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Jonathan Levy, Juan R. Vidal, Robert Oostenveld, Ian Fitzpatrick, Jean-Francois Démonet, et al.. Alpha-band suppression in the visual word form area as a functional bottleneck to consciousness.: A functional bottleneck to consciousness. NeuroImage, 2013, 78C, pp.33-45. 10.1016/j.neuroimage.2013.04.020 . inserm-00819667

HAL Id: inserm-00819667

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Submitted on 2 May 2013

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Alpha-band Suppression in the Visual Word Form Area as a Functional Bottleneck to Consciousness

Jonathan Levy,[1,2,3,4,5,† ,*] Juan R Vidal,[1,6,7,†] Robert Oostenveld,[1,10] Ian FitzPatrick,[1,8] Jean-Francois Démonet,[2,3,4,9,¥] and Pascal Fries [1,10,¥]

[1] Donders Institute for Brain, Cognition and Behaviour; Radboud University Nijmegen, Nijmegen, the Netherlands, [2] Inserm UMR825, Imagerie cerebrale et handicaps neurologiques, Toulouse, France, [3] Université de Toulouse, UPS, Toulouse, France, [4] Centre Hospitalier Universitaire de Toulouse, Pôle Neurosciences, CHU Purpan, Toulouse, France, [5] The Gonda Multidisciplinary Brain Research Center, Bar Ilan University, Ramat Gan, Israel, [6] Lyon Neuroscience Research Center, INSERM U1028, CNRS UMR5292, Brain Dynamics and Cognition Team, Lyon, France, [7] Université Claude Bernard, Lyon 1, Lyon, France, [8] Heinrich Heine University, Institut für Sprache und Information, Duesseldorf, Germany, [9] Leenaards Memory Center, Department of Clinical Neurosciences, CHUV and University of Lausanne, Lausanne, Switzerland, [10] Ernst Strüngmann Institute (ESI) for Neuroscience in Cooperation with Max-Planck-Society, Frankfurt, Germany.

† Jonathan Levy and Juan R Vidal have contributed equally to this work.

¥ Pascal Fries and Jean-Francois Démonet have contributed equally to this work.

*** Correspondence: Jonathan Levy, The Gonda Multidisciplinary Brain Research Center, Bar Ilan University, Ramat Gan, Israel. Email: yoniilevy@gmail.com**

1. Abstract

The current state of empirical investigations refers to consciousness as an all-or-none phenomenon. However, a recent theoretical account opens up this perspective by proposing a partial level (between nil and full) of conscious perception. In the well-studied case of single-word reading, short-lived exposure can trigger incomplete word-form recognition wherein letters fall short of forming a whole word in one's conscious perception thereby hindering word-meaning access and report. Hence, the processing from incomplete to complete word-form recognition straightforwardly mirrors a transition from partial to full-blown consciousness. We therefore hypothesized that this putative functional bottleneck to consciousness (i.e. the perceptual boundary between partial and full conscious perception) would emerge at a major key hub region for word-form recognition during reading, namely the left occipito-temporal junction. We applied a real-time staircase procedure and titrated subjective reports at the threshold between partial (letters)

and full (whole word) conscious perception. This experimental approach allowed us to collect trials with identical physical stimulation, yet reflecting distinct perceptual experience levels. Oscillatory brain activity was monitored with magnetoencephalography and revealed that the transition from partial-to-full word-form perception was accompanied by alpha-band (7-11 Hz) power suppression in the posterior left occipito-temporal cortex. This modulation of rhythmic activity extended anteriorly towards the visual word form area (VWFA), a region whose selectivity for word-forms in perception is highly debated. The current findings provide electrophysiological evidence for a functional bottleneck to consciousness thereby empirically instantiating a recently proposed partial perspective on consciousness. Moreover, the findings provide an entirely new outlook on the functioning of the VWFA as a late bottleneck to full-blown conscious word-form perception.

2. **Keywords:** Consciousness, VWFA, Reading, Neuronal oscillations, Alpha-band, MEG.

3. Introduction

Understanding how the brain creates conscious perception is probably one of the hardest challenges faced by modern science. Currently, it remains equivocal whether there can be a strict dissociation between unconscious and conscious processing. However, neuroimaging has recently shed important insight into that matter by providing sound evidence that such dissociation can be observed as a sharp nonlinear transition in brain activity (Sergent et al., 2005; Del Cul et al., 2007; Dehaene and Changeux, 2011). Subjective reports of perception can be tightly reflected by such transitions to such an extent that individual trials, reported or not as consciously seen, can be categorically distinguished by their activation pattern. The bifurcation between unconscious and conscious processing follows the 'winner-takes-it-all' rule, and is therefore indicative of consciousness as an "all-or-none" phenomenon clearly distinct from the graded panel of possible prior sensory inputs.

Nevertheless, it has been very recently suggested that an important transition phase, namely partial consciousness, separates nil and full conscious perception (Kouider et al., 2010). Partial consciousness is

described as a perceptual state with high subjective confidence about the informational content, but only at a limited level of the full percept. Accordingly, partial consciousness is assumed to be accessed independently from full (or nil) consciousness, thereby allowing low-level, not high-level representational contents to arise in conscious perception. Notably, partial consciousness may still reflect an all-or-none access, but in contrast to full consciousness – only to a limited level of representation. Hence, the partial hypothesis is indicative of consciousness as a graded phenomenon, yet without compromising its all-or-none mechanism. Importantly, the partial consciousness hypothesis has not yet been demonstrated at the brain activation level. Here, we reasoned that in order to result in distinct, yet closely-matched subjective reports, the neural correlates of partial and full conscious perception ought to have different dynamic neural signatures. Namely, we assumed here that contrasting full to partial consciousness should recruit neuronal substrates, selectively reflecting the access to higher-level informational contents.

To investigate the neural substrates involved in conscious processes, authors have used a variety of paradigms (for reviews see Lamme, 2006; Dehaene and Changeux, 2011), of which a common strategy has been contrasting perceived versus unperceived words (e.g. Gaillard et al., 2009). Importantly, using single-words for probing consciousness can be particularly suitable in the case of partial consciousness due to the graded organization of words from partial (letters) to full (whole word) processing (Selfridge, 1959; McClelland and Rumelhart, 1981) which is mapped onto separate localized functional cerebral clusters (Levy et al., 2008; Mainy et al., 2008; Vidal et al., 2012). Namely, the two perceptual levels involved in word reading (i.e. letter perception and whole word perception) can be exploited as two levels of conscious perception (i.e. partial and full blown perception, respectively).

Thus, we probed the oscillatory neural responses marking the transition from partial to full conscious word-form perception, and tested whether this transition could be generally accounted as a functional bottleneck to consciousness. In the present context, a functional bottleneck to consciousness refers to the perceptual boundary separating partial and full conscious perception. We expected that contrasting full and partial word recognition should majorly recruit neuronal substrates selectively involved in word processing. Our major candidate was the left occipito-temporal junction, as it is by far considered as a key brain region to word processing, despite the ongoing debate running around its specificity and its exact coordinates (Dehaene and Cohen, 2011; Price and

Devlin, 2011). We reason that this neural substrate can be straightforwardly extrapolated as a putative functional bottleneck to consciousness.

During the experiment, participants viewed a sequence of foveally-presented masked words (Figure 1A) while oscillatory brain activity was monitored with magnetoencephalography. Participants reported the level of perception in a forced-choice procedure. The combinations of perceptual report yielded four possible outcomes: if a word was fully perceived, the report was through a semantic decision on meaning (animate/inanimate). If by contrast, a word was partially perceived, i.e. no meaning yet vague orthographic information was perceived, the report was through an orthographic detection task (letters/no-letters) (Figure 1A). Noteworthy, in the latter task, subjects were required to report whether they were able to recognize one or more letters. Subject were not required to report the identity of the letter(s), but rather to press 'yes' or 'no' for the presence of letters. Specifically, the instruction was (with the counterbalancing of fingers' order across individuals) as follows: "Please press the button below your right middle finger whenever you fully see a word referring to an animate item; please press the button below your right index finger for a word referring to an inanimate item; please press the button below your left middle finger whenever you do not perceive any word, but instead you do perceive one letter or more; finally, please press the button below your left index finger whenever you do not perceive any word or any letter either. Alternatively, sample words were replaced by a blank screen in one sixth of the total trials (catch trials), for which subjects had to press the button corresponding to the absence of words/letters.

The critical manipulation was the adjustment of masks' contrast as a function of participants' reports (see Figure 1B for a sample from one single experimental sequence). Such procedure is also referred to as "staircase" (Levitt, 1971), pointing to the real-time adaptation of physical stimulation to subjective reports. Hence, this experimental strategy allowed us to obtain two types of subjective reports (partial or full) for an identical level of physical stimulation, thereby straightforwardly testing our hypothesis of a functional bottleneck to consciousness.

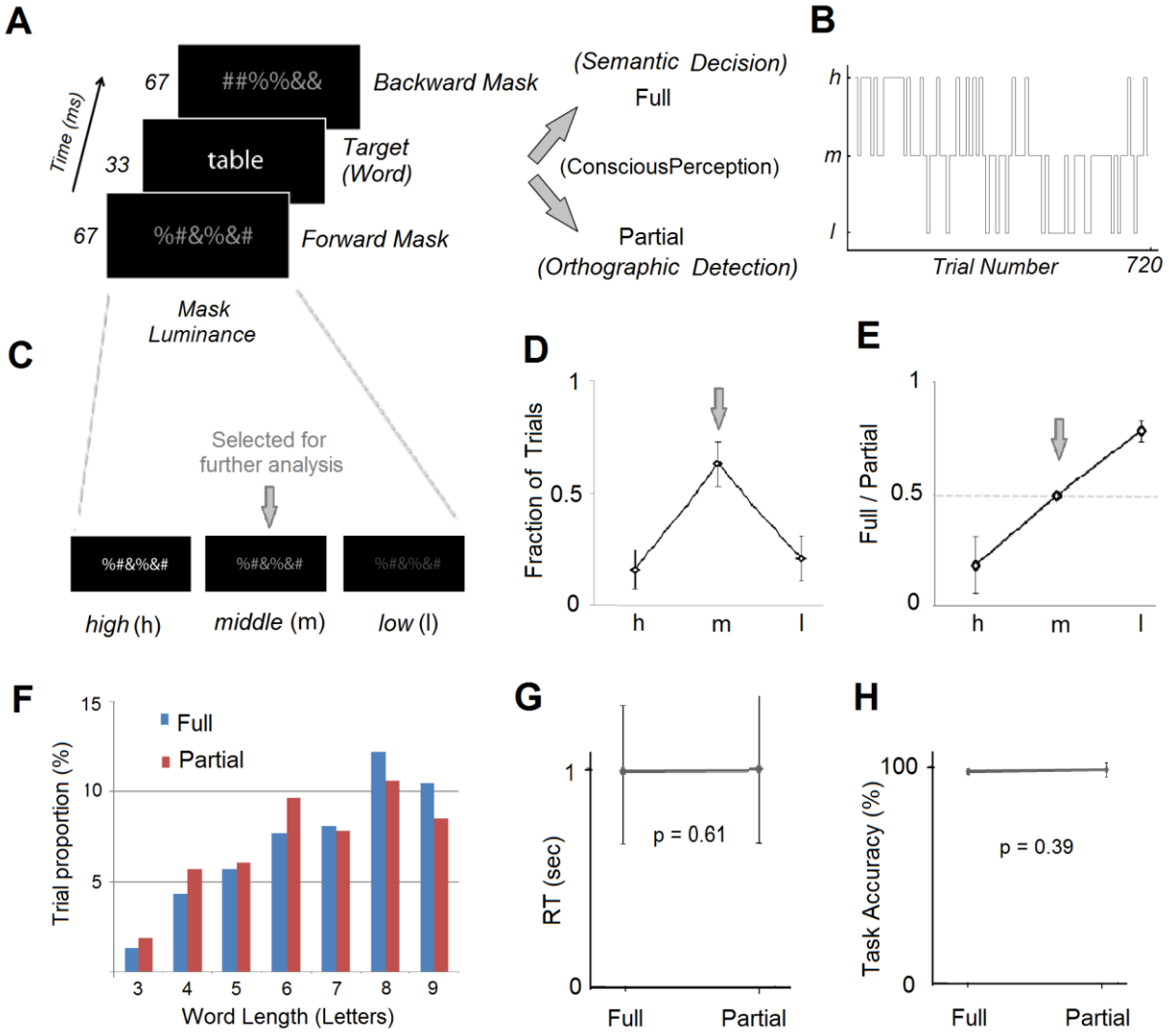


Figure 1. Experimental Design and behavioral results

(A) Design. Experimental paradigm used to present masked words in a stair-case procedure resulting in two levels of conscious perception: Full and Partial. The two levels were reflected by either a forced-choice task of semantic decision or of orthographic detection, respectively. (B) A sample of mask luminance fluctuation during an entire experimental trial sequence. (C) Masks. The luminance of the forward and backward masks fluctuated between three levels (h: high, m: middle, l: low) and was individually determined for each participant depending on the reported percept. (D) Trial distribution across subjects in the three masking conditions. (E) Ratio between the two levels of reported percept (Full vs. Partial) in the three masking conditions. The dashed horizontal bar indicates the optimal balanced ratio of 0.5. (F) Trial proportion in the two perceptual conditions as a function of the presented stimuli's (i.e. words) length (in number of letters). (G) Mean response times and (H) accuracy in the two perceptual tasks. Error-bars represent ±1 SD. Vertical arrows pointing to the mask level 'm' illustrate the selected trials for further MEG analyses.

4. Materials and Method

2.1 Participants

Thirteen healthy right-handed and native-Dutch subjects (eight males, average age 23.92 ± 4.54 years) with normal or corrected-to-normal vision participated in the experiment. None of the participants had a history of neurological or psychiatric disorders. The study was approved by the local ethics committee, and a written informed consent was obtained from the subjects before the experiment according to the Declaration of Helsinki, and received monetary compensation.

2.2 Stimuli

Stimuli were generated using Presentation software (Neurobehavioral systems, Albany, USA) in a dimly lit room and subtended a horizontal visual angle of ~2.5°. They were projected on an LCD monitor placed at a viewing distance of 70 cm. Responses were delivered by response pads. Stimuli were Dutch nouns (300 animate, 300 inanimate) between 3 and 9 letters in length with a lemma frequency between 100 and 300 occurrences per million (Baayen et al., 1993). Animate and inanimate words were balanced with respect to their word frequency of apparition and the number of letters they contained. The animacy character of the selected words was unequivocal. Words were presented only once to prevent automatic stimulus–response learning or repetition-suppression effect.

2.3 Experimental Procedure

Each trial began with a fixation cross presented for 600-933.33 ms (first presentation after pause presented for 2600-2933.33 ms), followed by the presentation of a forward mask (66.66 ms), a word (33.33 ms) and a backward mask (66.66 ms). The random time controlled for plausible anticipation of stimulus onset timing. In 16.67% of the totality of trials, we replaced the words with blank screens to avoid subject's habituation or anticipation and to control for the orthographic detection task (letters/no-letters). All stimuli were presented randomly. After stimuli presentation, a larger fixation crosshair prompted the subject to respond. Responses indicated trials' termination and lasted no longer than 2100 ms. A smaller subsequent crosshair spanned1000ms and signaled the interval linking the next trial. Participants were allowed to make eye movements or blinks during that inter-trial interval. In order to avoid guessing during the task, subjects were explicitly asked to categorize the word only when they had clearly recognized it, and were trained on the task with 90 training trials (different words than during the experiment) before measurement. During the task, subjects received visual feedback on the correctness of their response, so as to discourage them from guessing. Furthermore, in the unlikely event in which the semantic category (animate vs. inanimate) of a given word appeared equivocal, participants were instructed to avoid response, and hence exclude such trials from the analysis. After blocks of

30 trials, participants were allowed to pause. They initiated the start of each new trial block by a button press. In total, each subject performed 720 trials in a total measurement time of approximately 55 min. The reports were through button press on a response pad; they were counterbalanced across subjects between right/left hands and middle/index fingers (four response buttons in total, and hence eight possible combinations of response press, in the aim of controlling for differences in the motor representations of each finger.

To maximize and to balance attentional engagement, the subjects' task was to report (i) full or (ii) partial word-form perception by semantically categorizing the word (animate/inanimate) or if failed to perceive the word, by orthographically categorizing the percept (letters/none), respectively. Correctness in word detection was probed using the semantic categorization task (Animate or Inanimate), whereas correctness in letter detection was probed based on the ability to report the presence of letters during word trials (hit) or during blank trials (false alarm). To achieve maximal sensitivity of the neural signal and the statistical tests, the procedure aimed at collecting trials with a 50% distribution for each of the two reports. A modified "stair-case" version of the threshold estimation procedure described by Levitt (Levitt, 1971) was determined individually in real-time. The staircase effect was obtained by varying the contrast of a mask of scrambled characters (see Figure 1C) every six trials based on the given subjective response. Noteworthy, in order to obtain optimal parameters resulting in a 50/50 distribution of the two perceptual tasks, prior to this study we conducted pre-study piloting in which we obtained optimal stimulation/masking (i) latency and (ii) illumination, as well as (iii) optimal amplitude (masking intensity) of stair-case steps.

2.4 MEG recordings

Ongoing brain activity was recorded (sampling rate, 1200 Hz) using a whole-head CTF MEG system with 275 DC SQUID axial gradiometers (VSM MedTech Ltd., Coquitlam, British Columbia, Canada). Head position was monitored using three coils that were placed at the subject's left ear, right ear, and nasion. Bipolar EEG channels were used to record horizontal and vertical eye-movements as well as the cardiac rhythm for the subsequent artifact rejection.

2.5 Stratification

To minimize effects of fluctuations in response time on our analyses, we performed a *post hoc* stratification of the data based on the response time (RT) values. The goal of procedure was to assure that RT variance would

not bias the tested contrast (i.e. full versus partial). We therefore obtained from each of the two perceptual reports (partial and full), a subset of trials with an identical distribution of RT values across the subsets in each of the two report conditions. This approach has been adjusted from Roelfsema et al. (Roelfsema et al., 1998) and a similar strategy has been successfully applied before to control for EMG fluctuations (Schoffelen et al., 2005). For every participant, we binned the observations in each condition, while the bin centers were obtained by dividing the range of all RT values into four equally spaced bins with equal bin centers. In this way, each of the observations fell within one of the bins, for which we selected a subset of observations such that across the two conditions, the number of observations was identical. From the condition with the lowest number of observations in a given bin, all N observations constituting that particular bin were selected for the stratified sample. From the other condition, a subset of N observations was randomly drawn from the observations constituting that particular bin.

2.6 Spectral Analysis

The analysis was performed using Matlab 7 (MathWorks, Natick, MA, USA) and the FieldTrip toolbox (Oostenveld et al., 2011). Only correct trials with an identical contrast level were kept for spectral analysis (Figure 1C). They consisted in the largest fraction of report trials (Figure 1D) and were equally distributed (Figure 1E). Trials containing eye blinks, saccades, muscle artifacts and signal jumps were rejected from further analysis.

We applied tapers to each time window and calculated Time-Frequency Representations (TFRs) of power for each trial using a Fast Fourier Transform (FFT) applied to short sliding time windows; data was analyzed in alignment to stimulus onset. Power estimates were then averaged across tapers. Because the width of the frequency bands observed in physiological responses typically scales with the center frequency, we analyzed two frequency ranges separately: 2–40 and 40–150Hz. For the frequencies 2–40 Hz, we used a Hanning taper and applied a fixed time window of 0.5 s, resulting in a spectral resolution of slightly less than 2 Hz. For the higher-frequency band (40–150 Hz), we applied multitapers (Percival and Walden, 1993) using a fixed window length of 0.2 s, resulting in a frequency smoothing of 12.5 Hz.

The power values were calculated for the horizontal and vertical component of the estimated planar gradient and then summed (Bastiaansen and Knösche, 2000). The horizontal and vertical components of the planar gradients were calculated for each sensor using the signals from the neighboring sensors thus approximating the

signal measured by MEG systems with planar gradiometers. The planar field gradient simplifies the interpretation of the sensor-level data because the maximal signal typically is located above the source (Hämäläinen et al., 1993). The planar gradient power estimates were subsequently averaged over trials for a given condition.

2.7 Source analysis

For the analysis of the neuronal sources, we used an adaptive spatial filtering method called beamforming (Gross et al., 2001) and relied on partial canonical correlations. Subjects' brain volume was divided into a regular grid. The grid positions were obtained by a linear transformation of the grid positions in a canonical 1cm grid. This canonical grid was based on a template brain (Montreal Neurological Institute), and for each subject, we computed the linear transformation optimally aligning the subject's brain volume to the template brain, using SPM8 (http://www.fil.ion.ucl.ac.uk/spm). We applied the inverse of this linear transformation to the grid positions of the canonical grid to obtain subject-specific dipole grids. This procedure facilitates the group analysis, because no spatial interpolation of the volumes of reconstructed activity is required.

For each grid position, we constructed spatial filters. These filters have the property that they optimally pass activity from the location of interest, while other activity, which is present in the data, is suppressed. To compute the lead field matrices, we used a single-shell volume conduction model, based on the shape of the inside of the skull (Nolte, 2003). The inside of the skull was derived from each individual subject's structural magnetic resonance image, which was spatially aligned to the MEG sensors. Despite the fact that, in this volume conduction model, there is no truly magnetically silent direction, we excluded the most silent direction from the lead fields, since this direction potentially picks up a lot of noise.

To analyze the location of the sources accounting for the significant sensor level effects, we computed the CSD matrix between all MEG sensor pairs from the Fourier transforms of the tapered data epochs at the three frequency-bands where we had found significant sensor-level effects, i.e. the alpha, beta and gamma bands. For each subject, and within each of the frequency bands, we identified the frequency bin that yielded the most extreme *t* value (for power comparisons), averaged across sensors. Spatial filters were constructed for each grid location, based on the identified frequency bin, and the Fourier transforms of the tapered data epochs were projected through the spatial filters.

When analyzing at the coordinate level (virtual channel), we proceeded similarly with beamforming but this time we relied on a linear constrained minimum variance beamformer. Time frequency analysis was performed with the virtual channel at the coordinates of interest.

2.8 Statistical Analysis

Statistical significance of the power values was assessed similarly at the sensor and at the source levels. It was assessed using a randomization procedure (Maris and Oostenveld, 2007). This nonparametric permutation approach does take the cross-subject variance into account, because this variance is the basis for the width of the randomization distribution. This approach was chosen as it does not make any assumptions on the underlying distribution, and it is unaffected by partial dependence between neighboring time-frequency pixels. Specifically, the procedure was as follows: t-values representing the contrast between the conditions were computed per subject, channel, frequency and time. Subsequently, we defined the test statistic by pooling the t-values over all subjects. Here, we searched time-frequency clusters with effects that were significant at the random effects level after correcting for multiple comparisons along the time and the frequency dimensions. Testing the probability of this pooled t-value against the standard normal distribution would correspond to a fixed effect statistic. However, to be able to make statistical inference corresponding to a random effect statistic, we tested the significance of this group-level statistic by means of a randomization procedure: We randomly multiplied each individual t-value by 1 or by -1 and summed it over subjects. Multiplying the individual t-value with 1 or -1 corresponds to permuting the original conditions in that subject.

This random procedure was reiterated 2000 times to obtain the randomization distribution for the group-level statistic. For each randomization, only the maximal and the minimal cluster-level test statistic across all clusters were retained and placed into two histograms, which we address as maximum (or minimum, respectively) cluster-level test statistic histograms. We then determined, for each cluster from the observed data, the fraction of the maximum (minimum) cluster-level test statistic histogram that was greater (smaller) than the cluster-level test statistic from the observed cluster. The smaller of the two fractions was retained and divided by 2000, giving the multiple comparisons corrected significance thresholds for a two-sided test. The proportion of values in the randomization distribution exceeding the test statistic defines the Monte Carlo significance probability, which is also called a p-value (Nichols and Holmes, 2002; Maris and Oostenveld, 2007). This cluster-based procedure allowed us to obtain a correction for multiple comparisons at all sensor and source analyses. At the virtual sensor level, however, such procedure was not possible given the analysis at a single coordinate;

therefore, correction for multiple comparisons was performed by controlling the false discovery rate (FDR) (Benjamini and Hochberg, 1995).

5. Results

The critical manipulation was the adjustment of masks' contrast as a function of participants' reports (see Figure 1B for a sample from one single experimental sequence). Such procedure is also referred to as "staircase" (Levitt, 1971), pointing to the real-time adaptation of physical stimulation to the subjective reports. Mask contrasts fluctuated between three levels for most participants (eight), while the remaining five encountered only two levels. We selected for further analyses the middle luminance level, namely *m*, trials (Figure 1C) which accounted for the largest trial fraction (Figure 1D) and additionally presented a balanced distribution between the two perceptual reports (Figure 1E). Notably, the distribution error bar in the *m* contrast was virtually nil (±0.0044), thereby indicating low variance across subjects for the selected contrast. On average, 26.06 ±4.11% of the totality of trials were maintained for further analysis for each of the two conditions (full and partial). Mean response time after the stratification procedure was 999.84 ± 331.85 ms and 999.72 ± 343.45 ms for the full and partial conditions respectively, without significant ($p = 0.61$) difference (Figure 1, G). Mean accuracy for the two tasks was 97.38 ± 1.55 % and 98.16 ± 3.60 % in the full and partial conditions respectively, without significant ($p = 0.39$) difference (Figure 1, H).

Furthermore, to test whether intrinsic bottom-up (word-length in letters) or top-down (frequency of apparition) features of the presented stimuli (i.e. words) had any significant influence on their probability of being perceived fully or partially, a non-parametric Spearman rank correlation was performed. Significant negative correlation was found between word length and perception ($r = -0.08$, $p < 0.001$), yet no significant correlation between word frequency of apparition and perception ($r = -0.01$, $p = 0.43$). It was also found that full perception was biased towards longer words for 7-letter words (and longer) (Figure 1F). Nevertheless, the (theoretical) average word length (6.77 letters) yielded a balanced distribution (49.11/50.88%) in full/partial perception, respectively.

3.1 Frequency-localizer contrast

Neuronal network dynamics are characterized by rhythmic oscillatory activity (Buzsaki and Draguhn, 2004). In the case of word-form perception, locally-organized cortical oscillations have been previously reported as reliable markers of full conscious processing (Gaillard et al., 2009). Here, we measured brain activity with MEG and estimated neuronal oscillations during a double-task design of conscious perception. To constrain the coming analyses to functional rhythmic activity, we first quantified the post-stimulus neural response as compared to its pre-stimulus baseline response level. We therefore averaged power responses across all sensors ($p<0.05$, corrected for multiple comparisons across all time and frequency samples). Figure 2 illustrates time-frequency statistical maps of the MEG activity recorded over all sensors during the course of the trial, in the low (2-40 Hz) and high (40-150 Hz) frequency ranges. The neural response time-frequency statistics map highlights effects ($p<0.001$, corrected) in four standard frequency bands: Alpha (7-11 Hz), Beta (15-30 Hz), Narrow-band Gamma (60-90 Hz) and Broad-band Gamma (60-130 Hz). As trials lasted on average one second from stimulus onset to button press, one could note that in the lower frequency range (<40 Hz) spectral perturbations were down-regulated over the mid-part of the trial's epoch (approx. 500ms). In contrast, activity peaked in the first part of the trial (<500ms) in a transient broad-band gamma burst, and in the second part of the trial (>500ms) in a more sustained, narrow-band gamma burst. This clear-cut temporal division in the higher frequencies is suggestive of two distinct functional processes, one for sensory processing and the other for decision and response-related processing.

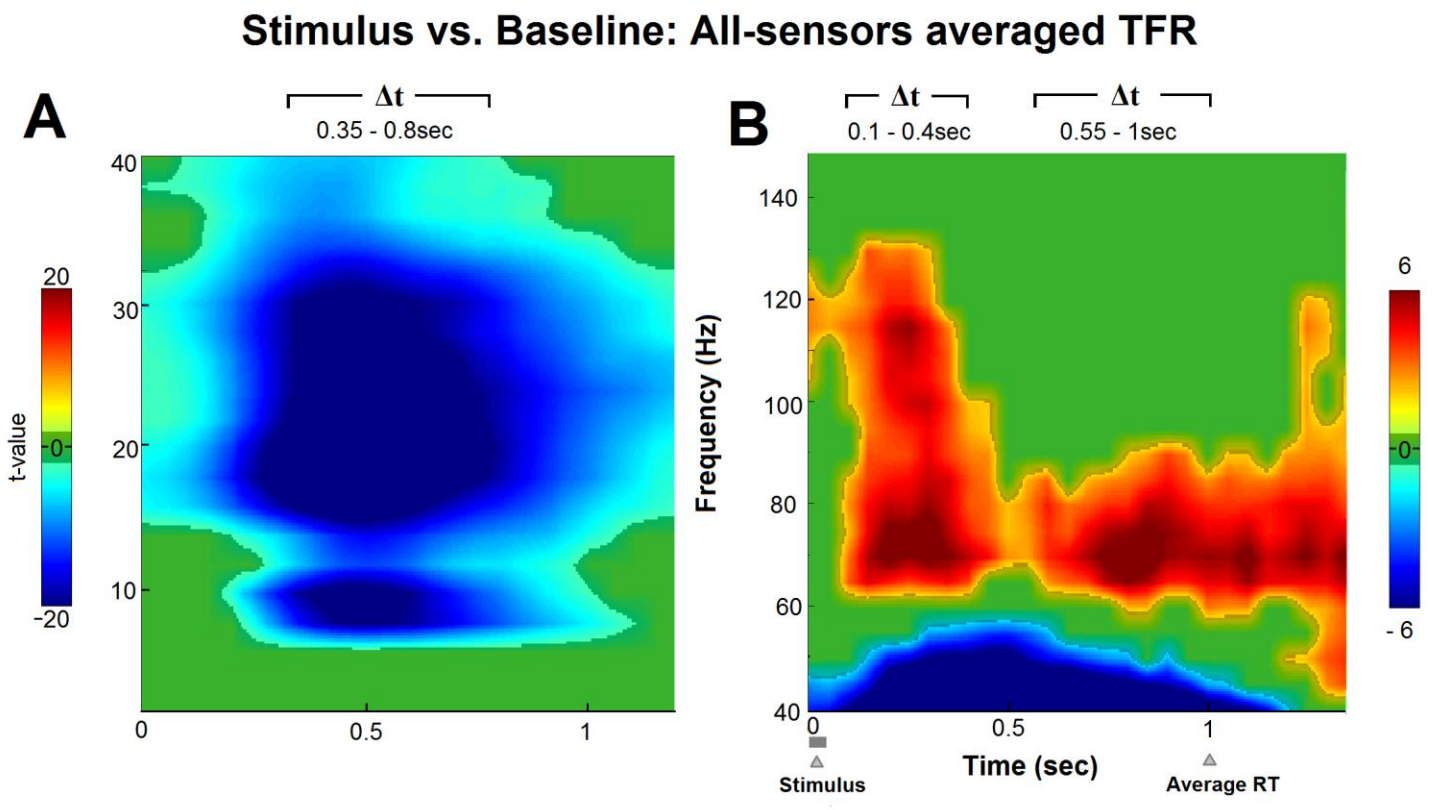


Figure 2. Frequency-localizer contrast: Stimulus (Full and Partial) vs. baseline activity

Time-Frequency statistical maps of (A) 2-40Hz and (B) 40-150Hz frequency ranges averaged across all sensors. Color bars illustrate masked significant modulations (p<0.05, corrected for multiple comparisons). The maps illustrate activity modulation during masked word presentation (Full and Partial) as contrasted with its baseline activity ([-0.5 -0.05] sec). The analysis was performed with stimulus-aligned data and was stratified for reaction time. Stimulus onset and average response time (0.9973sec) are indicated with a gray triangle, while stimulus latency is represented in the time line with a grey rectangle.

These sensor-level patterns were subsequently investigated at the source level. Figure 3 illustrates source reconstruction maps applied to the four frequency bands by means of adaptive spatial filters: alpha power changes localized to the junction of the bilateral occipital, temporal and parietal cortices; beta power changes localized to bilateral parietal, bilateral primary somatosensory (S1), left primary motor (M1) and left premotor (PM) cortices; narrow-band gamma was expressed in right M1, left S1 and left PM; finally broad-band gamma was expressed in the middle occipital gyri. The functional localization of these four spectral sources suggests that they may be assigned to different processes. Globally, alpha and broad-band gamma oscillations may

correspond to sensory processing whereas beta and narrow-band gamma may be more assigned to motor-related processing.

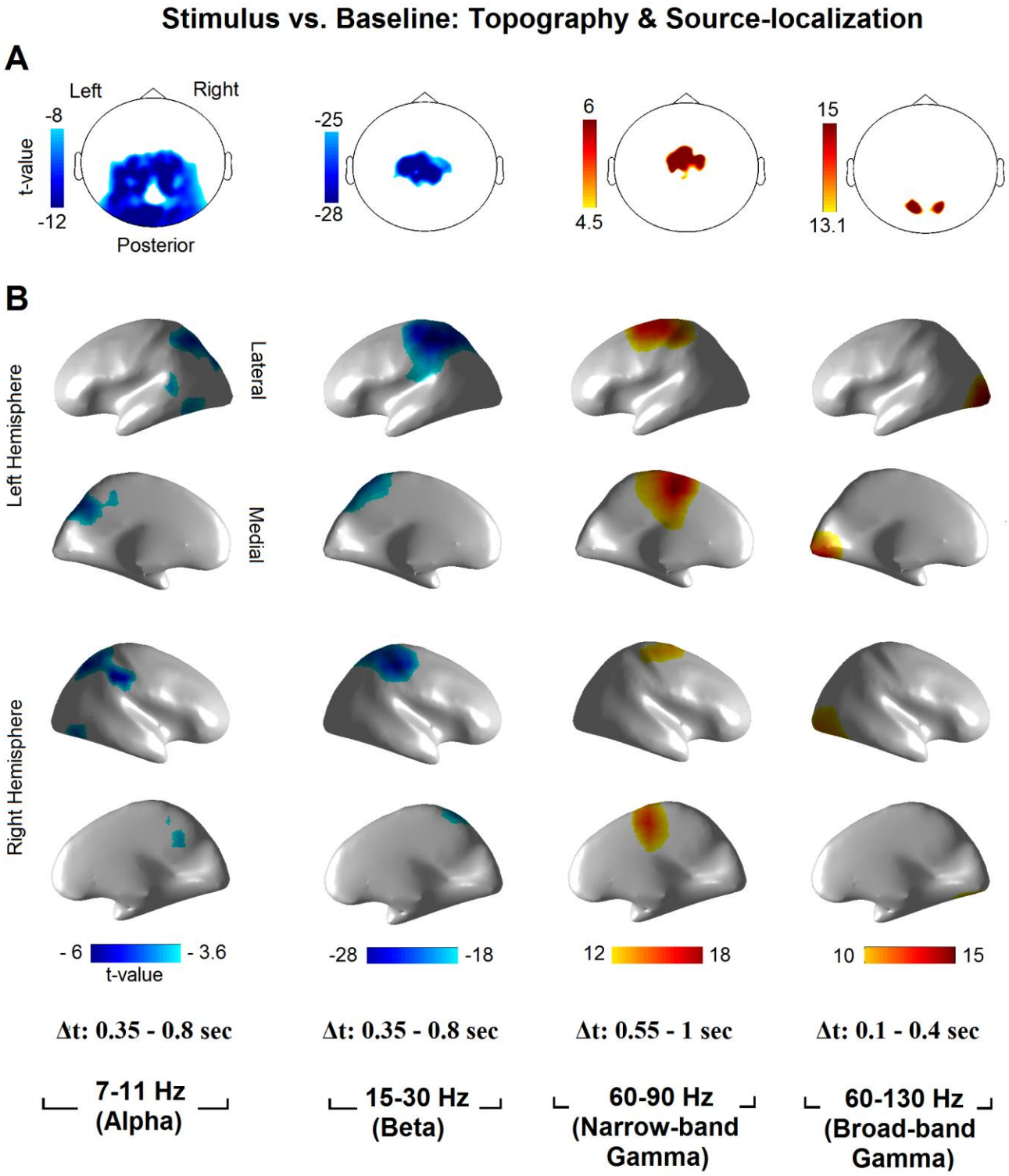


Figure 3. Frequency-localizer contrast: Stimulus (Full and Partial) vs. baseline sensor and source activity

(A) Scalp topographies and (B) overlaid cortical surface (MNI template) representations, both illustrate significant clusters ($p < 0.05$, corrected) during masked word presentation (Full and Partial) as contrasted with its baseline activity ([-0.5 -0.05] sec). The spatial

representations are averaged in the four frequency bands of interest and the maximum time-frequency windows (see at the bottom) as revealed in Figure 2.

3.2 Full versus partial conscious perception

To probe the neural processing underlying the transition from partial to full conscious perception, we contrasted the two conditions while averaging across all channels in the frequency bands of interest revealed by the previous time-frequency analysis. Even though there was only an insignificant difference ($p=0.27$) in reaction time distributions between the two perceptual reports (partial and full), we further minimized the effects of reaction time variance on spectral power by applying a *post hoc* reaction time stratification ($p=0.85$, after stratification). Figure 4 illustrates the time-course of the resulting t-values during the course of the trial; the graph highlights a late yet sharp buildup of effect size followed by a sustained effect over the second part of the trial (see significance bars at the bottom of the panel) for the three frequency-bands. It also points to the opposite polarity of this effect in the low (<40 Hz) compared to the high (>40 Hz) frequencies. We did not include in this analysis the previously mentioned broad-band gamma (Figure 2) as it did not reach significance for this contrast ($p>0.2$). Time-frequency and source maps associated this effect with early visual processing (Figures 2 and 3, respectively). Together with the low t-values during the early stages of trial processing in the three frequency bands ($t = -0.18$ cross-frequency averaged at 0 - 0.4sec), this is suggestive of visual processing common to both reports (partial and full). T-values reached significance ($p<0.05$, corrected) around 0.5sec post stimulus onset (Figure 4). This late buildup of neural processing suggests that sensory evidence could be identical during the two reports. This result pattern is in line with our expectation based on the experimental strategy of maintaining bottom-up resources at steady-level stimulation.

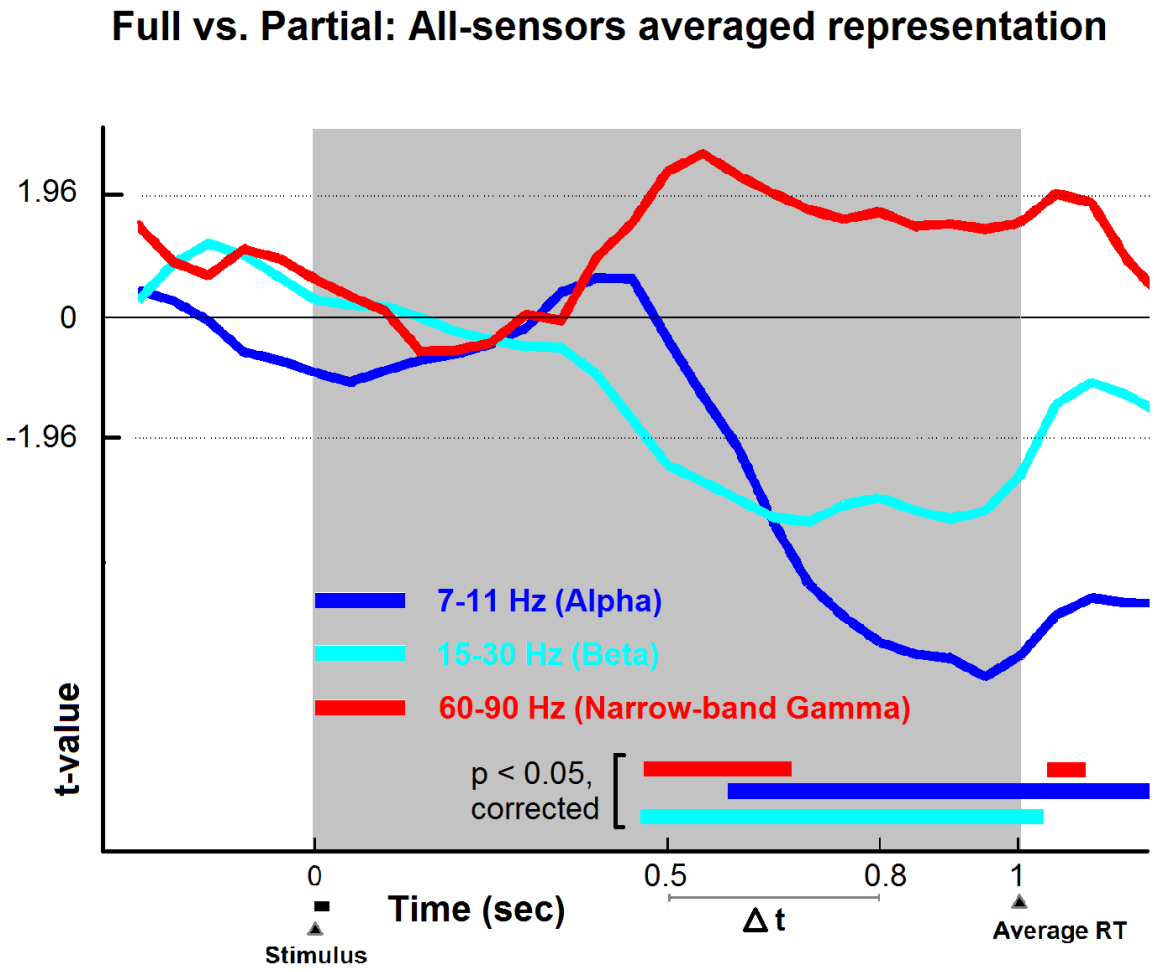


Figure 4. Full vs. Partial: temporal representation in the alpha, beta and gamma bands
Time course of t-values of the group test statistic for Full vs. Partial, averaged over all sensors and separately in the alpha, beta and gamma bands (blue, turquoise and red colors, respectively). The gray shading indicates the time interval from stimulus onset to average reaction time. The horizontal dashed lines indicate significance levels (p = 0.05, corrected), while the three lower horizontal bars indicate significant values (p < 0.05, corrected) on the time axis for each of the three frequency bands. The time interval 0.5 – 0.8 sec was significant for the three frequency bands and therefore selected for further analyses.

To further analyze the corresponding source level activity, we chose a time window (0.5-0.8 sec), which contained the perturbations in all three frequency bands (Figure 4). Scalp topographies revealed the (peak) sensors of interest of the full versus partial effects in the three frequency bands (Figure 5A). Source representations (Figure 5B) show differential activity in clusters expressed: at the left middle occipital gyrus and the left precuneus (Alpha), at the left cuneus (Beta), the left middle temporal gyrus (Beta) and at the left

inferior parietal lobule (Beta), and finally, at the left S1 and the left PM (Gamma). Figure 6 illustrates the TFRs specific to the sensors of interest revealed in Figure 5A, together with their right hemispheric homologs and the sensors of interest revealed in the stimulus versus baseline analysis in the broad-band gamma (Figure 3A, right panel). These sensor-specific TFRs straightforwardly convey the activity in partial and full conditions, separately, as well as the full versus partial contrast (Figure 6). This supplementary analysis strengthens the previous findings by revealing full versus partial effects only in the left hemispheric alpha, beta and narrow-band gamma (note, however, a weakened alpha effect in the right hemispheric sensors (Figure 6A, right panel)). It also shows a certain spatial overlap in the alpha and beta effects (Figure 6AB, left panels).

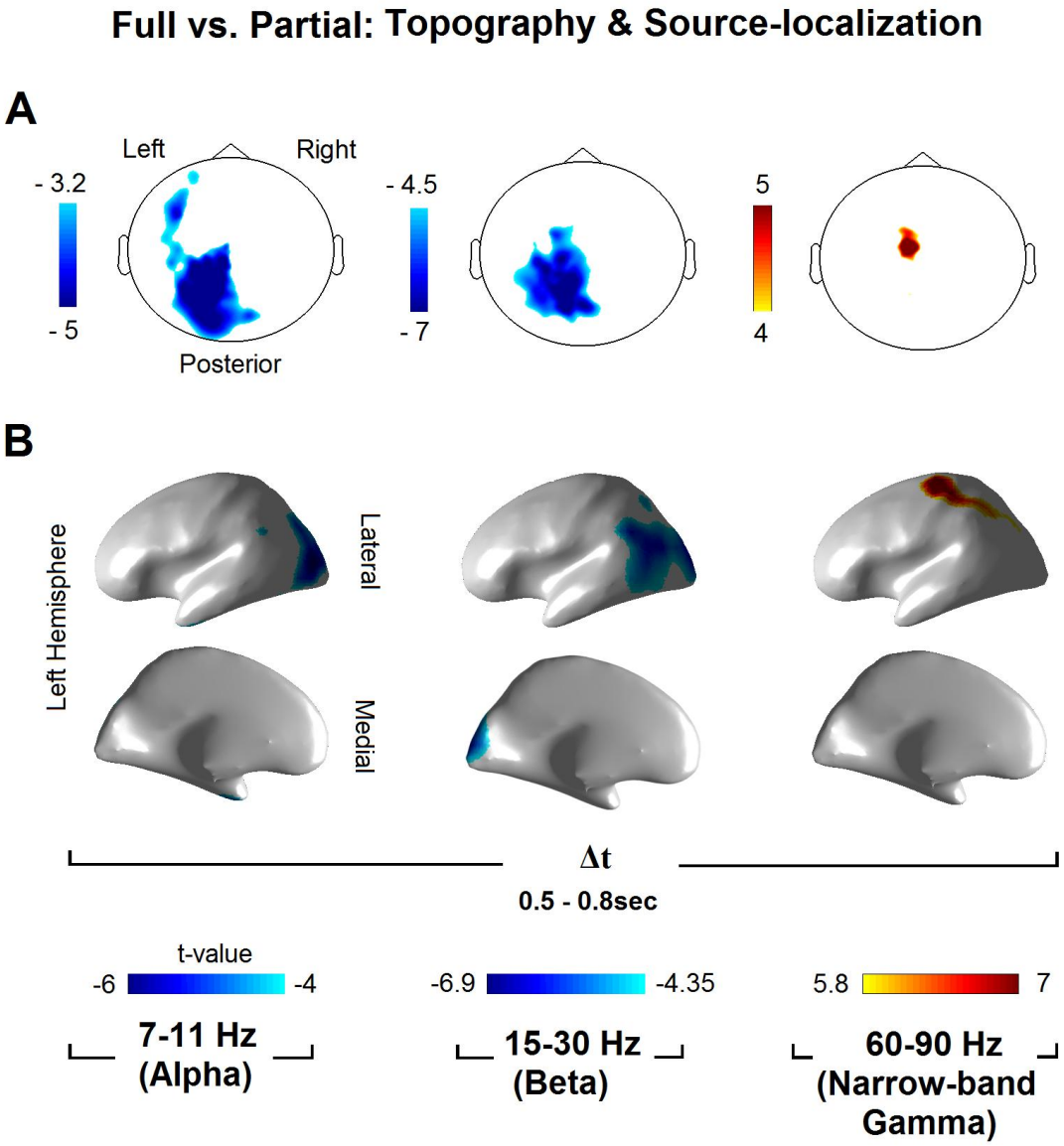


Figure 5. Full vs. Partial: Source-localization in the alpha, beta and gamma bands
(A) Scalp topographies and (B) overlaid cortical surface (MNI template) representations, both reveal topographic and cortical clusters ($p < 0.05$, corrected) in the selected time interval of interest (i.e. 0.5 – 0.8 sec) as revealed in Figure4.

To further probe the observed cortical response patterns, we separated subjects who reported full conscious perception with their right hand (and therefore partial conscious perception with their left hand), and those who reported it with their left hand (and therefore partial conscious perception with their right hand). This strategy leans on the observation that modulation in neural oscillations is typically enhanced in the motor cortex contralateral to the responding hand relative to the ipsilateral one (Donner et al., 2009). Thus, a contralateral

bias would be mainly indicative of motor-related activity, whereas spectral perturbations remaining unaffected as a function of response hand would be indicative of an effect which is largely unbiased by motor activity. Clusters of activity at both the sensor and the source level were left-lateralized irrespective of response-hand at the alpha band (Figure 7A), in contrast to a significant contralateral bias in the beta (Figure 7B) and gamma (Figure 7C) bands. Furthermore, statistically significant clusters of sensors (contralateral to button press) and their symmetrical homologues in the other brain hemisphere (ipsilateral to button press) were averaged. The resulting t-values for the different bands are shown as insets and provided additional evidence that the alpha band modulation was always left lateralized, while the beta and gamma modulation was always contralateral to the response hand. Source reconstruction further determined that the alpha-power perturbation originated in the left occipito-temporal-parietal junction. By contrast, the beta-power perturbation originated in right S1, left M1 and left inferior parietal lobule, and the gamma-power perturbation in the right PM and left M1. Hence, neural activity peaked in regions with a known contralateral motor bias in the beta (except for the left inferior parietal lobule) and gamma bands. Such sensori-motor activity therefore exhibited robust lateralized effector selectivity of opposite polarity in the beta and gamma bands. By contrast, alpha-band suppression peaked in a region specific for word processing, namely, the left occipito-temporal cortical junction (LOT) and exhibited robust left-lateralized selectivity unaffected by response hand (Figure 7A).

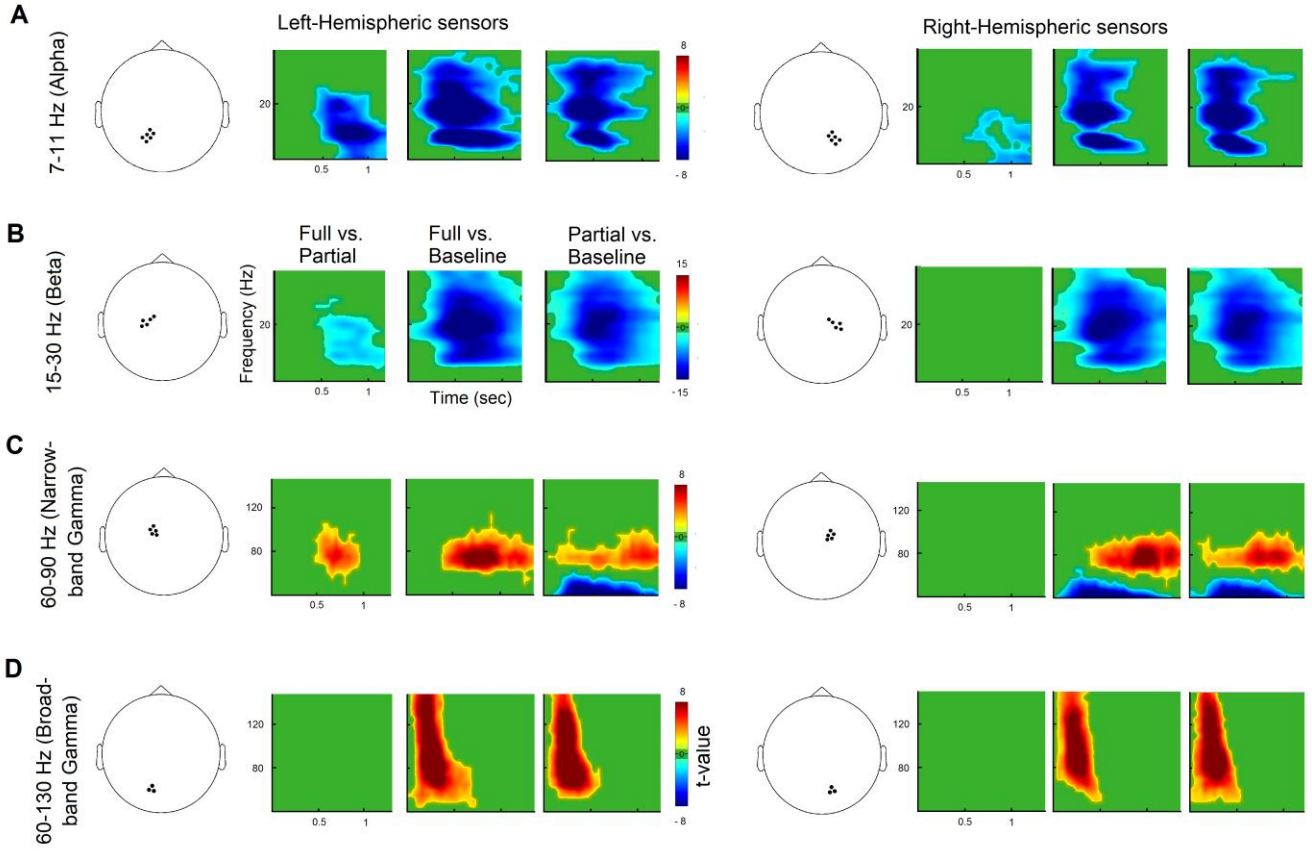


Figure 6. Time-frequency representations (TFRs) across the sensors of interest
The left panels illustrate time-Frequency statistical maps averaged across the sensors of interest as revealed in figure 5 for the (A) alpha, (B) beta and (C) narrow-band gamma, and in figure 3 for the (D) broad-band gamma. The right panels illustrate the maps of the right hemispheric sensor homologs. The maps describe activity modulation for the full vs. partial contrast (left TFRs), the full vs. baseline (middle TFRs) and the partial vs. baseline (right TFRs). The analysis was performed with stimulus-aligned data and was stratified for reaction time. Color bars illustrate masked significant modulations (p<0.05, corrected).

3.3 Virtual sensor analysis in the LOT and in the VWFA

Although activity peaked in the posterior LOT (the left middle temporal gyrus, BA 39, MNI coordinates -38 -78 12), (Figure 8A, upper panel), it also reached statistical significance in the anterior LOT (Figure 8B, upper panel), in a region also known as the visual word form area (VWFA; the left fusiform gyrus, BA 37, MNI coordinates -42 -55 -9) (Cohen et al., 2000). We computed two virtual sensors in each one of the posterior and anterior LOT coordinates. TFRs revealed that the main effect peaked in the alpha-band in both partial and full conditions (Figure 8, lower panels). Temporal power curves (Figure 8, blue/red curves) additionally revealed that the full versus partial alpha effect became statistically significant at 0.5sec in the posterior LOT, and at

0.7sec in the anterior LOT, i.e. the VWFA. These analyses advocate that a transition from partial to full conscious (word) perception can be measured with the use of a staircase procedure. Specifically, the transition is highlighted as a neural signature expressed through a late suppression of alpha-oscillations in the LOT. The present experimental approach and the characteristics of the observed neural signature are discussed in the context of prior evidence and future directions.

6. Discussion

The present study tested the validity of a graded perspective on consciousness. This was achieved with the emblematic case of word reading. We hypothesized that the putative functional bottleneck to consciousness (from partial to full) would emerge at a major key hub region for reading, namely the left occipito-temporal junction (LOT). We report that the transition from partial to full conscious (word) perception is marked by alpha-band oscillation suppression in the LOT. We propose that the findings empirically support a recent theoretical proposal of an intermediate perceptual level between conscious and non-conscious perception (Kouider et al., 2010). Furthermore, the findings not only confirm that consciousness can be graded into a partial level, but additionally shed new light on the functioning of the LOT/VWFA as a bottleneck region to full-blown conscious word-form perception. Specifically, the bottleneck would first emerge (at 0.5sec) in the posterior LOT and would extend anteriorly later on (at 0.7sec) to the VWFA.

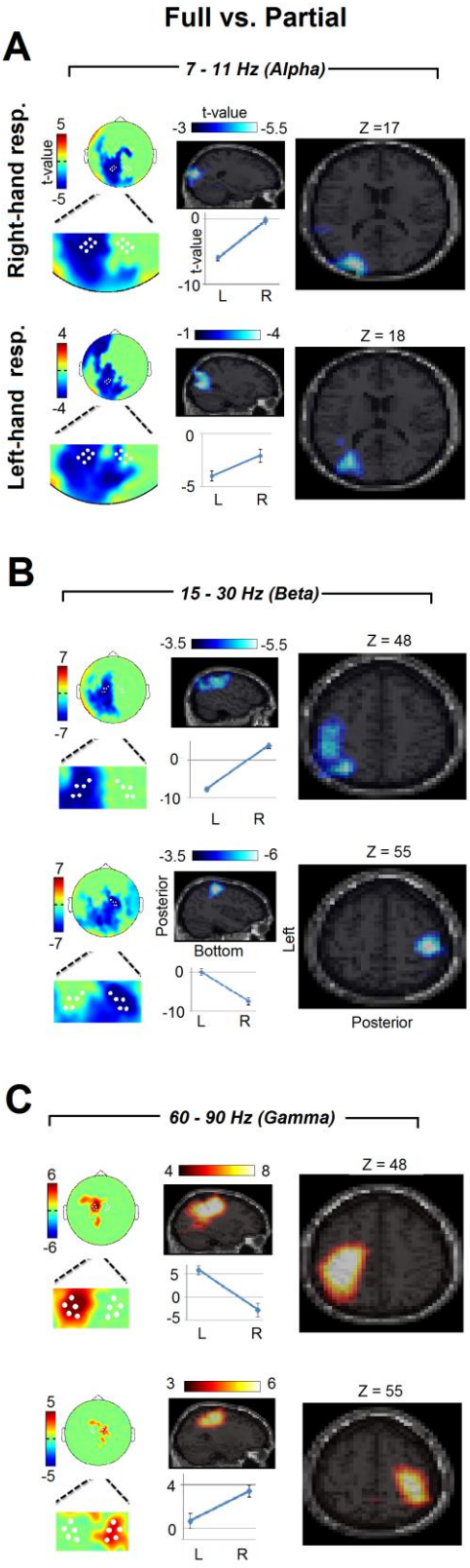

Full vs. Partial
A
7 - 11 Hz (Alpha)
Right-hand resp.
t-value
5
-5
-3
-5.5
Z =17
0
-10
L
R
Left-hand resp.
4
-4
-1
-4
Z = 18
0
-5
B
15 - 30 Hz (Beta)
7
-7
-3.5
-5.5
Z = 48
-6
Posterior
Bottom
Left
Z = 55
C
60 - 90 Hz (Gamma)
6
-6
4
8
5
3
Z = 48
Z = 55

Figure 7. Full vs. Partial: the alpha, beta and gamma effects as a function of response-hand laterality
Scalp topographies and brain views (sagittal and axial planes) in the (A) alpha, (B) beta and (C) gamma bands illustrate statistically significant ($p < 0.05$, corrected) topographical and cortical clusters. Topoplots refer to a group of statistically significant clusters of sensors (contralateral to button press) and their symmetrical homologues in the other brain hemisphere (ipsilateral to button press) that were highlighted in the topography. Insets illustrate pooled t-spectra were averaged across the highlighted left-hemispheric (represented by L) and right-hemispheric (represented by R) clusters. The upper and lower panels illustrate results pooled across subjects reporting Full conscious perception with a right-hand button press (N=7) and with a left-hand button press (N=6), respectively. Alternately, subjects reported Partial conscious perception with a left-hand button press (N=7) and with a right-hand button press (N=6), respectively.

Previous studies commonly compared trials in which stimuli were consciously perceived (i.e. full consciousness) versus trials in which stimuli were not consciously perceived (i.e. nil consciousness) (Supèr et al., 2001; Sergent et al., 2005; Del Cul et al., 2007; Melloni et al., 2007; Gaillard et al., 2009). However, recent theoretical approaches posit that such experimental strategy highlights neural activity driven by various processes unspecific to conscious perception (Aru et al., 2012; de Graaf et al., 2012). Here, we attempted to bypass the bias of non-specificity by focusing on a near-threshold transition from partial to full word-form perception. Additionally, exogenous stimulation was adjusted to endogenous perceptibility in real-time, thereby achieving stable stimulation. Importantly, the putative transition was expected once sufficient sensory evidence was accumulated. Previous research has revealed that such accumulation of evidence is reflected through a gradual buildup of neural processing reaching its peak near the perceptual threshold (Heekeren et al., 2008). Hence, under the current near-threshold stimulation, we expected the putative neural responses to reflect late high-level word processing rather than sensory processing. Accordingly, a notable aspect of the full versus partial contrast was its late rise of significance (approx. 0.5sec) in the three frequency bands (Figure 4). We therefore propose that the two reports (partial and full) reflect identical sensory processing and that a selective late neural process gates fully conscious perception of words under stimulation conditions of near perceptual threshold.

The present finding of a late neural processing marking the rise of full conscious perception is rather consistent with the predictions made by the global neuronal workspace (for a late review, see Dehaene and Changeux, 2011) and with other experimental data showing a late divergence between conscious and nonconscious processing (Sergent et al., 2005; Del Cul et al., 2007; Melloni et al., 2007; Gaillard et al., 2009). The global neuronal workspace, however, typically reports the divergence (between nil conscious and full consciousness) to arise at approximately 0.3sec post stimulus onset whereas the current experiment revealed an even later

divergence (between partial and full consciousness), i.e. at approximately 0.5sec. Thus, the present finding sheds novel light on the temporal dynamics of conscious perception by suggesting that the gateway to fully-blown conscious is even later than what has been previously considered – if the intermediate (i.e. partial) conscious level is taken into account. Furthermore, the global neuronal workspace makes predictions also regarding the cortical signature of conscious access, namely involving the fronto-parietal network (Dehaene and Changeux, 2011). In the present study the main non-motor activity (i.e. at the alpha-band) resulting from stimulus presentation in general (Figure 3, left panels), or from partial to full conscious perception in particular (Figure 5A, left panel) was not parieto-frontal, but rather occipital with temporal and parietal ramifications. Nevertheless, the effect did extend towards left-hemispheric parietal and even frontal sensors (Figure 5A, left panel). The most plausible explanation for the lack of more robust frontal activity could be accounted for by several experimental parameters: the paradigm (near-threshold presentation of masked words), the nature of the tasks (semantic and orthographic decisions), the analysis applied (local time-frequency) and the neuroimaging technique (MEG). Although Gross and colleagues reported a fronto-parietal enhancement in the beta band (Gross et al., 2004), their paradigm relates to a different experimental paradigm, namely the attentional blink, consisting in triggering quite different sensorial and cognitive processes. By contrast, word presentation has been previously shown to rather trigger alpha/beta suppression in similar regions as illustrated in the present study (Pammer et al., 2004; Cornelissen et al., 2009; Gaillard et al., 2009). Another matter to consider is that the fronto-parietal recruitment is rather predicted (Dehaene and Changeux, 2011) and observed (Melloni et al., 2007; Gaillard et al., 2009) in terms of long-range neuronal synchrony; the current paper, however, investigates the effects in terms of local neural oscillations. Future investigations should also keep in mind the distinct nature of local oscillations and long-range synchrony when testing the predictions of the global neuronal workspace or of other frameworks. Finally, one should also acknowledge the difference between electrophysiological source localization and haemodynamic cerebral mapping: word processing often does not trigger frontal activations when measured by MEG in comparison to fMRI (Vartiainen et al., 2011).

Despite the finding of insignificant processing modulation between the two perceptual reports during the first half second (Figure 4), we also probed activity in that early time window for both perceptual reports (Figure 2). We found that local rhythmic activity (alpha, beta and gamma bands) emerged early (Figure 2) at bilateral occipito-temporo-parietal cortices (Figure 3). This early oscillatory activity could be taken as an indication of the elementary visual and language processes taking place at the first half second of word processing. This

observation is in line with the scarce prior evidence of spatio-temporal oscillatory data during visual word processing (Pammer et al., 2004; Cornelissen et al., 2009). Considering the activity modulation observed here during the second half second (Figure 4), the report-driven divergence is suggestive of a critical threshold gating complete word-form perception.

As a consequence of the experimental strategy adopted here, contrasting full versus partial did not aim at including sensory processing. Furthermore, the counterbalanced response in both tasks and the *post-hoc* stratification for RT minimized the effect of eventual differences in reaction time distributions between conditions onto our data analysis. At the design level, response-hand laterality was task dependent and counterbalanced so as to highlight motor-independent effects; this strategy yielded the alpha power suppression observed here. Furthermore, the contralateral bias of the beta and gamma effects (of opposite polarity) suggested that they were related to motor response preparation (Figure 7BC); this observation is consistent with previous reports of the motor-driven gamma activation (Gruber et al., 2001; Kranczioch et al., 2006; Kranczioch et al., 2007; Donner et al., 2009) and beta deactivation (Kaiser et al., 2007; Donner et al., 2009) above central sensors. Notwithstanding the sound evidence of motor-related activity in the beta and gamma bands, the two hand-dependent sub-groups are most likely prone to reflect motor-driven effects whereas the whole group would rather reflect non-motor driven effects (e.g. semantic or conscious perception related effects). This could explain the presence of beta-band activity, at the whole group level, in cortical areas which are typically not assigned to motor activity, such as the left cuneus and the left middle temporal gyrus (Figure 5B, middle panels). By contrast, beta-band activity, at the hand laterality group level, rather emanated from motor-related cortical areas such as S1 or M1 (Figure 7B). We therefore recapitulate by stating that given the differential cortical mapping of the beta effect at the whole group level (Figure 5B, middle panels) versus at the hand laterality group level (Figure 7B), beta-band activity may have partially accounted for the partial to full conscious perception effect probed in this study. This is further corroborated by the beta effect detected at the level of the alpha-band sensors of interest (Figure 6A), and with previous reports of beta-band activity for higher linguistic functioning (for a review, see Bastiaansen and Hagoort, 2006). Nevertheless, the robust lateralized effector selectivity at the beta-band (Figure 7B) compared to non-lateralized effector selectivity at the alpha-band (Figure 7A) convincingly argues for the alpha-band effect observed here as the main candidate for the partial to full conscious perception transition.

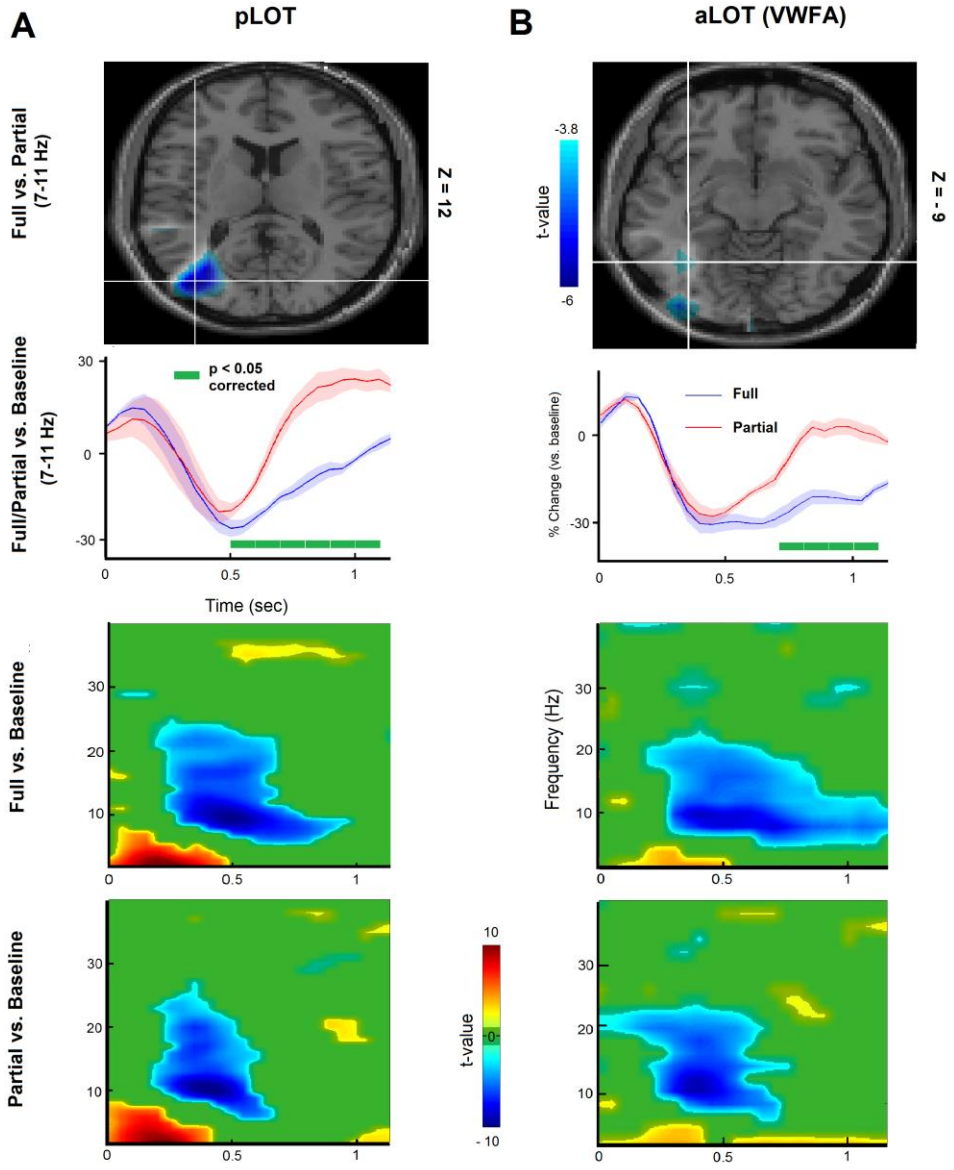


Figure 8. Virtual sensor analyses
Analyses were carried out on activity filtered from coordinates in (A, left panels) the posterior left occipito-temporal (pLOT) junction and in (B, right panels) the anterior LOT (aLOT), namely the visual word form area (VWFA). Source-localization (upper panels) illustrates on MNI templates statistical effects (Full vs. Partial) in the two coordinates. Underneath, plots represent the temporal evolution of power change vs. baseline of the two conditions averaged in the alpha band. Shades represent standard error of the mean power values, while green rectangles indicate statistically significant values ($p < 0.05$, corrected) on the time axis when contrasting Full vs. Partial. Below are shown TFRs of the Full and Partial conditions vs. baseline.

The current results propose that the LOT alpha suppression was not driven by motor activity. This could be convincingly pointed out by its left-lateralized activity pattern irrespective of response-hand laterality (Figure

7A), and by the non-motor region in which it was generated, namely, the LOT. Noteworthy, a recently proposed framework postulates that alpha activity reflects functional inhibition (Jensen and Mazaheri, 2010). This interpretation was derived from reports of alpha power suppression in task-engaged brain areas (van Gerven and Jensen, 2009; Handel et al., 2010), and alternatively of alpha power enhancement in non-engaged areas (Haegens et al., 2010). Thus, alpha suppression as observed here could be indicative of the functional engagement of the LOT as a selective activation pattern gating fully conscious perception of words. Sharing the same logic, previous reports of alpha suppression highlight its crucial role in high-level language processing (Roehm et al., 2001; Klimesch et al., 2001; Bastiaansen and Hagoort, 2006). Finally, a most recent review is highly consistent with the findings shown here, as it features the role of alpha suppression in enabling conscious access to semantics (Klimesch, 2012).

Contemporary models of reading propose that the LOT cortex acts as a neural gateway from vision to language (Jobard et al., 2003; Price, 2012). Ample evidence points out that the functional role of this area is primarily constrained to specific word-form perception (Dehaene and Cohen, 2011) within an anterior segment of the LOT, namely the VWFA. Here, we note that the essence of the partial to full conscious perception effect emerged in the posterior LOT (Figure 8A). Yet, we also note that this activity extends towards the anterior LOT, namely the VWFA (Figure 8B) about 0.2sec later. Accordingly, our findings generate a novel outlook on word processing dynamics: the VWFA would not only be recruited at an early stage for allowing low-level (script processing) word processing as has been previously instantiated (Pammer et al., 2004; Dehaene and Cohen, 2011), but also at a later stage for gating high-level (lexico-semantic) processing. Such late semantic gateway would not be selective to the VWFA but rather emerge in the posterior LOT and extend anteriorly to the VWFA. Notably, Cornelissen and colleagues have investigated the oscillatory activity at the alpha and beta bands during the first half second of passive word viewing (Cornelissen et al., 2009). Their findings revealed significant activity suppression concentrated at the VWFA during the 0.2-0.5sec time window. Hence, the activity observed here as a gateway to higher language processing, namely, alpha band suppression in the VWFA starting at 0.7sec, probably accounts for a late stage of the processing cascade which is triggered in this area as early as at 0.2sec. Specifically, the present evidence of a gateway from lower to higher processing is congruent with the observation of simultaneous early activity in the VWFA and in frontal language areas (Cornelissen et al., 2009). This "second go" in the VWFA is likely to be enhanced under the particular experimental conditions of the present paradigm, namely near-threshold conscious word perception. Further

support for the outlook generated here can be drawn from the joint evidence that forward and backward connections are essential for allowing conscious perception (Lamme, 2006) and for interfacing lower with higher language processes (Price and Devlin, 2011). Future connectivity modeling should exploit the fine temporal sampling of MEG to further probe the neural dynamics gated through the alpha suppression in the LOT region.

Moreover, zooming into the LOT activation source, one could note not only an extension of activity towards the ventral pathway, but also towards dorsal pathways (Figure 5B, left panel). The crucial role of the ventral and dorsal pathways during reading has been highlighted before (Pugh et al., 2000). Interestingly, in a previous effective connectivity (fMRI) study, it was shown that this same region was acting as a mediator of information trafficking to those two pathways, and thereby optimizing reading performance (Levy et al., 2009). Other connectivity studies also highlight the role of these pathways during reading (Cao et al., 2008; Richardson et al., 2011). In the major endeavor of comprehending the complex neural dynamics sustaining reading, these findings propose that future studies should take particular note of the forward and backward connections emanating from the LOT towards the ventral and dorsal pathways.

The results reported here reflect the grading of consciousness to a partial level, between nil and full, without compromising its all-or-none mechanism. In other words, partial or full stimulus representations can trigger an all-or-none neural response (Kouider et al., 2010). Although it is impossible to rule out random attentional fluctuations during the course of experiment may have generated fluctuations between full and partial perception, our analyses showed that these were most probably due to a bottom-up feature, namely word-length (Figure 1F), in agreement with previous experimental psychology data (Samuel et al., 1982). Furthermore, our data shows that fluctuations in perception could not have been significantly predicted by early baseline power activity (Figure 4) as previous studies near-threshold stimulus or a TMS-induced phosphene perception have reported (Romei et al., 2008; van Dijk et al., 2008; , Mathewson et al., 2009; Dugue et al., 2011). Yet, these studies often refer to baseline phase change as a predictor to subsequent perceptual level. Although phase analysis is beyond the scope of the present study, future analyses may reveal a plausible link between baseline phase activity and a bottleneck to perceptual consciousness. Finally, the word-length effect found here should be taken into account when selecting word stimuli in future experiments testing for conscious perception.

7. Acknowledgements

The present work was supported by both the European Science Foundation's European Young Investigator Award Program, and by the French allowance “Allocation de Recherche Ministérielle”. We would like to thank Bram Daams and Sander Berends for technical support, as well as Jan-Mathijs Schoffelen and Stan van Pelt for their previous advice on the analysis scheme.

8. References

Aru, J., Bachmann, T., Singer, W., Melloni, L., 2012. Distilling the neural correlates of consciousness. Neurosci. Biobehav. Rev. 36,737-746.

Bastiaansen, M.C., and Knösche, T.R., 2000. Tangential derivative mappingof axial MEG applied to event-related desynchronization research. Clin. Neurophysiol. 111, 1300-1305.

Bastiaansen, M., and Hagoort, P., 2006. Oscillatory neuronal dynamics during language comprehension. Prog. Brain Res. 159, 179-96. Review.

Baayen, H., Piepenbrock, R., van Rijn, H., 1993. The CELEX lexical database [CD-ROM]. Philadelphia, PA: University of Pennsylvania, Linguistic Data Consortium.

Benjamini, Y., and Hochberg, Y., 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. J Roy Stat Soc 57: 289–300.

Buzsaki, G., and Draguhn, A., 2004. Neuronal oscillations in cortical networks. Science 304, 1926–1929.

Cao, F., Bitan, T., Booth, J.R., 2008. Effective brain connectivity with reading difficulties during phonological processing. Brain Lang. 107, 91-101.

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.A., Michel, F., 2000. The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain 123, 291-307

Cornelissen, P.L., Kringelbach, M.L., Ellis, A.W., Whitney, C., Holliday, I.E., Hansen, P.C., 2009. Activation of the left inferior frontal gyrus in the first 200 ms of reading: evidence from magnetoencephalography (MEG). PLoS One 4, e5359.

Del Cul, A., Baillet, S., Dehaene, S., 2007. Brain dynamics underlying the nonlinear threshold for access to consciousness. PLoS Biol. 5, e260. doi:10.1371/journal.pbio.0050260

Dehaene, S., and Cohen, L., 2011. The unique role of the visual word form area in reading. Trends Cogn Sci. 15, 254-262.

Dehaene, S., and Changeux, J.P., 2011. Experimental and theoretical approaches to conscious processing. Neuron 70, 200-227.

Donner, T.H., Siegel, M., Fries, P., Engel, A.K., 2009. Buildup of choice-predictive activity in human motor cortex during perceptual decision making. Curr. Biol. 19, 1581-1585.

Dugue, L., Marque, P., VanRullen, R., 2011. The phase of ongoing oscillations mediates the causal relation between brain excitation and visual perception. J. Neurosci. 31, 11889- 11893

Gaillard, R., Dehaene, S., Adam, C., Clémenceau, S., Hasboun, D., Baulac, M., Cohen, L., Naccache, L., 2009. Converging intracranial markers of conscious access. PLoS Biol. 7, e61.

de Graaf, T.A., Hsieh, P.J., Sack, A.T., 2012. The 'correlates' in neural correlates of consciousness. Neurosci. Biobehav. Rev. 36,191-197.

Heekeren, H.R., Marrett, S., Ungerleider, L.G., 2008. The neural systems that mediate human perceptual decision making. Nat. Rev. Neurosci. 9, 467-479.

Gross, J., Kujala, J., Hämäläinen, M., Timmermann, L., Schnitzler, A., Salmelin, R., 2001. Dynamic imaging of coherent sources: Studying neural interactions in the human brain. Proc. Natl. Acad. Sci. U S A 98, 694-699.

Gross J, Schmitz F, Schnitzler I, Kessler K, Shapiro K, Hommel B, Schnitzler A., 2004. Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. Proc. Natl. Acad. Sci. U S A 101, 13050-13055.

Gruber, T., Keil, A., Müller, M.M., 2001. Modulation of induced gamma band responses and phase synchrony in a paired associate learning task in the human EEG. Neurosci. Lett. 316, 29-32.

van Gerven, M., Jensen, O., 2009. Attention modulations of posterior alpha as a control signal for two-dimensional brain–computer interfaces. J. Neurosci. Methods 179, 78–84.

Haegens, S., Osipova, D., Oostenveld, R., Jensen, O., 2010. Somatosensory working memory performance in humans depends on both engagement and disengagement of regions in a distributed network. Hum. Brain Mapp. 31, 26–35.

Hämäläinen, M., Hari, R., Ilmoniemi, R.J., Knuutila, J., Lounasmaa, O.V., 1993. Magnetoencephalography – theory, instrumentation, and applications to noninvasive studies of the working human brain. Rev. Mod. Phys. 65, 413-497.

Handel, B., Haarmeier, T., Jensen, O., 2010. Alpha oscillations correlate with the successful inhibition of unattended stimuli. J. Cogn. Neurosci. doi: 10.1162/jocn.2010.21557

Jensen, O., and Mazaheri, A., 2010. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. Front. Hum. Neurosci. 4, 186.

Jobard, G., Crivello, F., Tzourio–Mazoyer, N., 2003. Evaluation of the dual route theory of reading: a metanalysis of 35 neuroimaging studies. Neuroimage 20, 693-712.

Kaiser, J., Lennert, T., Lutzenberger, W., 2007. Dynamics of oscillatory activity during auditory decision making, Cereb. Cortex 17, 2258-2267.

Klimesch, W., Doppelmayr, M., Wimmer, H., Gruber, W., Röhm, D., Schwaiger, J., Hutzler, F., 2001. Alpha and beta band power changes in normal and dyslexic children. Clin. Neurophysiol. 112, 1186-1195.

Klimesch, W., 2012. Alpha-band oscillations, attention, and controlled access to stored information.

Trends Cogn Sci., 16(12):606-17. doi: 10.1016/j.tics.2012.10.007.

Kouider, S., de Gardelle, V., Sackur, J., Dupoux, E., 2010. How rich is consciousness? The partial awareness hypothesis. Trends Cogn. Sci. 14, 301-307.

Kranczioch, C., Debener, S., Herrmann, C.S., Engel, A.K., 2006. EEG gamma-band activity in rapid serial visual presentation. Exp. Brain Res. 169, 246-254.

Kranczioch, C., Debener, S., Maye, A., Engel, A.K., 2007. Temporal dynamics of access to consciousness in the attentional blink. Neuroimage 37, 947-955.

Lamme, V.A., 2006. Towards a true neural stance on consciousness. Trends Cogn. Sci. 10, 494-501.

Levitt, H., 1971. Transformed up-down methods in psychoacoustics. J. Acoustical Soc. Am. 49, 467-477.

Levy, J., Pernet, C., Treserras, S., Boulanouar, K., Berry, I., Aubry, F., Demonet, J.F., Celsis, P., 2008. Piecemeal recruitment of left- lateralized brain areas during reading: a spatio-functional account. Neuroimage 43, 581–591.

Levy, J., Pernet, C., Treserras, S., Boulanouar, K., Aubry, F., Demonet, J.F., Celsis, P., 2009. Testing for the Dual-Route Cascade Reading Model in the Brain: An fMRI Effective Connectivity Account of an Efficient Reading Style. PLoS ONE 4, e6675. doi:10.1371/journal.pone.0006675.

Maris, E., and Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Meth. 164, 177-190.

Mainy, N., Jung, J., Baciu, M., Kahane, P., Schoendorff, B., Minotti, L., Hoffmann, D., Bertrand, O., Lachaux, J.P., 2008. Cortical dynamics of word recognition. Hum. Brain Mapp. 29, 1215-1230.

Mathewson, K.E., Gratton, G., Fabiani, M., Beck, D.M., Ro, T., 2009. To see or not to see: prestimulus alpha phase predicts visual awareness. J. Neurosci. 29, 2725-2732

McClelland, J. L., and Rumelhart, D.E., 1981. An interactive activation model of context effects in letter perception: Part 1. An account of basic findings. Psychol. Rev. 88, 375-407.

Melloni, L., Molina, C., Pena, M., Torres, D., Singer, W., Rodriguez, E., 2007. Synchronization of neural activity across cortical areas correlates with conscious perception. J. Neurosci. 27, 2858-2865.

Nichols, T.E., and Holmes, A.P., 2002. Nonparametric permutation tests for functional neuroimaging: a primer with examples. Hum. Brain Mapp. 15,1-25.

Nolte, G., 2003. The magnetic lead field theorem in the quasi-static approximationand its use for magnetoencephalography forward calculation in realistic volume conductors. Phys Med Biol 48, 3637-3652.

Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational intelligence and neuroscience 2011, 156869.

Pammer, K., Hansen, P.C., Kringelbach, M.L., Holliday, I., Barnes, G., Hillebrand, A., Singh, K.D., Cornelissen, P.L., 2004. Visual word recognition: the first half second. Neuroimage 22, 1819-1825.

Percival, D.B., and Walden, A.T., 1993. Spectral analysis for physical applications: multitaper and conventional univariate techniques. Cambridge,UK:CambridgeUP.

Price, C., Devlin, J.T., 2011. The Interactive Account of ventral occipito-temporal contributions to reading. Trends Cogn. Sci. 15, 246–253.

Price, C.J., 2012. A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. Neuroimage 62, 816-847.

Pugh, K.R., Mencl, W.E., Jenner, A.R., Katz, L., Frost, S.J., Lee, J.R., Shaywitz, S.E., Shaywitz, B.A., 2000. Functional neuroimaging studies of reading and reading disability (developmental dyslexia). Ment. Retard. Dev. Disabil. Res. Rev. 6, 207-213.

Richardson, F.M., Seghier, M.L., Leff, A.P., Thomas, M.S., Price, C.J., 2011. Multiple routes from occipital to temporal cortices during reading. J. Neurosci. 31, 8239-8247.

Roelfsema, P.R., Lamme, V.A., Spekreijse, H., 1998. Object-based attention in the primary visual cortex of the macaque monkey. Nature 395, 376 -381.

Roehm, D., Klimesch, W., Haider, H., Doppelmayr, M., 2001. The role of theta and alpha oscillations for language comprehension in the human encephalogram, Neurosci. Lett. 310, 137-140.

Romei, V., Brodbeck, V., Michel, C., Amedi, A., Pascual-Leone, A., Thut, G., 2008. Spontaneous fluctuations in posterior alpha-band EEG activity reflect variability in excitability of human visual areas. Cereb. Cortex 18, 2010-2018

Samuel, A.G., van Santen, J.P., Johnston, J.C., 1982. Length effects in word perception: we is better than i but worse than you or them. J. Exp. Psychol. Hum. Percept. Perform. 8, 91-105.

Schoffelen, J.M., Oostenveld, R., Fries, P., 2005. Neuronal coherence as a mechanism of effective corticospinal interaction. Science 308, 111–113.

Selfridge, O., 1959. Pandemonium: a paradigm for learning. Symposium on the Mechanization of Thought Processes, HM Stationery Office, London, 513-526.

Sergent, C., Baillet, S., Dehaene, S., 2005. Timing of the brain events underlying access to consciousness during the attentional blink. Nat. Neurosci. 8, 1391-1400.

Supèr, H., Spekreijse, H., Lamme, V.A., 2001. Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). Nat. Neurosci. 4, 304-310.

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

Vartiainen J, Liljeström M, Koskinen M, Renvall H, Salmelin R., 2011. Functional Magnetic Resonance Imaging Blood Oxygenation Level-Dependent Signal and Magnetoencephalography Evoked Responses Yield Different Neural Functionality in Reading. J. Neurosci. 31, 1048-1058.

Vidal, J.R., Freyermuth, S., Jerbi, K., Hamamé, C.M., Ossandon, T., Bertrand, O., Minotti, L., Kahane, P., Berthoz, A., Lachaux, J.P., 2012. Long-distance amplitude correlations in the high γ band reveal segregation and integration within the reading network. J. Neurosci. 32, 6421-6434.