli close to the perception threshold (Van Vugt et al., 2018). Finally, the ability to measure an attention-related activity in real-time suggests that online attention monitoring devices are clearly feasible, provided that VLPFC activity can be assessed non-invasively with efficient source-reconstruction algorithms, especially in MEG since the region is lateral and lies in a sulcus.

Declaration of competing interest

The authors declare no conflict of interest.

I have read and have abided by the statement of ethical standards for manuscripts submitted to NeuroImage.

CRediT authorship contribution statement

S. El Bouzaïdi Tiali: Formal analysis, Resources, Writing - original draft, Writing - review & editing, Visualization. **J.R. Vidal:** Software, Formal analysis, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization. **M. Petton:** Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition, Resources, Writing - original draft. **A.C. Croize:** Resources, Writing - original draft. **P. Deman:** Resources, Writing - original draft. **S. Rheims:** Resources, Writing - original draft. **L. Minotti:** Resources, Data curation, Writing - original draft, Writing - review & editing. **M. Bhattacharjee:** Resources, Writing - original draft, Writing - review & editing. **M. Baciu:** Resources, Writing - original draft. **P. Kahane:** Resources, Data curation, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition. **J.P. Lachaux:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.116574.

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