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Evidence from iEEG of an adaptative transient constriction of spatial attention

Attentional suppression of peripheral vision

Keywords : inattention blindness, attention, primary visual cortex, suppression, ECoG

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Abbreviation

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Summary for Social Media if Published

When reading or focusing attentively at details of a visual scene, we often fail to notice visual events occurring in the periphery. At the neural level, it coincides with reduced neural processing of peripheral locations in the visual cortex. Our study investigated the subsecond dynamics of that phenomenon for the first time in humans and revealed a highly flexible mechanism that restores peripheral vision as soon as attention is released from the central stimulus. In practice, we provide a clear explanation for numerous traffic accidents occurring during sustained attention to the central visual field, especially while using smartphones.

Abstract

Attention-related suppression refers to a transient inhibition of neurons in the representation of the peripheral visual field in response to a centrally-flashed stimulus. Using intracranial EEG recordings in Human area V2, we were able to record that suppression during a reading task while varying the behavioral relevance of word stimuli. We showed that suppression duration is flexibly modulated by task-demands to reduce the response to peripheral distractors while the stimulus of interest is processed by higher-level visual areas. Our study demonstrates for the first time a transient constriction of the attentional-spotlight controlled by top-down process.

Introduction

When a high-contrast stimulus is attended in the central visual field, the main effect of attention in primary visual areas is a suppression of neural activity representing peripheral locations. This phenomenon - called attention-related suppression has been well documented both in humans and non-human primates (NHP), with fMRI and electrophysiological recordings¹⁻⁸. It corresponds to a suppressive peripheral attention field, or peripheral field inhibition (PFI)^{7,9} causing a sudden constriction of the famous attentional 'spotlight'¹⁰ and erasing unattended spatial locations.

At the behavioral level, that PFI is associated with a reduced discriminability and detectability of peripheral stimuli¹¹⁻¹³, which yields a phenomenon known as inattention blindness¹⁴: in real-life conditions, we famously fail to react to and notice important and sometimes life-threatening events in unattended locations. Far from a laboratory curiosity, inattention blindness has become such an important cause of traffic accidents, that several nationwide campaigns have warned road-users against that phenomenon, in relation to smartphone usage¹⁵.

To properly assess the behavioral consequences of the attention-related PFI, it is critically important to understand its precise dynamics, including its latency and duration. Yet, most reports in humans have described negative BOLD responses in primary visual areas with a slow time-course which fails to reveal the actual dynamics of the phenomenon (e.g.^{5,7}). In Non-Human Primates, direct neural recordings have shown that the suppression starts at an early latency (around 100 ms) and can last several hundreds of ms⁸. In humans, that dynamics has not been described so far, probably because it can only be observed with direct intracranial EEG (iEEG) recordings in the visual cortex, almost never performed except in rare epileptic patients, during their pre-surgical evaluation. Using iEEG fifteen years ago, we reported anecdotally a transient suppression of the peripheral field in the primary visual cortex, in response to centrally flashed face-stimuli⁶, but the paradigm did not allow to assess whether the duration adjusted to task demands. Given the behavioral impact of inattention blindness - and its potential danger - that question is nevertheless critical, as an efficient attention system should in principle allow the attention field to open up as soon as possible, that is, as soon as all necessary information has been extracted from the visual stimulus. In particular, central stimuli should trigger a shorter surround-suppression when they contain no information relevant to the task. The aim of the present study was specifically to test that prediction.

Methods & Results

We recorded iEEG in five participants suffering from epilepsy and implanted with iEEG electrodes in the parietal, occipital and temporal cortex, including area V2. They viewed a series of words flashed one by one every 700 ms in the center of a dark computer screen (200 low-contrast and 200 high-contrast gray words, in random order) and were asked to ignore the latter and read only low-contrast words which unfolded a story to be told afterwards (details in figure 1)¹⁶. We computed the variations of High-Frequency Activity induced by to-be-read and to-be-ignored word stimuli flashed in the central visual field (HFA, between 50 Hz and 150 Hz) as a proxy of population-level spiking activity¹⁷ and compared pre- vs. post-stimulus activity to detect significant positive or negative responses (Wilcoxon test $p < 0.01$, fig1) and measure their duration. We found that all stimuli elicited a suppression of

activity in representations of the peripheral field in V2¹⁸ (i.e. V2 sites where clinical electrical stimulations at 50 Hz induced peripheral phosphenes). Most important was the significantly shortened suppression for non-relevant stimuli: HFA decreases starting around 100ms reaching a negative plateau around 200ms, then it returns to baseline immediately if the stimulus was non-relevant and up to 400ms later if the stimulus was relevant. This deactivation coincides with an increase in HFA for basal temporal lobe (cf fig.2).

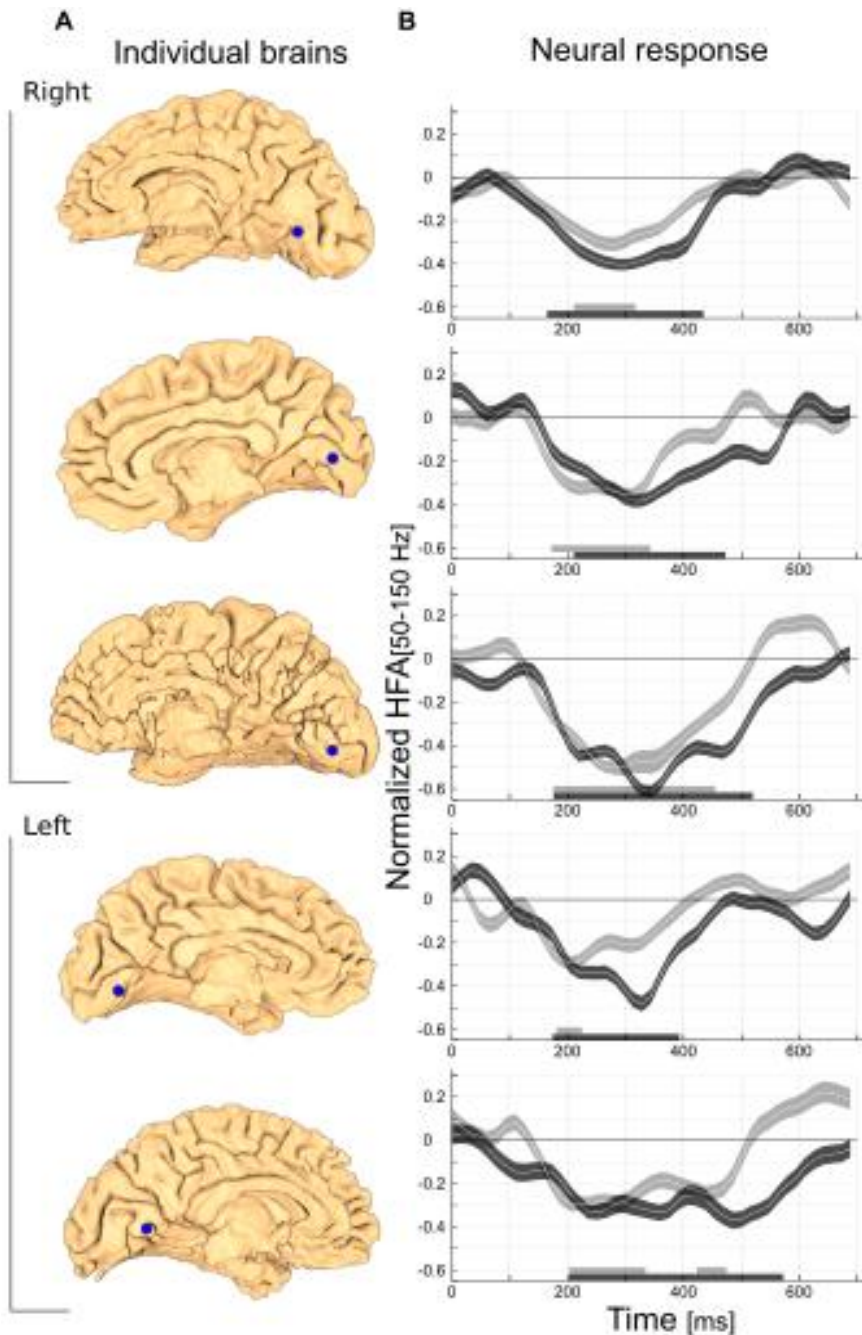


Figure 1 : Central visual stimuli elicit a suppression of neural activity in V2, enhanced by attention. (A) Precise location of the recording sites for each patient (2 males, 3 females, 16 to 33 y.o.). In all sites, standard clinical electrical stimulations at 50 Hz elicited peripheral visual phosphenes. (B) Participants were presented with white and grey words flashed for 200 ms at the center of a computer screen : white words had to be ignored (IGN,

grey plots) while grey words had to be read (ATT, in black) and formed a story that the participant had to report at the end. Right graphs show normalized HFA for each recording site between 0 and 700 ms following stimulus onset averaged across 200 words (\pm s.e.m). Bars above the time axis indicated time windows with significant deactivation relative to prestimulus baseline (-200:0 ms; Wilcoxon test, $p < 0.01$).

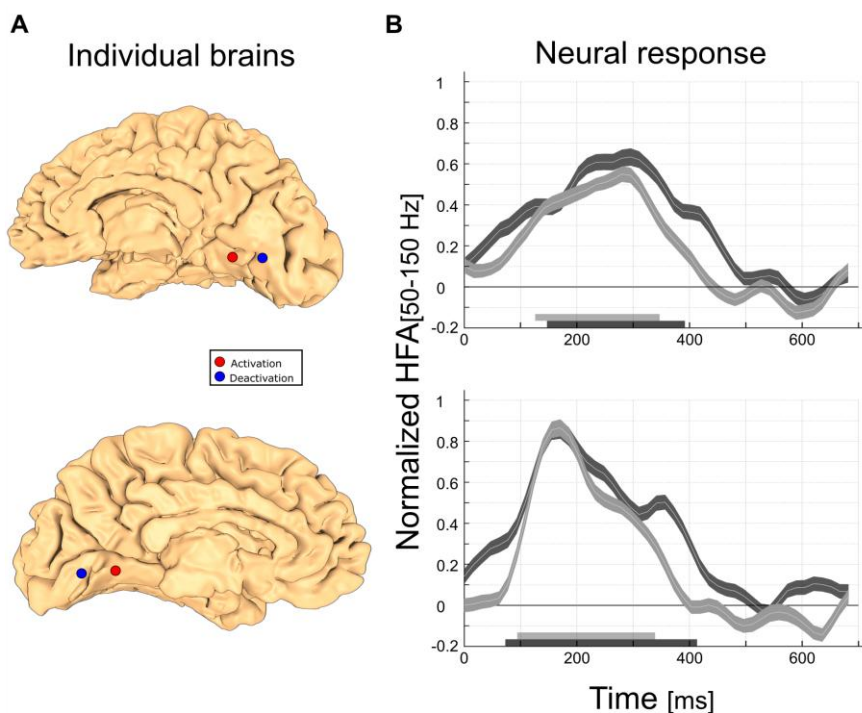


Figure 2 : Timing of neural activation induced by visual stimuli (A) individual anatomy for 2 patients showing sites in which central visual stimuli trigger an increase (red) vs. a decrease (blue) of neural activity. (B) Normalized HFA[50-150 Hz] for each recording site in the 700 ms following stimulus onset (onset at 0 ms) (median \pm s.e.m, $n = 200$ trials). Horizontal bars indicate time windows with significant HFA increase relative to pre-stimulus baseline level (-200:0 ms; Wilcoxon test, $p < 0,01$).

Discussion

We therefore confirmed that the peripheral suppression induced by a central stimulus in the primary human visual cortex is a transient mechanism. That systematic return to prestimulus baseline level between consecutive stimuli is somewhat counterintuitive from a purely functional point of view, given that peripheral vision is behaviorally irrelevant throughout the task: from the sole point of view of that task, the peripheral inhibition could be maintained throughout the task. Yet, we showed that attention is never durably focal, which suggests a dynamic mechanism to limit peripheral neglect to a minimum and thus avoid inattentive blindness.

We also showed that the suppression coincided precisely in time with word-recognition processes in higher-level visual areas, such as the basal temporal lobe. Those processes, which dynamics has been exquisitely detailed by Self et al.⁸ are essential for letter recognition and reading. The PFI likely prevents interference from irrelevant peripheral visual inputs.

Most importantly, we found that the duration of the inhibition of peripheral locations is flexibly adjusted on a trial-to-trial basis to re-open the attention field as soon as possible. A recent analysis of the same task by our group showed that the distinction between targets and distractors involved Inferior Frontal Sulcus around 200-250 ms¹⁶, which corresponds to the peak latency of the suppression induced by

distractors in area V2. Therefore, the peripheral suppression is relieved as soon as a stimulus is recognized as non-relevant, which is optimal to minimize inattention blindness. This raises the interesting possibility that the dynamical opening/closing of the attention field might be controlled by prefrontal areas - which hold the task-set and attention-set representations, possibly through a top-down influence on the pulvinar, which is thought to enable the attention-dependent suppression⁷.

We conclude that the PFI in response to central stimuli is not an encapsulated reflex, but a time-adjusted adaptation of the attentional system to match behavioral demands: an optimal compromise between selectivity and openness, which quickly alternates at the subsecond level. Yet, that mechanism might be challenged in specific situations delivering fast and rhythmic task-relevant central stimuli - such as reading or texting - in which case the peripheral suppression might be sustained and cause potentially fatal inattention blindness. It remains to be determined whether that obvious flaw in the system can be compensated by the superior colliculus, which receives direct visual inputs from the retina and could in principle bypass the suppression and trigger attentional reorientation and escape/avoidance behaviors, at least for salient peripheral events¹⁹.

Acknowledgments

ICMJE Statement

Authorship contribution

J.-P.L., P.K. and S.R. conceived and designed the study, M.P and B.C acquired the data under supervision of S.R. and P.K., B.C. and D.M.-A. analyzed the data with the engineering assistance of B.B. and A.G.. Then J.-P.L. and B.C. took the lead in writing the manuscript while all authors provided critical feedback.

Ethical statement

The present study received the approbation of the CPP Ile de France XI on the 06/01/2017 and the authorisation of the ANSM (Agence National de Sécurité du Médicament, the French national agency for medical safety) on the 04/07/2017. The clinical trial received the following ID : NCT03094312

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