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Alpha suppression and connectivity modulations in left temporal and parietal cortices index partial awareness of words

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ABSTRACT

The partial awareness hypothesis is a theoretical proposal that recently provided a reconciling solution to graded and dichotomous accounts of consciousness. It suggests that we can become conscious of distinct properties of an object independently, ranging from low-level features to complex forms of representation. We investigated this hypothesis using classic visual word masking adapted to a near-threshold paradigm. The masking intensity was adjusted to the individual perception threshold, at which individual alphabetical letters, but not words, could be perceived in approximately half of the trials. We confined perception to a pre-lexical stage of word processing that corresponded to a clear condition of partial awareness. At this level of representation, the stimulus properties began to emerge within consciousness, yet they did not escalate to full stimulus awareness. In other words, participants were able to perceive individual letters, while remaining unaware of the whole letter strings presented. Cortical activity measured with MEG was compared between physically identical trials that differed in perception (perceived, not perceived). We found that compared to no awareness, partial awareness of words was characterized by suppression of oscillatory alpha power in left temporal and parietal cortices. The analysis of functional connectivity with seeds based on the power effect in these two regions revealed sparse connections for the parietal seed, and strong connections between the temporal seed and other regions of the language network. We suggest that the engagement of language regions indexed by alpha power suppression is responsible for establishing and maintaining conscious representations of individual pre-lexical units.

Introduction

How conscious perception relates to sensory processing in the human brain is a major unanswered question in cognitive neuroscience. In recent years, various influential theoretical frameworks have stimulated a lot of experimental work to identify the neural correlates of consciousness (NCC; Crick and Koch, 1998). One prominent theory, the global neuronal workspace (GNW; Baars, 2005; Dehaene et al., 1998), proposed that a stimulus can be consciously perceived when, after activating essential nodes in sensory regions, the signal is distributed globally in the cortex and reverberates among high-level cortical areas, including frontal, temporal and parietal regions (Dehaene et al., 2001; Dehaene and Changeux, 2005; Nakamura et al., 2005). Crucially, neuronal activity confined to specific early sensory areas would thus not suffice for conscious perception.

Interestingly, Kouider et al. (2010) recently suggested that perception of a stimulus can result in different levels of conscious representation. According to the partial awareness hypothesis (Kouider et al., 2010; Kouider and Dupoux, 2004), objects are not necessarily perceived in an all-or-none manner, but rather we could be aware of certain object features while being unaware of others (see also Cleeremans, 2007; Overgaard et al., 2006; Sergent and Dehaene, 2004, on the debate of whether consciousness is a graded or dichotomous phenomenon). Therefore, we could become conscious of different properties of an object, organized hierarchically from low-level to complex forms of representation, independently.

To investigate this hypothesis, we developed a paradigm that exploits the strengths of two different approaches in the tradition of consciousness research (Dehaene et al., 2006), namely near-threshold (NT) and visual masking paradigms. The outstanding value of NT paradigms consists of providing researchers with the opportunity to isolate the neuronal processes that reflect qualitative changes in perception.

Abbreviations: MEG, Magnetoencephalography; NCC, Neural correlates of consciousness; GNW, Global neuronal workspace; NT, Near-threshold; CoLFIS, Corpus e Lessico di Frequenza dell'Italiano Scritto; DLP, Digital light processing; HPI, Head-position indicator; ANOVA, Analysis of variance; ERF, Event-related field; FFT, Fast Fourier transform; DICS, Dynamic imaging of coherent sources; MNI, Montreal Neurological Institute; MRI, Magnetic resonance image; CI, Confidence interval; BA, Brodmann area; VWFA, Visual word form area; TMS, Transcranial magnetic stimulation.

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The opportunity is achieved by presenting physically identical stimuli at the individual perceptual threshold, which results in stimuli being consciously perceived in only a proportion of trials. However, as a consequence of the threshold-level reduction of stimulus intensity, NT paradigms can hardly preserve the more fine-grained features of complex stimuli. To circumvent this problem, visual masking techniques have been extensively employed (see Breitmeyer and Ogmen, 2000; Enns and Di Lollo, 2000; Kouider and Dehaene, 2007 for reviews), particularly in the study of language processing (see Dehaene et al., 2001 for an example). Conventionally, the strength of the mask interference is changed to make stimuli either completely visible or completely invisible, thereby retaining all or none of their characteristics into consciousness.

We designed a word masking paradigm in which the mask's strength was adjusted to a constant threshold level, similar to the NT approach. In agreement with the partial awareness hypothesis, we defined our threshold as the chance-level probability of detecting letters in masked word presentations. Hence, we prevented participants from perceiving the entire word, and expected them to report seeing letters in only a proportion of trials. Our manipulation provided us with an ideal scenario to study the neural basis of a clearly characterized condition of partial awareness.

Specifically, the perception of letters marks the transition between two distinct levels of stimulus representation. On the one hand, letters become consciously visible by virtue of combining basic geometrical shapes into meaningful patterns. On the other hand, neuronal activation in response to letter patterns is not yet sufficient to trigger full stimulus awareness, and perception does not escalate to accessing the lexical and semantic properties of the word. In line with the GNW model outlined above, we predicted that partial awareness of words would be reflected by the engagement of core language-processing regions, also referred to as essential nodes (Zeki and Bartels, 1999; see Tong et al., 1998 for an example). To investigate this, we compared neuronal oscillatory activity, measured with MEG, between perceived and not perceived stimuli. We hypothesized that differences in oscillatory power would be found in cortical regions of the left hemisphere that represent the stimulus features disentangled by our experimental manipulation. Based on the anatomical locations showing the greatest power effects, we then used a seeded functional connectivity analysis approach to explore the functional interactions between nodes of the language network.

Materials and methods

Participants

Twenty right-handed healthy volunteers (mean age $\pm$ standard deviation: 25 $\pm$ 5.2; ten females) took part in the study after giving informed consent. Following behavioral data analysis, three participants were excluded due to inadequate task performance (two of them because of unbalanced proportion of perceived and not perceived stimuli, and one of them because of too many false alarms, see Behavioral data analysis below). Therefore, the analysis of MEG data was performed on seventeen out of the initial twenty participants. All participants were native Italian speakers and, to prevent confounding effects in the lexical decision task, were required to have no to very poor knowledge of the Spanish language. All participants had normal or corrected-to-normal vision and reported no known history of neurological or psychiatric disorders. The experimental procedure was approved by the local ethics committee and participants received monetary reimbursement for their participation.

Stimuli and procedure

The experiment consisted of the adaptation of a visual masking paradigm, in which masked linguistic stimuli were presented at the individual threshold for the detection of letters, pre-estimated with two independent one-up one-down staircases converging to 50% detection rate. The visibility of the letters was manipulated by adjusting the luminance contrast of the masks. Prior to beginning the main experiment, participants completed 20 training trials that served to test if the contrast threshold had been estimated successfully. Two different sets of stimuli (each including both words and pseudowords) were used for the threshold and training procedures, none of which was presented in the main experiment. In the main experiment, participants had to perform two sequential tasks. Firstly, they had to report whether they were able to identify at least one letter in the stimulus presentation. This constituted the perceptual decision, or detection task. Secondly, they were required to perform a lexical decision and classify the stimulus as word or pseudoword. Participants were instructed to also respond when the stimulus was not perceived, i.e. irrespectively of whether they had perceived letters or not. The total time of the experimental session, including preparation, was less than 2 h.

The trial structure of the experiment is illustrated in Fig. 1. Target stimuli were presented with three different intensities (320 trials at threshold, 40 supra-threshold catch trials and 40 empty trials), in random order and equally distributed across eight blocks (~5 min each). Participants were allowed to take breaks between blocks. Target stimuli consisted of strings of four letters forming either a word or a pseudoword (two stimulus classes, see Stimuli and procedure below). In threshold trials, letters were presented in medium-contrast gray. In catch trials, letters were presented in white to increase their visibility. In empty trials, letters were presented in black and were therefore invisible. Each trial began with a white fixation cross ($0.8 \times 0.7°$ visual angle) presented centrally on a black background for a jittered period of 3 to 6 s, with shorter intervals being more common than longer ones. The target stimulus was presented centrally ($3 \times 1°$ visual angle) for 33 ms, and was immediately preceded and followed by a forward and a backward mask of 67 ms duration each. Masks consisted of a fixed number of different shapes (squares, diamonds, triangles and circles) drawn with the same line thickness as the text font (Arial) and covering the same approximate area. The size and position of the shapes was pseudo-randomly generated on a trial-by-trial basis, but with forward and backward masks of the same trial remaining identical. The fixation cross disappeared at forward mask onset and reappeared at backward mask offset. After a 500 ms interval, two questions were displayed consecutively on the screen for up to 2 s each, or until a response was given. Participants responded 'perceived' or 'not perceived' to detection and 'word' or 'pseudoword' to classification by raising the index or middle finger of their right hand. The responses associated with the index and the middle finger were counterbalanced in all possible combinations, both across participants and between the first and second response.

The two classes of target stimuli consisted of words and pseudowords, equally distributed across levels of stimulus intensity (threshold, catch, and empty trials) and experimental blocks. Words were selected from the CoLFIS database (Bertinetto et al., 2005) and consisted of Italian disyllabic nouns only, syllables having consonant–vowel structure. Pseudowords were created by substituting the second consonant of each word stimulus, following the phonotactic restrictions of the Italian language. Pseudowords that were English words and pseudowords that would become Italian words by adding an accent to the final vowel were excluded. Words and pseudowords did not differ statistically in bigram frequency ($t_{(398)} = 1.28$, $p = 0.2$) and neighborhood size ($t_{(398)} = 1.02$, $p = 0.3$).

All stimulus presentations were programmed in Matlab (MathWorks) using the Psychophysics Toolbox (Kleiner et al., 2007). Stimuli were back-projected onto a translucent screen using a DLP projector (Panasonic PT-D7700E) located outside the magnetically shielded room. The projected area was $17 \times 13.6°$ visual angles (with a resolution of 1280×1024 pixels) and the refresh rate was 60 Hz. A photodiode was placed at the upper left corner of the projection screen in order to record the exact onset of the visual stimulation.