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Reading the mind's eye: Online detection of visuo-spatial working memory and visual imagery in the inferior temporal lobe

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ABSTRACT

Several brain regions involved in visual perception have been shown to also participate in non-sensory cognitive processes of visual representations. Here we studied the role of ventral visual pathway areas in visual imagery and working memory. We analyzed intracerebral EEG recordings from the left inferior temporal lobe of an epileptic patient during working memory tasks and mental imagery. We found that high frequency gamma-band activity (50–150 Hz) in the inferior temporal gyrus (ITG) increased with memory load only during visuo-spatial, but not verbal, working memory. Using a real-time set-up to measure and visualize gamma-band activity online – BrainTV – we found a systematic activity increase in ITG when the patient was visualizing a letter (visual imagery), but not during perception of letters. In contrast, only 7 mm more medially, neurons located in the fusiform gyrus exhibited a complete opposite pattern, responding during verbal working memory retention and letter presentation, but not during imagery or visuo-spatial working memory maintenance. Talairach coordinates indicate that the fusiform contact site corresponds to the word form area, suggesting that this region has a role not only in processing letter-strings, but also in working memory retention of verbal information. We conclude that neural networks supporting imagination of a visual element are not necessarily the same as those underlying perception of that element. Additionally, we present evidence that gamma-band activity in the inferior temporal lobe, can be used as a direct measure of the efficiency of top-down attentional control over visual areas with implications for the development of novel brain-computer interfaces. Finally, by just reading gamma-band activity in these two recording sites, it is possible to determine, accurately and in real-time, whether a given memory content is verbal or visuo-spatial.

Introduction

The definition of certain brain regions as perceptual, motor or associative, has been based mostly upon functional criteria. For example, regions of the human brain showing selective responses to visual stimuli would usually be labeled as ‘visual areas’. However, the human visual system is known to be involved not only in perception of environmental stimuli, but also in mental visual imagery (Kreiman et al., 2002; Le Bihan et al., 1993) and in working memory retention of visual information (Awh and Jonides, 2001; Haxby et al., 1994; Serences et al., 2009).

Visual imagery refers to the maintenance of a stable conscious visual representation independent of visual inputs (Moulton and Kosslyn, 2009), very much like the maintenance of a visual event in working memory, a theoretical construct that refers to memory stores and executive processes supporting our capacity to keep ‘in mind’ information no longer available in the environment (Baddeley, 1992; Baddeley and Hitch, 1974). Indeed, behavioral studies have shown that increasing working memory load impairs the capacity of subjects to mentally create and/or manipulate visual images (Atkinson and Shiffrin, 1968; Baddeley and Andrade, 2000; Gyselinck et al., 2007), suggesting that visual imagery and visual working memory share common cognitive and neural resources. These findings are in agreement with the ‘sensory recruitment hypothesis’, which states that information to

Abbreviations: BCI, brain-computer interface; MVIS, visuo-spatial working memory task; MVEB, verbal working memory task; ITG, inferior temporal gyrus; TMS, transcranial magnetic stimulation; WFA, word form area.

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be recalled is temporarily stored in the sustained activity of brain regions involved in perception of that information (Awh and Jonides, 2001; Serences et al., 2009). In fact, the disruption of neural activity in the early visual cortex with single TMS pulses affects performance in both visual imagery and short-term memory tasks (Cattaneo et al., 2009). Moreover, apart from the sensory recruitment hypothesis, several authors have proposed that visual imagery and visuo-spatial working memory might rely on the same large-scale network connecting the frontal executive system with occipito-temporal visual areas, possibly via the parietal lobes (Cabeza and Nyberg, 2000; Ranganath and D'Esposito, 2005; Zimmer, 2008). Nevertheless, how and to what extent visual brain regions participate in imagery and working memory remains unknown.

In the present study, we focus primarily on the neural implementation of visual imagery and working memory maintenance in the inferior temporal lobe. We hypothesized that visual areas which activity increases with memory-load should also be active during visual imagery. We tested this hypothesis in an epileptic patient implanted with intracerebral electrodes for clinical reasons. We recorded the patient during a simple visuo-spatial working memory task and searched for cortical sites active during memory maintenance. We then monitored the activity of those sites online and found an instantaneous and systematic increase in gamma-band neural activity (50–150 Hz) when the patient voluntarily engaged in visual imagery.

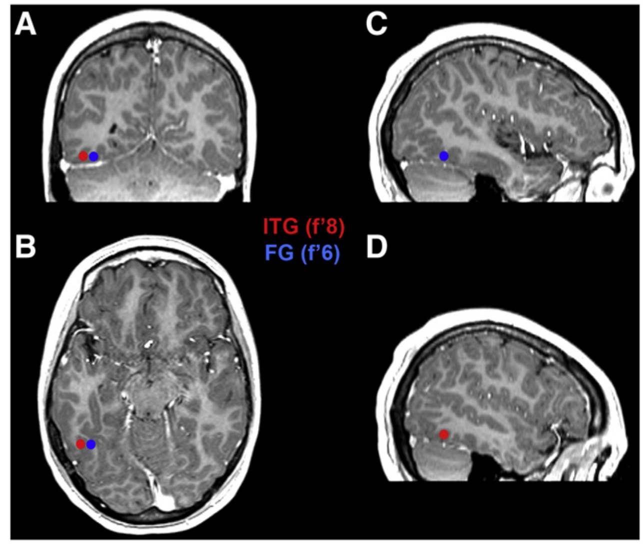

Fig. 1. Patient preoperative MRI and electrode positions. A) Coronal and B) horizontal view of MRI showing recording sites f′6 and f′8. C) Sagital, view in the preoperative MRI highlighting localization of contact site f′6 in the fusiform gyrus, Tailarach coordinates: −42, −55, −11. D) As in C, but highlighting localization of contact site f′8 in the inferior temporal gyrus, Tailarach coordinates: −49, −55, −11.

Methods

Participant

Subject was a right-handed 16 year old female undergoing resective neurosurgical treatment for drug-resistant epilepsy. Neuropsychological examination was normal, with intellectual abilities and memory in the normal range. A thickening of the right superior temporal sulcus was suspected, though repeated MRI proved inconclusive. 18-FDG-PET demonstrated a right posterior temporo-perisylvian hypometabolism. Interictal EEG mainly showed right temporal slow waves. In order to precisely identify the epileptic focus, the patient was stereotactically implanted with 15 multi-lead depth-EEG electrodes. The implantation strategy favored the posterior temporal cortex of both sides with 9 electrodes on the right side, and 6 electrodes on the left, chosen solely by clinical criterion. The patient was electrophysiologically monitored for a three-week period by a team of clinicians at Grenoble University Hospital (see Kahane et al., 2004 for method description). During this period, parents and subject provided informed consent for participation in the study. Research was approved by the Regional Ethical Committee (CPP Sud-Est V). After clinical examination, the epileptogenic area proved to be right temporo-basal. Fig. 1 depicts the patient's MRI showing location of the electrode contacts of interest for this study, f′6 and f′8.

Intracerebral recordings

A multi-channel video-EEG acquisition and monitoring system (Micromed, Treviso, Italy) was used to record neural activity from 15 semi-rigid uni-linear electrode arrays. Each array comprises from 6 to 15 contact sites separated by 3.5 mm (Dixi, Besançon, France) bilaterally spanning temporal and occipital lobes. The intracerebral EEG signal was acquired at a 512 Hz sampling rate and bandpass filtered between 0.1 and 200 Hz. A contact site placed in white matter was chosen as monopolar reference for the acquisition. However, and in order to increase spatial resolution, a bipolar montage (i.e., difference between adjacent contacts) was applied for online analysis and display. After real-time exploration of gamma-band response (50–150 Hz) in different cognitive and behavioral conditions (Jerbi et al., 2009b; Lachaux et al., 2007a), a left fusiform (f′6) and an inferior temporal gyrus (ITG) (f′8) recording sites were selected for further study, due to their selective response to load manipulations during working memory tasks. Activity in these recording sites was verified to be free from epileptiform activity, eye movements, and electromyographic artifacts. Structural MRIs were acquired before implantation, post-implantation (i.e., with electrodes in place) and after resective surgery. The post-implantation MRI was analyzed with custom Matlab (Mathworks, Natick, MA, USA) routines to precisely localize electrodes and contact sites. Talairach and Tournoux (1988) atlas was used to identify and report recorded brain regions as standard coordinates.

Offline time-frequency analysis

Time courses of gamma-band (50–150 Hz) amplitude (i.e., envelope or band-limited power) were calculated offline for the electrophysiological signal acquired during visuo-spatial and verbal working memory tasks (see below for an explanation of procedures). Continuous data was first band-pass filtered between 50 and 150 Hz in steps of 10 Hz to obtain 10 consecutive frequency bands from 50–60 Hz to 140–150 Hz. Afterward, the envelope of each of these band-passed filtered signals was calculated using the standard Hilbert transform (c.f. Le Van Quyen et al., 2001). To normalize across frequency bands, amplitude values for each 10 Hz band were divided by their mean throughout the entire session and then multiplied by 100. The resulting values are thus presented as a percentage of increase or decrease in activity relative to the entire recording period. Finally, the 10 envelopes were averaged across frequency yielding a single time-series for broad-high-gamma (50–150 Hz).

Event-related modulations of gamma envelope were obtained by averaging its amplitude across trials for a given experimental condition. For visualization purposes, envelopes were smoothed using a sliding-window moving average of 250 ms and then displayed relative to a common pre-stimulus baseline of −400 to −100 ms.

All spectral analyses, display and related statistical tests were performed using Matlab custom routines.

Real-time visualization of gamma-band activity

A real-time visualization system, dubbed BrainTV (detailed description in Lachaux et al., 2007a, 2007b), was used for online analysis and