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Category-specific visual responses: an intracranial study comparing gamma, beta, alpha, and ERP response selectivity

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INTRODUCTION

Several studies have shown that high-frequency neuronal activity in the brain is a marker of active information processing involved in perception, action, and cognition (Engel et al., 2001; Fell et al., 2001; Fries et al., 2001; Varela et al., 2001; Pesaran et al., 2002; Fries, 2009). Electroencephalography (EEG) and magnetoencephalography (MEG) have enabled observation of the behavior of this spectral signature in a variety of tasks, revealing its functional role not only in local neuronal processing but also in large-scale neuronal communication (Bauer et al., 2006). Other studies have turned to the high spatial resolution and high signal-to-noise ratio of intracerebral electroencephalography (iEEG) to describe fine amplitude modulations invisible to scalp EEG/MEG while preserving millisecond time resolution (Voytek et al., 2010). Recordings with these in cerebro implanted electrodes in humans have shown local broadband gamma activity modulated by visual perception (Lachaux et al., 2005; Canolty et al., 2006; Jacobs and Kahana, 2009), language processing (Canolty et al., 2006; Sahin et al., 2006; Jung et al., 2008; Lachaux et al., 2008; Mainy et al., 2008; Sahin et al., 2009), attention (Lachaux et al., 2005; Tallon-Baudry et al., 2005), and different types of memory (Sederberg et al., 2006, 2007; van Vugt et al., 2010).

Although spectral analysis has become a well-established technique in cognitive neuroscience, an important debate remains regarding whether low-amplitude GBR is more informative than high-amplitude intracerebral evoked response potentials (iERPs) as a neural marker of underlying mental processes. Reports often focus on either GBR or iERPs (Allison et al., 1994b; Halgren et al., 1994a,b, 1995a,b; McCarthy et al., 1999; Puce et al., 1999; Prinzman et al., 2007; Jacobs and Kahana, 2009) to reveal the high specificity of response to stimulation conditions, but recent studies combined both markers (Fisch et al., 2009; Engell and McCarthy, 2010). These markers show different stimulus response characteristics in terms of amplitude and latency, and it is still unknown whether they systematically reflect the same information processing. To investigate this issue, we decided to study the GBR patterns in relation to iERP and ABR amplitude in an experimental context requiring a high level of neuronal response specificity: visual object recognition.
Here we set out to examine neuronal activity involved in discriminating visual objects. We examined iEEG recordings from 18 epileptic patients while engaged in a simple visual detection task using stimuli from different visual object categories. We analyzed the data with the goal of revealing the multiple degrees of specialization elicited by different neuronal markers within a few hundred milliseconds after stimulus onset. The cerebral region that concentrated most specific neural responses was the posterior temporal cortex. Interestingly the GBR, iERP, and ABR that were selective for the same visual object showed very little spatial overlap across all recording sites.

**MATERIALS AND METHODS**

**PATIENTS AND RECORDINGS**

Eighteen patients (9 women, group mean age 35 ± 10 years) with drug-resistant partial epilepsy and candidates for surgery were considered in this study and recruited from Neurological Hospitals in Grenoble and Lyon. Because the location of the epileptic focus could not be identified using non-invasive methods; the patients underwent intracerebral recordings by means of stereotactically implanted multi-lead electrodes (SEEG). Recording sites were selected solely according to clinical indications, with no reference to the current experiment; however, enrolled patients were primarily those with electrodes sampling visual areas. All the patients had previously given their informed consent to participate in this experiment and research recordings were approved by the National French Science Ethical Committee (CPPRB). All had normal or corrected to normal vision.

**ELECTRODE IMPLANTATION**

Eleven to 15 semi-rigid electrodes were implanted per patient in cortical areas which varied depending on the suspected origin of their seizures. Each electrode had a diameter of 0.8 mm and was comprised of 10 or 15 contacts of 2 mm length, depending on the target region, 1.5 mm apart (Dixi, Besançon, France). Therefore, various medial and lateral cortical areas were evaluated for each patient (see Figure 1B), the coordinates of each electrode contact with their stereotactic scheme was measured (in the Talairach coordinate system). The coordinates were used to anatomically localize the contacts using the proportional atlas of Talairach and Tournoux (Talairach et al., 1993), after a linear scale adjustment to correct size differences between the patient’s brain and the Talairach model. These locations were further confirmed by overlying a post-implantation CT scan (showing contact sites) with a pre-implantation structural MRI with VOXIMR (IVS Solutions, Chemnitz, Germany), allowing direct visualization of contact sites relative to brain anatomy.

These patients voluntarily participated in a series of short experiments to identify local functional responses at the recorded sites. The results presented here were obtained from a test exploring visual recognition. All data were recorded using approximately 120 implanted depth electrode contacts per patient with a sampling rate of 512 Hz. Data were obtained in a total of 1760 recording sites, distributed as follows: temporal cortex (962 recording sites), frontal cortex (515), dorsal visual pathway, which includes parietal and motor cortices (220) and occipital cortex (42) (Figure 1B).

**STIMULI AND TASK**

The visual recognition task lasted about 15 min. Patients were instructed to press a button each time a picture of a fruit appeared on screen (visual oddball paradigm). Non-target stimuli consisted of pictures of objects of eight possible categories: houses, faces, animals, scenes, tools, pseudowords, consonant strings, and scrambled images. The latter were not included in this analysis. All stimuli had the same average luminance except for pseudowords and consonant strings which consisted of a white letter string on a black background. All categories were presented within an oval aperture (Figure 1A). Stimuli were presented for a duration of 200 ms every 1000–1200 ms in series of 5 pictures interleaved by 3-s pause periods during which patients could freely blink. Patients reported the detection of a target through a right-hand button press and were given feedback of their performance after each report. A 2-s delay was placed after each button press before presenting the follow-up stimulus in order to avoid mixing signals related to motor action with signals from stimulus presentation. Importantly, we only analyzed here the neural responses to all non-target stimuli that did not elicit a button press. Each visual category was presented 50 times during the whole experiment.

**DATA ANALYSIS**

The iERP estimated for all subjects was obtained by filtering the raw data between 1 and 25 Hz. We further analyzed the spectral signatures of the data in two steps. First we calculated the full time–frequency representations of the data to estimate the frequency intervals of interest that would then be used to estimate subsequently the instantaneous spectral response amplitude with the Hilbert Transform (Le Van Quyen et al., 2001; Bruns, 2004). To quantify signal power modulations across time and frequency we used standard time–frequency (TF) wavelet decomposition (Tallon-Baudry et al., 1996). The signal s(t) is convoluted with a complex Morlet wavelet \( w(t, f, \sigma) \), which has Gaussian shape in time \((\sigma)\) and frequency \((\sigma_f)\) around a central frequency \(f_0\) and defined as:

\[
\begin{align*}
A & = \frac{1}{\pi \sigma} \\
& = \frac{1}{\sqrt{2 \pi \sigma}} \\
\end{align*}
\]

The wavelet transform of the data is then given by the convolution of the input signal with the wavelet transform.

The investigated frequency range was 1–200 Hz. To estimate a gamma frequency range of interest of neural responses, we applied a matched-pairs Wilcoxon test for each time–frequency bin comparing power estimates after stimulus presentation to averaged baseline power between −300 and −100 ms. We used this interval to estimate instantaneous amplitude of the signal with the Hilbert transform, according to the following procedure: we band-pass filtered the entire recording dataset in consecutive non-overlapping frequency bands (for instance, 50–60, 60–70, ..., 140–150 Hz to cover the gamma-band 50–150 Hz), and for each band we extracted the amplitude envelope using an Hilbert transform (thus applied to the entire recording session). For each frequency band, the envelope was then divided by its mean value over the entire recording session, channel-wise, and multiplied by 100 to be expressed in percentage of the mean amplitude of the session. This provided 10 amplitude time-series between 50 and 150 Hz (one for each frequency band) which were averaged together to obtain a single 10 min time-series...
FIGURE 1 | Paradigm, electrode implantation and neural responses. (A) Example of the visual detection paradigm. (B) Lateral view of general implantation scheme of all 18 patients. Red arrows indicate xyz axis reference. (C) Time–frequency representations of Wilcoxon Z-values (post-stimulus power vs baseline power) elicited by different complex stimuli. The values are masked by a significance threshold (not corrected). Each example pertains to a different patient. All gamma-band responses within the 50–150 Hz interval are pronounced, while the low-frequency power interval is negative (vs baseline). (D) Examples of intracerebral evoked response potentials to different visual categories from different patients (paired conditions).
of gamma amplitude (the duration of the task). Finally this amplitude was then epoched into data segments centered on each stimulus, between −300 and +1000 ms relative to stimulus onset, and then averaged together for each stimulus category.

For the alpha-beta band (ABR), the same procedure was applied to the 8–24 Hz interval (4 Hz wide consecutive frequency intervals). After all time–frequency analyses and data filtering operations, we downsampled all time-series to increase statistical power for comparisons applying corrections for multiple comparisons when testing for a difference between conditions through time. The final data precision was maintained at 16 ms per sample.

To display all responses within MNI brain space as in Figure 3, we plotted averaged activities from all categories for each electrode within a sphere volume. The color of each node codes for the averaged activity over all recording sites located within a 1.5 cm distance from the node. This allowed active electrode responses to appear on medial and lateral cortices of a topographical representation of the MNI brain. This visualization of the data served as a preliminary step to identify regions of interest or more precise analyses at the individual level.

**STATISTICAL EVALUATIONS OF NEURAL RESPONSE SPECIFICITY**

Previous studies in animals and humans analyzed neuronal activity to complex visual stimuli and developed statistical strategies to demonstrate response specificity to visual stimuli of neuronal selectivity to complex visual stimuli and developed statistical strategies to identify the temporal clustering of responses. We extended this analysis to the 8–24 Hz interval (4 Hz wide consecutive frequency intervals).

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**RESULTS**

For each electrode and visual object category, time–frequency analyses revealed broadband high-frequency power increases between 50 and 150 Hz (Figure 1C). Low-frequency band power decreases were observed between 8 and 24 Hz. Figure 1C illustrates a few examples of GBR to different visual object categories from temporal lobe recording sites in different patients. These frequency ranges coincide with previous intracerebral observations by our group (Lachaux et al., 2005; Jerbi et al., 2009; Jung et al., 2010) and others (Crone et al., 2006) and will be used in this study to evaluate systematically spectral responses across recording sites within different patients. This initial identification of prominent spectral components allowed us to concentrate on a single spectral data estimate per time sample and per frequency.
Interestingly, iERP responses were mainly present at recording sites that also showed a GBR with or without an ABR (see Figure 1D for examples of iERP).

We estimated a response index (RI) per electrode which indicated the number of visual object categories for which an electrode produced a statistically significant neurophysiological response. Figure 3A shows the spatial distribution of the RI for all recording sites with a RI from 1 to 7, for GBR, ABR, and iERP. We observe that recording sites responding to most visual object categories (RI 5–7) clustered within posterior temporal cortex for all three neural markers GBR, ABR, and iERP (left hemisphere: AP and AD $p<0.001$; right hemisphere: AP $p<0.001$, AD $<0.001$ for ABR only).

**NEUROPHYSIOLOGICAL RESPONSES**

About 83.9% of all recording sites (1760) did not show statistically significant responses to stimulus presentation (Figure 2A). As shown in Figure 2A, among the remaining sites, 16.9% solely produced GBR, 2.7% only iERP, and 14.5% only ABR. Around 18.1% produced iERP and GBR, 19.1% produced GBR and ABR. In 16.3% of cases, all three markers coincided on the same electrode.

**FIGURE 2** Neural responses type proportionality and neuronal activity dynamics in temporal cluster. (A) Left, proportion of recording sites that gave at least one response to a stimulus; right, proportion of gamma-band, iERP, and ABR within the total percentage of responsive recording sites. (B) Left, percent of recording sites in temporal cluster that start responding in different time-windows after stimulus presentation. Right, percent of recording sites in temporal cluster that are active between 0 and >500 ms.
striking differences in sensitivity to visual categories between the different markers. To illustrate this response specificity to visual object category information in the gamma-band, Figure 4 and Figure S2 in Supplementary Material depict examples of single-trial responses at recording sites within the cluster. Each object category is represented by the amplitude time-course of 50 trials. We plotted the single-trial responses per category for GBR, ABR, and iERP at the same recording site in each example. Figure 4A shows a very specific GBR to faces in a fusiform gyrus, matched the localization of the fusiform face area (FFA) reported in another study (Grill-Spector et al., 2006) (Talairach coordinates: 41, −50, −8). All other object categories elicited very weak or no response. At this same electrode, a unique negative iERP to faces was observed, while all other object categories elicited a positive evoked response. Overall, ABR amplitude decreased in all visual object categories, with faces specifically inducing an earlier small amplitude. Figure 4B depicts responses measured in the fusiform face area in a second patient (Talairach coordinates: 42, −51, −16). All other object categories elicited very weak or no response. At this same electrode, a unique negative iERP to faces was observed, while all other object categories elicited a positive evoked response. Overall, ABR amplitude decreased in all visual object categories, with faces specifically inducing an earlier small amplitude. Figure 4B shows a very specific GBR to faces in a fusiform gyrus, matched the localization of the fusiform face area (FFA) reported in another study (Grill-Spector et al., 2006) (Talairach coordinates: 41, −50, −8). All other object categories elicited very weak or no response. At this same electrode, a unique negative iERP to faces was observed, while all other object categories elicited a positive evoked response. Overall, ABR amplitude decreased in all visual object categories, with faces specifically inducing an earlier small amplitude. Figure 4B depicts responses measured in the fusiform face area in a second patient (Talairach coordinates: 42, −51, −16). Despite the location of this electrode, GBR was stronger and more specific to animals and tools, while only weak and occasional single-trial responses could be observed for faces, houses, and scenes. The GBR distinguished the response preference of several recording locations at the single-trial level across different patients (Figure S2 in Supplementary Material). Of note, the strongest GBR corresponded to iERP components in some cases, e.g., face stimuli (Figure 4A), but most examples show a local dissociation between these two neural markers.

Figure 3B bar-plot shows the number of responses to visual object categories per electrode elicited for each neural marker throughout all recording sites. Surprisingly, although the number of responding sites decreased with increasing RI overall, RI = 7 elicited more responses than RI = 3 for both GBR and ABR.

We measured the time-course of neural activity for each neural marker at all recording sites within the posterior temporal cluster. GBR and iERP activated more recording sites than ABR in the cluster through time (Figure 2B). For both GBR and iERP the peak of activity onset (different from baseline level) emerged shortly after stimulus onset, i.e., within 100 and 200 ms (Figure 2A).

GBR dynamics across all patients were plotted on the MNI brain to obtain a global view (see Materials and Methods). Strongest GBR appeared most concentrated in posterior occipital-temporal cortex (medial and lateral cortices, including middle temporal gyrus, fusiform gyrus, middle occipital gyrus, and lateral occipital cortex) after 100 ms (Figure S1 in Supplementary Material) and increased in amplitude until 300 ms, declining in intensity after this latency. This allowed us to distinguish a limited spatial cluster covering medial and lateral cortices from left and right hemispheres. A smaller frontal cluster covering Brodmann areas 8 (frontal eye fields) and 6 also evolved in the same time-activation pattern, but we will only focus on the temporal cluster in this study.

RESPONSE SPECIFICITY AT SINGLE-TRIAL LEVEL

In the temporal cluster, GBR, iERP, and ABR responded differently to visual object categories. Visual inspection of single-trial neural responses at individual recording sites revealed

Figure 3 | Response score spatial distributions and histograms. (A) Response index for GBR, ABR, and iERP are plotted according to their spatial location (Wilcoxon test, for all responses, p < 0.05). (B) Histograms show the number of electrode sites that elicit significant responses to visual stimuli.
To convey a global overview of the spatial distribution of selective responses to visual objects, we estimated a selectivity index (SI) for each recording site (see Materials and Methods). A high SI (>1) indicates that the neural response induced by various visual object categories are statistically different from one another significantly (Friedman test, \( p < 0.05 \)).

Figure 6 shows the spatial distribution of SI for GBR, ABR, and iERP. All recording sites which elicited a SI >1 for GBR, ABR, or iERP formed a statistically significant cluster within the posterior temporal cluster (for all neural markers, left and right hemisphere, AP and ADR: \( p < 0.001 \)).

In order to measure the degree of overlap of response specificity between neural markers, we mapped all responses to categories that were significantly different from each other. The overlap was estimated as the proportion of responses at single recording sites showing the same difference between paired conditions. Percentage

**Partial distribution and overlap of selective neural responses**

After illustrating specific GBR to visual objects at the single-trial level that strongly dissociate from other neural markers we now focus on the spatial distributions of these responses in this temporal cluster as well as the entire brain. To convey a global overview of the spatial distribution of selective responses to visual objects, we estimated a selectivity index (SI) for each recording site (see Materials and Methods). A high SI (>1) indicates that the neural response induced by various visual object categories are statistically different from one another significantly (Friedman test, \( p < 0.05 \)).

**Spatial distribution and overlap of selective neural responses**

After illustrating specific GBR to visual objects at the single-trial level that strongly dissociate from other neural markers we now focus on the spatial distributions of these responses in this temporal cluster as well as the entire brain. To convey a global overview of the spatial distribution of selective responses to visual objects, we estimated a selectivity index (SI) for each recording site (see Materials and Methods). A high SI (>1) indicates that the neural response induced by various visual object categories are statistically different from one another significantly (Friedman test, \( p < 0.05 \)).

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In order to measure the degree of overlap of response specificity between neural markers, we mapped all responses to categories that were significantly different from each other. The overlap was estimated as the proportion of responses at single recording sites showing the same difference between paired conditions. Percentage
of overlap between neural markers was less than 6% in the temporal cluster and brain-wide. The spatial response specificity overlap between gamma-GBR and iERP was 2.9% in the cluster and 3.8% brain-wide, between GBR and ABR 4.4% in the cluster and 5.4% brain-wide, and between ABR responses and iERP 1% in the cluster and 2.7% brain-wide. This very low spatial overlap is visible on the global spatial map of these specific responses (Figure 7 and Figures S3–S8 in Supplementary Material).

Although most specific responses group within the posterior temporal cluster (bilaterally), many specific responses were recorded from anterior temporal lobe and frontal cortices. No single anatomical region concentrated all specific responses to a single category. We did however locate stimulus preference within regions that described a preference for complex stimuli such as for example specific GBR to faces within the fusiform face area and selective responses to letter strings (pseudowords and consonants) in a region described by fMRI studies as the word-form area (Cohen et al., 2000) (Figure S9 in Supplementary Material). Moreover, unique GBR to pseudowords mapped mainly to recording sites within the left hemisphere, spread over the temporal lobe and within frontal Broca’s area (Figure S10 in Supplementary Material), implying the active involvement of regions specialized in word reading and processing.

**HIGH FIDELITY INTRACRANIAL GBR**

In the same line as previous studies that showed how neural responses can be evaluated regarding their capacity to accurately describe stimulation features or behavioral response value (Britten et al., 1992; Donner et al., 2007; Liu et al., 2009; Wyart and Tallon-Baudry, 2009), we examined whether the specific GBR and iERP responses were able to objectively distinguish visual object category information based on the amplitude level of neural signals. With a binary classification procedure based on signal detection theory (Green and Swets, 1974), we extracted for each time sample an index of signal strength (termed here AUC index) which was statistically compared to a surrogate data set (see Materials and Methods). In Figure 8 are shown various illustrative examples of AUC index curves for all three neural markers at different temporal recording sites chosen based on their signal strength and selectivity toward specific visual objects determined in previous analyses.

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**Figure 5** | Local dissociations (temporal cortex) between GBR and iERP to represent category coding. (A) In one patient the iERP distinguishes faces from animals while GBR is the same for both type of stimuli. (B) In another patient GBR dissociates houses from faces, while iERP fails to do so. Shaded areas represent ±1 SEM.
visible either in the GBR or in the iERP, in separate sites. Most of these effects were identified in our study with a pool of 18 patients. This had been observed locally in a previous intracerebral study (Lachaux et al., 2005) but has been more rigorously and extensively extended of activated neuronal networks. It has been shown that single neurons in temporal and frontal cortical regions respond selectively to complex visual information (Desimone et al., 1984; Tanaka, 1996; Freedman et al., 2001; Quiroga et al., 2005), contrasting with neurons in sensory areas which code and respond primarily to low-level features of stimuli, e.g., contrast, size, color, and motion (Albright et al., 1984; Hubel and Livingstone, 1987). At a larger neuronal population scale, fast evoked responses have shown high specificity toward category information, revealing the capacity of neuronal groups to quickly extract invariant conceptual information from a wide variety of stimulus configurations (Allison et al., 1993, 1994a; Halgren et al., 1994a,b, 1995a,b; McCarthy et al., 1999; Puce et al., 1999; VanRullen and Thorpe, 2001; Liu et al., 2009). The particular case of evoked potential selectivity for face stimuli has been extensively investigated with intracranial recordings in humans (Allison et al., 1993, 1994a; Halgren et al., 1994a,b, 1995a,b; McCarthy et al., 1999; Puce et al., 1999; Liu et al., 2009). In our study, we identified similar face and pseudoword selective effects, within face and word-form selective areas (Cohen et al., 2000; Kanwisher and Yovel, 2006), in agreement with a previous intracerebral study (Lachaux et al., 2005). We report selective neural responses – GBR, ABR, as well as iERP – to visual object categories spatially distributed across cerebral cortex. This had been observed locally in a previous intracerebral study (Lachaux et al., 2005) but has been more rigorously and extensively identified in our study with a pool of 18 patients.

A recent study has shown that regional stimulus selectivity can be lower than expected if scrutinized with high spatial resolution MRI (Grill-Spector et al., 2006). This study showed that subregions of the FFA additionally respond to faces amongst a large panorama of non-face stimuli. We observed similar results, for the first time with intracranial gamma-band responses in two
Vidal et al. Gamma modulation by visual objects

patients with recording sites located in the FFA. Moreover, we report specific GBR related to character string processing (pseudowords and consonants) in left inferior temporal lobe. This is in agreement with previous findings on specific word processing activity detected in the word-form area (Cohen et al., 2000) in cerebro with iERP (Nobre et al., 1994; Nobre and McCarthy, 1995) and GBR (Mainy et al., 2008) as well as non-invasively with fMRI (Mechelli et al., 2003).

Many previous studies by our group and others reported human intracranial gamma-band selective stimulus-induced activity in higher-order visual brain regions and frontal regions that were in addition modulated by perceptual, attention, memory, and awareness processes (Crone et al., 1998; Lachaux et al., 2005, 2008; Canolty et al., 2006; Jensen et al., 2007; Jung et al., 2008; Mainy et al., 2008; Fisch et al., 2009; Gaillard et al., 2009; Jacobs and Kahana, 2009; van Vugt et al., 2010). In our study, we analyzed stimulus-induced neural activity which was not task-relevant and thus did not request the same attentional resources. We suggest that the stimulus-induced GBR observed within most regions, especially posterior temporal cortex, were partly generated by the bottom-up activation of local neural representation. However, we cannot dismiss the possibility of top-down effects of attention and perceptual awareness. Recent intracranial studies have shown that masked visual stimuli (either complex category or character strings) that were not consciously perceived by the patients elicited limited GBR (especially in frontal regions) as compared to unmasked stimuli which were fully perceived and actively matched to a target template (Fisch et al., 2009; Gaillard et al., 2009). A similar observation has been made concerning gamma-band modulation when the degree of attention on word reading is controlled (Jung et al., 2008). Interestingly, we observed overall more GBR for visual objects from category animals and tools, especially in frontal cortex. These effects might be caused by the natural saliency of these stimuli in capturing human attention in natural environment (Bar, 2004). The same argument applies to the sustained GBR to pseudowords, which might trigger enhanced attentional processing in order to engage active reading of the stimulus.

An ECoG study in patients (Jacobs and Kahana, 2009) revealed recently similar stimulus-specific GBR observable at single-trial and single subject level. These authors used single letter stimuli within a memory task and found that letter shape was able to

**FIGURE 7** | Spatial distribution of recording sites eliciting selective non-overlapping (upper) and overlapping (lower) responses between GBR, ABR, and iERP, for visual object category tools.
elicit graded GBR, mainly in occipital lobe recordings. They report
less specific responses in temporal lobe than we do. The level of
processing requested by a stimulus may depend on its complexity
and task-relevance, but also on the variety of their physical struc-
tures. This could explain why processing letter shape differences
might request less high-level visual processing and thus less overall
gamma-band activation as compared to experiments using stimuli
from multiple visual object categories. Neural responses can dif-
ferentiate stimuli to various degrees. This differentiation capacity
of neural markers can be measured by evaluating differences between
neural responses elicited by two or more groups of stimuli and
grouped according to this classification. However, testing without
a priori condition grouping criteria requires objective classification
of neural signals based on amplitude readout methods. Many pre-
vious studies have used these techniques to read out fMRI signals
during similar perceptual tasks (Kamitani and Tong, 2005; Kay
et al., 2008; Haynes, 2009). Previous intracranial studies showed
that this technique allowed very accurate separation of iERP signals
pertaining to different categories (Hung et al., 2005; Liu et al., 2009).
Other MEG studies in healthy subjects used this same technique

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**FIGURE 8 | AUC index curves.** (A–F) Six temporal recording sites illustrate the capacity of the three studied neural markers to sustain effective paired category readout. Left boxes represent AUC index curves through time. Right small boxes represent the average maximal absolute AUC indices extracted from each curve (star location) for each neural marker. The red dots represent 2 SEM around the average (black dots).
to evaluate perceptual and behavioral content of beta and gamma responses (Donner et al., 2009; Wyart and Tallon-Baudry, 2009). Here we used this method to assess the high reliability of single-trial intracranial GBR amplitudes in describing information content from visual object stimuli.

Unlike narrow band gamma oscillations reported in various recent MEG studies (Hoogenboom et al., 2006, 2010; Vidal et al., 2006; Dalal et al., 2008, 2009; Wyart and Tallon-Baudry, 2008), intracranial gamma-band activity recorded here with stereotactically implanted depth electrodes in deep cortical layers is broadband signal extending between ~50 and ~150–200 Hz. Previous reports (Miller et al., 2009a,b) suggested that cerebral gamma activity induced by stimulation could be the result of a global increase of local neuronal population firing rate, and a recent intracranial study (Manning et al., 2009) showed that broadband gamma activity increase correlated with local increases of neuronal firing rate. Single-neuron recordings have shown that visual category information can be unambiguously and selectively represented by the firing rate of neurons in human medial temporal lobe (Kreiman et al., 2000). Intracranial gamma-band selective visual category responses might thus reflect these local neuronal population firing rates in response to neural representations. Despite their high level of specificity in conveying conceptual and meaningful information on stimuli, these neuronal populations may be part of a broad network operating with sparse neural representation coding along the lines of recent findings based on unit recordings in humans (Quiroga et al., 2008).

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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FIGURE S1 | Global dynamics of GBR across all recording sites (18 patients, 1760 recording sites). After 100 ms post-stimulus, a posterior region in occipital-temporal cortex starts responding. This GBR increases in time until 400 ms, when its starts decaying. A small frontal cluster is also visible. The brain space covered using a 1.5-cm radius inflated sphere around each electrode is shown in green. Frontal and temporal cortex are well-covered, though other regions are sparsely sampled, such as the primary visual cortex and parietal cortex (in blue).
FIGURE S2 | Examples of single-trial neural activity to visual categories in different temporal sites (within the temporal cluster) in four different patients. Same display type as in Figure 4. Within a global response GBR can be “tuned” to respond more to certain categories than others. In (A) the strongest gamma-band response is elicited by Tools, in (B) by Scenes, in (C) by Animals and in (D) by houses. Although most of the time the onset appears to be simultaneous for all categories, the amplitude and duration of the response may vary. All reported GBR effects are amplitude increases as compared to average baseline amplitude. On the contrary, most ABR effects consist in amplitude decreases as compared to average baseline amplitude.
FIGURE S3 | Similar to Figure 5, for house stimuli.
Object Category: Faces

Non-overlapping responses

Overlapping responses

FIGURE S4 | Similar to Figure 5, for face stimuli.
Object Category: Animals

Non-overlapping responses

Overlapping responses

FIGURE S5 | Similar to Figure 5, for animal stimuli.
Object Category: Scenes

Non-overlapping responses

Overlapping responses

FIGURE S6 | Similar to Figure 5, for scene stimuli.
Vidal et al. Gamma modulation by visual objects

Object Category: Pseudowords

Non-overlapping responses

Overlapping responses

FIGURE S7 | Similar to Figure 5, for pseudoword stimuli.
FIGURE S8 | Similar to Figure 5, for consonant stimuli.
FIGURE S9 | Specific averaged GBR amplitude profile to word-like stimuli. The amplitude profiles are elicited by an electrode located in the word-form area (Talairach coordinates: $-46, -47, -10$). Shaded regions indicate ±1 SEM.

FIGURE S10 | Anatomical locations of unique GBR and iERP specific to faces, pseudowords, and consonants.