

The dynamics of cortical interactions in visual recognition of object category: living vs non-living

Brief running title: Animacy alters visual recognition flows

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Abstract

Noninvasive brain imaging studies have shown that higher visual processing of objects occurs in neural populations that are separable along broad semantic categories, particularly living vs non-living objects. However, because of their limited temporal resolution these studies have not been able to determine whether broad semantic categories are also reflected in the dynamics of neural interactions within cortical networks. We investigated the time course of neural propagation among cortical areas activated during object naming in 12 patients implanted with subdural electrode grids prior to epilepsy surgery, with a special focus on the visual recognition phase of the task. Analysis of event-related causality (ERC) revealed significantly stronger neural propagation among sites within ventral temporal lobe (VTL) at early latencies, around 250 ms, for living objects compared to non-living objects. Differences in other features, including familiarity, visual complexity, and age of acquisition, did not significantly change the patterns of neural propagation. Our findings suggest that visual processing of living objects relies on stronger causal interactions among sites within VTL, perhaps reflecting greater integration of visual feature processing. In turn, this may help explain the fragility of naming living objects in neurological diseases affecting VTL.

Key words:

High-gamma activity; event-related causality; causal interaction; picture naming

1 Introduction

2 Although visual cortex spans much of occipital and posterior temporal lobes in humans and its
3 circuitry in non-human primates has been mapped in extraordinary detail, little is known about
4 how neural activity is propagated across this vast functional-anatomic domain during common
5 tasks such as recognizing and naming objects seen in our environment. We do know that visual
6 processing of objects can occur in neural populations that are separable for object animacy
7 (living vs. non-living objects) (Connolly et al. 2012), real-world size (Konkle and Oliva 2012),
8 retinotopic eccentricity (Levy et al. 2001), and other factors (Grill-Spector and Weiner 2014).
9 Indeed, functional MRI and lesion studies have demonstrated category-specific responses in the
10 posterior ventral temporal lobe, including a medial to lateral bias for non-living vs. living objects
11 within ventral temporal cortex (Martin et al. 1996; Chao et al. 1999; Humphreys and Riddoch
12 2003; Mahon et al. 2009; Wierenga et al. 2009; Chouinard and Goodale 2010; Zannino et al.
13 2010; Grill-Spector and Weiner 2014). However, patients suffering from neurological diseases,
14 including viral encephalitis and dementia, that affect the temporal lobes more broadly, without
15 regard to category-specific areas, often manifest more impaired naming of living than non-living
16 objects (Capitani et al. 2003; Humphreys and Riddoch 2003; Kivisaari et al. 2012; Ritchie et al.
17 2021). An attractive hypothesis to explain this discrepancy is that there is something special
18 about the network dynamics of processing living objects that render this category susceptible to
19 widespread injury or degeneration. For example, stronger propagation of neural activity within
20 and across visual areas may be needed for processing living objects than non-living objects.
21 Testing this hypothesis, however, requires measurements of task-related changes in neural

1 propagation at spatial and temporal resolutions higher than those afforded by MEG and fMRI,
2 respectively.

3 To compare the fine temporal dynamics of changes in both neural activation and neural
4 propagation during category-specific visual object naming, we recorded electrocorticographic
5 (ECoG) signals from subdural electrode grids implanted in 12 patients for epilepsy surgery. We
6 measured task-related neural activation of stimulus-locked high-gamma (HG; 80-150 Hz), which
7 has been shown to closely track changes in neuronal population firing rates (Ray et al. 2008;
8 Manning et al. 2009; Crone et al. 2011; Buzsaki and Wang 2012). Having identified sites with
9 task-related neural activation, we applied event-related causality analysis (ERC) (Granger 1969;
10 Korzeniewska et al. 2008), a multichannel extension of the Granger causality concept (Granger
11 1969), to study the dynamics of neural propagation at high-gamma frequencies (Korzeniewska et
12 al. 2011; Flinker et al. 2015; Nishida et al. 2017; Korzeniewska et al. 2020), and to detect
13 differences the dynamics of high-gamma propagation in brain networks for category-specific
14 object recognition. Moreover, we tested whether object features other than object category
15 (familiar vs unfamiliar, simple vs. complex forms, and difference of age of acquisition - referred
16 and controlled in previous papers (Humphreys et al. 1989; Wierenga *et al.* 2009; Chouinard and
17 Goodale 2010; Shimotake et al. 2015; Chen et al. 2016)), affect visual recognition and influence
18 the pattern of neural propagation.

19 Although prior studies have used ERC to study neural propagation during speech
20 production tasks, including visual object naming (Korzeniewska *et al.* 2011; Flinker *et al.* 2015;
21 Korzeniewska *et al.* 2020; Korzeniewska et al. 2022), this is the first study to investigate the
22 effect of visual object category and other object characteristics (familiarity, visual complexity,

and age of acquisition) on neural propagation in visual association cortices and other cortical regions activated during visual object recognition at the scale of milliseconds.

Materials and Methods

Patients

Fourteen patients who underwent invasive presurgical evaluation with electrocorticography (ECoG) for intractable focal epilepsy since April 2010 through July 2019 in Kyoto University Hospital were recruited for this study. Twelve of these patients (age: 21-61, male/female = 6/6) were eligible for this study according to the below-mentioned criteria (**Table 1**) and provided written informed consent. Recordings from seven participants included here (Pt #1-7) were used previously for representation similarity analyses (Chen *et al.* 2016). The protocol conformed to the Declaration of Helsinki and was approved by the Ethics Committee of the Institute (IRB #C533). The placement of intracranial electrodes was decided solely according to clinical needs. The recording electrodes consisted of arrays of macroelectrodes (2.3 mm in diameter, 1 cm in interelectrode distance, AD-TECH, Wisconsin. Although 8 x 2 grids with 0.5 cm in interelectrode distance were included in the parietal lobe in Pt. #10, further analysis did not show any significant activation). The methods for identification of the implanted electrodes and coregistration to MNI standard space are described elsewhere (Matsumoto et al. 2004; Usami et al. 2015). The locations of the electrodes were confirmed by an MRI image after implantation. Then they were linearly co-registered into a pre-implantation image, and next non-linearly into MNI standard space (ICBM-152) with 2-mm resolution using the program of `fsl_anat` (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/fsl_anat). Anatomical labels of the electrodes in this study

were confirmed by both a pre-implantation image and MNI standard space in reference to the Harvard-Oxford cortical structural atlas (<https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Atlases>).

Task and Recording Procedure

Sitting comfortably on the bed, patients named pictured items aloud in Japanese (without articles or a carrier phrase) as quickly and accurately as possible. Note that the Japanese language does not use articles as a default when referring to a general name. 100 pictures appeared consecutively every 5 seconds on a computer monitor (52.5 cm wide x 29.5 cm height) (**Figure 1**) located 1.0 m in front of the patient. The visual angle of the stimulus items was 7.5°-10.6°. Stimuli consisted of black line drawings (50 living [animals including insects, ex. rabbit, butterfly] and 50 non-living objects [ex. airplane, guitar]) on a white background, as in previous studies (Morrison et al. 1997) (please see a full list of items in **Supplementary Table 1**). Living and non-living objects were also characterized by other variables derived from the previous norming studies: age of acquisition (AoA), visual complexity, familiarity, and word frequency, which were not significantly different across categories according to independent two-tailed *t*-test analyses (Chen *et al.* 2016). The 100 stimuli were pseudo-randomly ordered and presented once per object in one session. In total, four sessions were performed within approximately an hour. We confirmed that the patient watched the monitor through the recording and that no seizures occurred during the recordings by carefully monitoring video of patient behavior and ECoG signals. Verbal responses were recorded with a microphone placed in front of patient. ECoG signals and time stamps of visual stimuli were digitally recorded and stored on a hard drive in the recording system (EEG 1000, Nihon Kohden, Tokyo, Japan). ECoG signals were

referenced to a scalp electrode placed on the skin over the mastoid process contralateral to the side of electrode implantation, sampled at 1000 Hz with a band-pass filter of 0.08-300 Hz in Pt. #1-9, and at 2000 Hz with a band-pass filter of 0.08-600 Hz in Pt. #10-12.

Data analysis

Analytic tools and scripts

Spectral and ERC analyses were performed using a custom-made analysis pipeline (Fortran⁷⁷ C++, and R) developed at Johns Hopkins University (Franaszczuk and Jouny 2004; Korzeniewska *et al.* 2008). Statistical analyses were performed using in-house scripts in Matlab software (version 2019b, MathWorks, Natick, MA).

Selection of channels that show significant neural activities

First, electrodes with systemic artifacts, which cause no effective recoding from disconnection or overlapped multiple grids, were excluded from further analysis. Then, a common average reference was applied to the remaining electrodes, to remove common activity, to remove spatial biases due to varying distances from the reference electrode, and to emphasize local activity when analyzing activation and propagation (Korzeniewska *et al.* 2008). For each epoch within - 2000 to 1000 ms relative to stimulus onset in each trial, certified neurophysiologists carefully checked ECoG signals, excluding from subsequent analyses the trials that involved interictal epileptic discharges or artifacts. Electrooculograms were not recorded in this study. Because small artifacts from continuous eye movements can sometimes appear as changes in high

frequency activity in temporal lobe, especially at the anterior temporal pole (Kovach et al. 2011), raw signals in all recording sites in the anterior temporal lobe were carefully inspected, and trials contaminated with these artifacts were also removed. Two out of 14 patients were excluded in this process because they showed eye movement artifacts in the anterior temporal lobe throughout their recordings, such that we could not preserve enough trials for further analysis.

To detect cortical activation elicited by visual stimuli we focused on the high-gamma frequency range (HG: 80-150 Hz) (**Figure 2**). First, the data epochs (-2000 ms to ~ 1000 ms, with zero at visual stimuli) were separated into living and non-living trials and analyzed using short-time Fourier transform (STFT) with 50 ms Hann window shifting/sliding by 10 ms. Second, for each of these shifting windows the spectral power in high-gamma frequency bands (80, 100, 120, and 140 Hz) was calculated and averaged over trials. Third, the z-score of power changes in each post-stimulus window was calculated with respect to the mean power over all pre-stimulus baseline windows. Fourth, a cluster of consecutive windows where the change in HG power exceeded z-score equal 3 ($z = 3$) lasting at least 50 ms between 0 to 500 ms (to focus on visual processing, which occurs within 500 ms, and to avoid artifacts generated by vocalization) were found. Then, the z-scores in the clusters were summed separately for living and non-living objects in each recording site (in each electrode, please see **Supplementary Figure 1**). The largest sum (for living or non-living objects) was considered as the value that reflected the strength of neural activity evoked by visual stimuli in each recording site (electrode) in this study. This approach ensured the choice of electrodes responding to one or the other category i.e., living or non-living objects. Next, these values were ordered and the top 10% of all analyzed recording sites in each patient were used for subsequent causality analysis, to ensure sufficient number of data-points). Selection of recording sites to those which were activated by

the task was required by ERC analysis, which uses multivariate autoregressive modeling (MVAR) (please see section of **Event-related causality (ERC)** in **Methods**). If an electrode was located at a site in the anterior temporal lobe, which is anterior to the plane perpendicular to the long axis of the temporal lobe passing through the fusiform gyrus at $y = -20$, $z = -30$ and superior temporal gyrus at $y = 0$, $z = -5$ in MNI space defined by Rice, et al. (Rice et al. 2015), the electrode was excluded from further analysis because we wanted to avoid spurious causality caused by eye movement artifacts as much as possible. The anatomical regions of interest were defined independently of the results of high-gamma mapping. The focus of this study was the ventral temporal lobe and lateral occipital lobe. No electrodes in the medial occipital lobe were present in all 12 patients. The ventral temporal lobe (VTL: posterior to the plane defined by the border of anterior temporal lobe [ATL] in the paper by Rice, et al. (Rice *et al.* 2015) and anterior to the posterior transverse collateral sulcus) was first extracted based on previous studies emphasizing its importance for visual processing (Zannino *et al.* 2010; Grill-Spector and Weiner 2014). Then, the lateral occipital lobe (LO: posterior to the temporo-occipital sulcus) was demarcated. The lateral temporal lobe was defined as the area posterior to ATL and lateral to VTL in the temporal lobe.

Reaction time (RT) was defined as the onset of spoken words/responses including the tip of the tongue whether the answer was correct or not. We focused on neural activities and propagation elicited by visual stimuli, not those elicited by semantic processing or vocalization in this study although correct answer rates were calculated. These RT data were deemed to be solely useful to differentiate visual-induced network dynamics from subsequent network dynamics. RT in each patient was also converted to z-score to enable the global analysis across patients.

Statistical comparisons between living and non-living stimuli were performed by a two-tailed paired t -test for HG activities (as we paired the mean of HG activation evoked by living objects with the mean of HG activation evoked by non-living objects for each recording site) or unpaired t -test for RT (living and non-living trials were unpaired), and their effect sizes (r) were also calculated.

Event-related causality (ERC)

Details of event-related causality (ERC) analysis and its applications to visual recognition of objects may be found in previous papers (Korzeniewska et al., 2008; Korzeniewska et al., 2011; Korzeniewska et al., 2020; Korzeniewska et al., 2022). In short, this method is a multichannel extension of Granger causality concept, which states that an observed time series $x(t)$ causes another series $y(t)$, if knowledge of $x(t)$'s past significantly improves prediction of $y(t)$. A set of time series, in this study set of ECoG signals unveiling task-related increase in spectral power, is modelled with multivariate autoregression (MVAR) to obtain ERC values, which reflect the directions and statistically significant changes in the intensity of neural activity propagation between recording sites, as a function of frequency (80-150 Hz in this study), relative to baseline activity (-2000 ms to 0 ms). MVAR model assumes that the value of the x at a time t depends on its p previous values and the random component e . The MVAR process for vector signal x consisting of multiple ECoG signals can be expressed as:

$$x(t) = - \sum_{j=1}^p A_j x(t-j) + e(t)$$

In the frequency domain, the MVAR model is given by:

$$H(f) = \left(\sum_{j=0}^p \mathbf{A}_j e^{-2\pi j f \Delta t} \right)^{-1}$$

Here, H is a transfer function matrix, f is frequency, and Δt is the sampling interval.

The intensity and spectral content $z_{kl}(f, t)$ of the causal influence of signal l on signal k ($l \rightarrow k$) is estimated by:

$$z_{kl}(f, t) = \frac{|h_{kl}(f, t)| |c_{kl}(f, t)|}{\sqrt{\sum_f \sum_{kl} |h_{kl}(f, t)|^2 |c_{kl}(f, t)|^2}}$$

Where $h_{kl}(f, t)$ is an element of the transfer function matrix (M. J. Kaminski & Blinowska, 1991; Korzeniewska et al., 2003, 2022), a measure of the *directed* relationship between signal l and signal k , computed in a short time-window starting at time t , while $c_{kl}(f, t)$ is an element of the partial coherence matrix, a measure of the *direct* relationship between them, in the same short time-window. The combination of the two measures results in a measure of direct causal interactions between signals in a multi-channel recording. Therefore $z_{kl}(f, t)$ shows whether the k -signal component at a given frequency f is shifted in time with respect to an l -signal component of the same frequency, and whether the shifted components are coherent and are not explained by components of other signals. $z_{kl}(f, t)$ takes values from 0 to 1. Zero indicates a lack of direct causal relationships. The nonzero values of $z_{kl}(f, t)$ are interpreted as a flow of activity from recording site l to recording site k ($l \rightarrow k$). To investigate interactions that occur on brief time scales, such as during the picture naming task, an algorithm using multiple realizations of MVAR processes (or multiple repetitions of a task - n_t) was applied (Ding et al. 2000). To ensure a sufficient number of data samples, this can be estimated by the inequality:

$$\frac{K(p+1)}{N_s n_t} < 0.1$$

1 where K denotes the number of signals, p - MVAR model order, and N_s - the length of the time-
2 window (number of samples per one repetition epoch). Please note, that to investigate brief time-
3 scale dynamics a short window N_s is used, which requires a large number of task repetitions n_t ,
4 which may be impossible to obtain in a clinical setting. To compensate for an insufficient number
5 of repetitions, a smaller number of signals can be used. However, it is crucial to assure inclusion
6 of most of the recording sites activated during the task.

7 The dynamics of causal influence $z_{kl}(f, t)$ can be acquired by sliding the short time-
8 window over the time-course t of the investigated process. For each set of trials of one category,
9 aligned to stimulus onset, the MVAR model order p was determined using the Akaike
10 Information Criterion (AIC, Akaike, 1974). As the orders were the same or similar in individual
11 patients (e.g., 5 in one patient, 8-9 in another patient), the same model order was used for each
12 ERC analysis in each patient to allow comparisons between categories. MVAR coefficients were
13 computed for a 50 ms shifting window, overlapped by 10 ms over the 2500 ms trial (including
14 baseline -2000 ms to 0 ms and response period 0 ms to 500 ms).

15 Table 2 provides the numbers of directed connections between ROIs for all patients.
16 Please note, that there are two directed connections between each pair of recording sites k and l
17 (between two electrodes), from k to l ($k \rightarrow l$), and from l and k ($l \rightarrow k$). For each of these directed
18 connections the ERC value was calculated in each 50-ms window.

20 Statistical group analysis

21 ERC values were normalized in each patient to maximum equal one to allow for group level
22 statistics. Normalized ERC values reaching significance ($p < 0.05$, Bonferroni corrected) for

1 propagation within and between anatomical regions (frontal lobe, parietal lobe, lateral temporal
2 lobe, lateral occipital lobe [LO], ventral temporal lobe [VTL]) were pooled across patients,
3 separately for living and non-living trial categories.

4 Our null hypothesis was that there was no difference in HG propagation patterns between
5 living and non-living categories. A nonparametric permutation test (Maris and Oostenveld 2007)
6 was used for comparison of ERC values between categories in each time-window separately. It
7 is worth noting that ERC values were already tested in each patient, and represent statistically
8 significant change in neural propagation, as compared to the baseline. To evaluate group level
9 significance, ERC values between two variables (ex. living and non-living) were randomly
10 shuffled within each directed connection (e.g., LO -> VTL). Next, a two-tailed paired t-test
11 between the two surrogate variables was applied across time points (0 ms to 500 ms) to select
12 epochs where consecutive t values satisfied $p < 0.05$ for at least three consecutive 50-ms
13 windows. Then, we calculated the sum of the t values in each cluster and made cluster-level
14 statistics. This procedure was repeated 10,000 times and the null distribution of the maximum
15 cluster-level statistics was compared with the original cluster-level statistics in each propagation,
16 respectively. A p -value threshold was defined at < 0.05 . How to quantify the effect sizes in
17 cluster-based permutation results is discussed elsewhere (Meyer et al. 2021), although it remains
18 undefined. We calculated the Cohen's d at each time point involved within the cluster that
19 proved significant.

20 To evaluate group level significance of HG activation, pooled spectral powers of HG during
21 living or non-living stimuli were averaged within each region and compared by two-tailed paired

1 *t*-test. A *p*-value threshold was defined at < 0.05 . We corrected for multiple comparisons by
2 Holm's method.

4 **Analysis for the other picture properties**

5 Each picture stimulus was characterized not only by living/non-living category, but also by
6 familiarity, visual complexity, and age of acquisition. The median of category values of each
7 stimulus was calculated. Then the trials were regrouped into higher and lower halves to analyze
8 HG activation and ERC analysis, as well as their group level significance for the top half and
9 bottom half of trials for each of these stimulus properties.

11 **Results**

12 **Behavioral data**

13 Twelve Japanese patients performed picture naming task (**Figure 1A**) during chronic (~ 2 weeks)
14 ECoG recordings for presurgical evaluation of focal epilepsy (**Table 1**). Subjects were asked to
15 overtly name objects serially presented on a computer monitor, in their native Japanese. The
16 objects belonged to one of two categories, living (animals including insects, e.g., rabbit,
17 butterfly) or non-living (e.g., airplane, guitar), and varied within each category as to their
18 familiarity, visual complexity, and age of acquisition. Trials without artifacts and without
19 epileptic discharges were analyzed (17.5-82% of all the trials in each patient) (**Table 1**). The
20 numbers of remaining trials in the living/non-living categories were not significantly different
21 across patients ($p = 0.13$, paired *t*-test). The subjects' mean verbal response latencies were

significantly faster for living objects, although the effect size was small ($t(1541) = 2.365$, $p = 0.02$, effect size $r = 0.06$, unpaired t -test. Living 1700 ± 982 vs. Non-living 1728 ± 952 ms) (**Figure 1B**).

High-gamma activity and its propagation in the posterior cortex

We analyzed the propagation of HG activity among the top 10% of recording sites that showed significant task-related HG activation within 500 ms when living or non-living trials were analyzed independently, as per our criteria (**Figure 2A**. See **Methods** for detail). We tested whether the numbers of the selected electrodes from living or non-living category were different in LO and VTL in each patient, respectively. However, no significance was found ($p = 0.30$ in LO; $p = 0.14$ in VTL, paired t -test). Signals from 103 of 1,142 recording sites in all patients were analyzed. These included 33 recording sites clustered in the lateral occipital region (LO, posterior to the temporo-occipital sulcus) and 40 clustered in the ventral temporal lobe (VTL, posterior to the plane defined by the border of anterior temporal lobe [ATL] in the paper by Rice, et al. (Rice *et al.* 2015)) (please see **Supplementary Table 2** for the MNI coordinates of each electrode in each patient). VTL was firstly extracted based on previous studies implying its importance for visual processing. Then, LO was demarcated. Five electrodes in ATL were excluded because HG activities were potentially contaminated with eye movement artifacts (Kovach *et al.* 2011; Muthukumaraswamy 2013). HG activation within LO was significantly greater for living objects than for non-living objects across all patients between ~150 ms and ~250 ms (**Figure 2B**). This predominance of HG activity in LO for living objects was in line with previous invasive studies (Kojima et al. 2013; Kadipasaoglu et al. 2016), supporting the

1 validity of our methodology for electrode selection. In contrast, we found no significant
2 difference between categories for HG activation within VTL.

3 We next used the event-related causality (ERC) method to investigate the propagation of
4 HG activity within and between LO and VTL, or patterns of HG activity propagation, elicited by
5 living and non-living objects (**Table 2**. See **Figure 3** for the example of one patient. See
6 **Supplementary Figure 2** of the diagram presentation of Figure 3). The patterns of high-gamma
7 propagation, revealed by ERC, did not differ significantly between language-dominant and non-
8 dominant hemispheres (language laterality was defined by handedness and pre-surgical electrical
9 stimulation mapping).

10 Therefore, results from both sides were combined (**Figure 4**) for comparison of ERC
11 results for different object categories. We found significantly greater propagation among sites
12 within VTL for living objects than for non-living objects at 230-270 ms ($p < 0.05$, nonparametric
13 permutation test, effect size: $d = 0.29, 0.29, 0.27, 0.25$, and 0.23 at each 50-ms window within
14 the cluster). Propagation within LO, as well as between LO and VTL were not significantly
15 different between living and non-living objects. We did not observe significant differences
16 between living and non-living objects for the magnitude of propagation among the frontal lobe,
17 parietal lobe, or lateral temporal areas.

18 Each picture named by our subjects varied with respect to object familiarity, visual
19 complexity, and age of acquisition (AoA), independent of their living vs non-living category. To
20 investigate the effect of these characteristics on the propagation of HG activity, we reanalyzed
21 the data after regrouping trials within each patient into the higher half and lower half of the
22 values for each of these categories. As we did for living vs non-living object category, we
23 selected the top 10% of recording sites revealing HG activation within LO and VTL. For

familiarity, it was 32 recording sites within LO and 41 within VTL out of 100. One electrode in LO and three in VTL were different from those in living vs non-living categories. For visual complexity, it was 33 recording sites within LO and 42 within VTL out of 102. Two sites within LO and three within VTL were different from those in living vs non-living categories. For age of acquisition, 32 recording sites within LO and 40 in VTL were selected out of 103. One site within LO and two within VTL were different from the electrodes selected in living vs non-living categories. Objects with lower familiarity induced greater HG activation in LO starting ~ 100 ms until the end of the analysis period (+500 ms) (**Supplementary Figure 3**). Moreover, objects with higher visual complexity induced slightly greater HG activation in VTL ~300 ms after the stimulus (**Supplementary Figure 4**). However, we observed no significant differences in propagation patterns among LO and VTL (therefore data not shown) for both properties. However, the distance between 95% confidence intervals may suggest a tendency of greater propagation from LO to VTL for lower familiarity over higher familiarity around 300 ms (**Supplementary Figure 5**). Finally, age of acquisition did not affect HG and propagation patterns significantly.

Differences of HG activation within subregions of VTL for living vs non-living objects

We also analyzed HG activation within subregions of VTL, i.e., 10 recording sites within the inferior temporal gyrus [ITG], 29 within the fusiform gyrus [FG] and one site within parahippocampal gyrus (PHG). ITG in VTL showed larger HG activation for living objects ($t(9) = 2.44, p = 0.037, r = 0.77$), while FG and PHG did not show differences ($t(29) = -0.697, p =$

0.491, $r = 0.13$). The predominance of ITG activation for living objects was in line with previous invasive studies (Kojima *et al.* 2013; Kadipasaoglu *et al.* 2016).

ERC analysis was also performed among subregions (within and between ITG and FG/PHG) (**Table 3**), but we did not observe differences in patterns of HG propagation.

Discussion

Neural activation and propagation

Most prior studies of the neural dynamics of visual object perception and the effects of object category on these neural dynamics have focused on the magnitude of task-related increases in neural activation, measured either with BOLD responses in fMRI or with high-gamma responses in intracranial EEG (electrocorticography, or ECoG) (Martin *et al.* 1996; Chao *et al.* 1999; Mahon *et al.* 2009; Wierenga *et al.* 2009; Chouinard and Goodale 2010; Zannino *et al.* 2010; Kojima *et al.* 2013; Kadipasaoglu *et al.* 2016). Like BOLD signals measured at each voxel, high-gamma responses estimate changes in overall population firing rates at each recording electrode but do so with temporal resolutions on the order of tens of milliseconds, and are thus capable of unraveling the spatial-temporal dynamics associated with human behavior. Here we used advanced ECoG signal analyses of changes in event-related causality (ERC) to go beyond mere changes in the strength of activation at individual sites, to measure the degree to which neural activity is propagated between these regions. This measurement is important for understanding the neural mechanisms of object perception, as well as object naming, because of the dependence of downstream processing on upstream processing in cortical networks that span

1 large cortical areas and that have both hierarchical and parallel distributed architectural features
2 (Zeki and Shipp 1988; Van Essen et al. 1992). The presence of a hierarchical processing system
3 was demonstrated in a seminal study that showed that grouping processes can operate at a level
4 at which combined form information, not single-feature form information, is represented in
5 visual search (Humphreys *et al.* 1989). Indeed, the intensity of propagation by which neural
6 activity is transmitted from one node of a cortical area to another may reflect the specific way by
7 which the network processes information, and thus could uniquely identify network nodes that
8 are important to task performance. Although prior studies have used ERC to study neural
9 propagation during speech production tasks, including visual object naming (Korzeniewska *et al.*
10 2011; Flinker *et al.* 2015; Korzeniewska *et al.* 2020; Korzeniewska *et al.* 2022), this is the first
11 study of the effect of visual object category and other object characteristics (familiarity, visual
12 complexity, and age of acquisition) on neural propagation in visual association cortices and other
13 cortical regions activated during naming. Because intracranial electrodes were implanted in our
14 subjects for solely clinical purposes, no individual patient was implanted with enough electrodes
15 for conclusive hypothesis testing. Nevertheless, changes in high-gamma activity were
16 sufficiently robust to test the statistical significance of both activation and propagation within
17 each of our subjects, and this allowed us to aggregate results across subjects in order to test our
18 hypotheses.

20 **Network dynamics for living vs non-living objects**

21 Clinical-pathological correlations in the past have consistently pointed to the temporal lobe as an
22 important network for semantic knowledge, with greater susceptibility to injury or disease for

knowledge of living objects (Martin *et al.* 1996; Chao *et al.* 1999; Capitani *et al.* 2003; Humphreys and Riddoch 2003; Mahon *et al.* 2009; Chouinard and Goodale 2010; Grill-Spector and Weiner 2014). Therefore, we hypothesized that visual object naming would elicit not only neural activation in the temporal lobe, but also propagation of neural activity among activated sites. Moreover, we predicted that propagation would be stronger for living than for non-living objects. Although we did observe robust activation, and propagation of activation, in both temporal and occipital (VTL and LO) areas of visual association cortex, we only observed greater aggregate neural activation for living than for non-living objects in LO and did not observe a difference in VTL (HG z-values in Fig. 2B). Interestingly, we observed that living objects did evoke significantly greater propagation of high-gamma activity (80-150 Hz) within the ventral temporo-occipital area (VTL) ~230-270 ms after stimulus onset than non-living objects did. These findings suggest, at least in this study, that neural propagation was better than neural activation alone at capturing differences in category-specific processing dynamics within VTL. The number of recording sites, and consequently the numbers of analyzed directed connections between them, was greatest in VTL, which may have increased the sensitivity for detecting differences in this area. We focused on the propagation of high-gamma bands in this study. However, it may be of value in the future to analyze ERC in other (e.g., low) frequency bands, which may also be relevant for cortico-cortical communication.

Implications for neurological diseases affecting temporal lobe

Stronger neural propagation within VTL evoked by living stimuli may help explain why patients who suffer from neurological diseases that affect the ventral part of the temporal lobe,

1 posteriorly to ATL, demonstrate impairments particularly for naming living objects (Capitani *et*
2 *al.* 2003; Humphreys and Riddoch 2003; Kivisaari *et al.* 2012). Our findings suggest that
3 propagation within VTL revealed by ERC analysis reflects an intrinsic vulnerability of this
4 cortical region to dysfunction from degeneration and viral infection, because it relies on the
5 shared successive flows of information processing, particularly for living objects. In contrast to
6 the situation that occurred in LO, damage to one node will involve dysfunction of another node
7 within the area. In the context of the Conceptual-Structure account of semantic organization in
8 temporal lobes that has been used to explain differences in naming deficits for living relative to
9 non-living objects during neural degeneration (Tyler and Moss 2001), higher correlation between
10 features shared among living objects like faces or legs, relative to non-living objects, may also
11 help explain the differences we observed in ERC flows within VTL. Or, more interactions
12 among cortical sites within VTL may be needed to disambiguate the unique constellation of
13 visual features that is needed for identification and naming of living objects. From an
14 evolutionary point of view, it is possible that living objects are more salient for humans than non-
15 living. We observed faster reaction times for living objects, which may be partly due to more
16 processing to reassure shorter processing latencies. As such, greater impairments for recognition
17 (and naming) of living objects may occur when neurological diseases involve VTL. A reduction
18 in the shared dynamics of information flow may help explain the preferential deterioration of
19 detailed semantic knowledge for living objects in dementias affecting ATL (Lambon Ralph *et al.*
20 2010; Chen *et al.* 2016; Ralph *et al.* 2017), which is considered to be downstream of the temporal
21 lobe.

Other object properties and network dynamics

We did not find evidence that the degree of visual object familiarity, visual complexity, or age of acquisition affect the strength of network propagation in visual association cortices in this study, although the inclusion of more participants could have shown significant differences in propagation. Higher familiarity and earlier age of acquisition imply that subjects have had more experience with these objects visually or via other inputs than for ones with lower familiarity or later age of acquisition. Greater experience might have been expected to result in more efficient processing, reflected here by stronger neural propagation within visual association cortex, particularly in the ventral stream. However, we did not find support for this expectation. Our observation of stronger propagation in VTL for living objects may reflect specialization for processing living objects, independent of visual object familiarity, visual complexity, or age of acquisition, which may in turn have survival value to humans. Whether this depends on innate genetic expression (Mahon and Caramazza 2011) or specific experience for living objects after birth is unclear and beyond our scope here.

Although we did not observe difference in neural propagation within LO, or between LO and VTL, or between these areas and other brain regions, we observed greater neural activation for living objects (in LO) and for objects with lower familiarity (in LO) and higher visual complexity (in VTL). Greater activation for objects of low familiarity may have reflected more initial visual processing for object recognition. Moreover, we found a tendency of greater ERC flow from LO to VTL for lower object familiarity around 300 ms. This latency is similar to latencies at which we observed greater HG activation for lower object familiarity. This suggests continued visual processing and propagation of information from LO to VTL. Higher visual

complexity had a similar effect, but this effect was observed in VTL instead of LO. This may be consistent with VTL's serving as a set of filters that extract specific characteristics from complicated visual forms (Mani et al. 2008). Our results imply that some properties of visual objects have a great effect on the magnitude of neural activation, but not on neural propagation, during visual object processing. It may be that the magnitude of neural activation reflects local processing that does not necessarily rely on propagation across the large-scale cortical networks that are sampled using ECoG. On the other hand, we observed greater neural propagation, but not greater neural activation, in VTL for living objects relative to non-living objects. This suggests that neural propagation may sometimes offer a better index of functional specialization than neural activation alone, and it opens the door for pursuing a deeper understanding of how the neural dynamics of brain networks support complex human behaviors such as visual object naming.

Limitations

Our intracranial EEG data were necessarily recorded in patients with focal epilepsy. We carefully excluded trials with abnormal activity that could potentially affect cognition (Liu and Parvizi 2019). Although object category may have effects on HG activity in the frontal lobe, we did not observe significant effects on propagation to between frontal and occipital or temporal regions. Likewise, we were unable to discuss propagation regarding ATL, which is reportedly important for semantic processing, due to contamination by EOG. Generally, the number of electrodes implanted in ventral temporal areas is often low due to neurosurgical factors. Therefore, detailed cyto-architectural investigation of flows between the subregions in VTL and

LO was impossible compared to functional MRI studies with high spatial resolution (Grill-Spector and Weiner 2014). Nevertheless, we were able to adequately sample this and nearby visual association cortices for the purposes of this study. Lastly, we combined trials regardless of correct or incorrect answers because limiting number of trials would affect statistical significance of ERC. Thus, we analyzed data within 500 ms to focus on visual perception and its ERC. To compare correct vs. incorrect trials, or to study repetition priming effects (Korzeniewska *et al.* 2020), we would have needed to increase the number of trials in the task, which was not feasible after the fact.

Conclusions

During the early phase of visual processing of objects, propagation of HG activity within the ventral temporal lobe (VTL) is more intense for living than for non-living objects. Potential confounds in this comparison, including the degree of visual object familiarity, visual complexity, or age of acquisition did not significantly affect the patterns of network propagation in visual association cortices. These results suggest that living objects require stronger causal interactions at least in VTL devoted to visual object processing, making them more susceptible to naming deficits when these networks are affected by disease.

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- 11

1 **Table 1. Patient Profile and analyzed trials/electrodes**

	Age, gender, handedness	Epilepsy classification	Etiology, Pathology	Antiseizure medication	Performance (%)	The percentage of analyzed trials (%)	# of recording electrodes	# of electrodes used in ERC analysis of the living vs non-living category/recording electrodes in each region				
								Lateral occipital (LO)	Ventral temporal lobe (VTL)	Lateral temporal (LT)	Frontal (F)	Parietal (P)
1	29, M, L	L-TLE	HS, FCD 3A	CLB, PHT, ZNS	90.5	17.5	102	7 / 12	2 / 6	0 / 18	0 / 18	1 / 22
2	34, M, R	R-TLE +PLE	traumatic injury, HS	CBZ, LEV, TPM, ZNS	62.5	37.8	81	6 / 19	0 / 0	0 / 8	2 / 11	0 / 28
3	38, F, R	L-TLE	FCD 2A	CBZ, PHT, TPM, LEV	96.8	82	85	0 / 0	4 / 9	3 / 14	1 / 22	1 / 15
4	41, F, R	L-TLE	FCD 1	CBZ, TPM, PHT	91.3	31.3	94	0 / 2	7 / 11	0 / 14	0 / 26	0 / 18
5	52, M, R	L-TLE	arteriovenous malformation/gliosis/inflammatory infiltration	CBZ, LTG	42.3	49.3	104	3 / 7	6 / 17	1 / 22	0 / 16	0 / 15
6	27, F, R	R-TLE	FCD 1	CLB, LEV, PHT	93.8	24.5	76	3 / 4	5 / 15	0 / 18	0 / 9	0 / 6
7	61, M, R	L-PLE	oligoastrocytoma WHO grade II	CBZ, TPM	51.5	61.8	94	0 / 4	3 / 4	0 / 14	0 / 27	0 / 23
8	28, F, R	L-TLE	non-neoplastic brain tissue	CBZ, TPM, LEV	50.5	46	98	2 / 9	5 / 14	0 / 13	1 / 27	2 / 20
9	21, M, R	L-TLE	FCD 3A	LEV, CLB	93.5	41.5	81	1 / 1	4 / 8	0 / 13	2 / 25	0 / 4
10	34, M, R	L-TLE	FCD 3A	CBZ, LTG	81.0	47.5	102	3 / 7	2 / 6	0 / 18	4 / 27	0 / 18
11	49, F, R	L-TLE	HS + unknown etiology	PHT, PB, LEV	80.0	23.3	119	2 / 10	2 / 7	3 / 12	1 / 38	1 / 34
12	22, F, R	L-PLE +TLE	FCD 1C	VPA, TPM, PER, LCM	64.5	34.5	106	6 / 17	0 / 3	0 / 17	1 / 18	5 / 32

1 **Abbreviations** TLE: temporal lobe epilepsy PLE: parietal lobe epilepsy, HS: hippocampal sclerosis, FCD: focal cortical dysplasia.
2 CLB: clobazam, PHT: phenytoin, ZNS: zonisamide, LEV: levetiracetam, TPM: topiramate, LTG: lamotrigine, fPHT: fosphenytoin,
3 PB: phenobarbital, LCM: lacosamide.

4 *FCD classification is according to Blumcke's criteria published in Epilepsia, 2011.

5 # of recording electrodes represents all electrodes without systemic artifacts, including the electrodes in the anterior temporal lobe,
6 which were excluded for ERC analysis.

7

8

1 **Table 2. The number of directed connections within channels**

Directed connections	Lateral Occipital (LO)	Ventral temporal-lobe (VTL)
LO	124	71
VTL	71	148

2

3

1 **Table 3. The number of directed connections within channels in VTL**

Directed connections	Inferior temporal gyrus (ITG)	Fusiform gyrus (FG) + Parahippocampal gyrus (PHG)
ITG	8	29
FG + PHG	29	82

2

Captions to figures

Figure 1. ECoG signals data during visual naming task. **(A)** Patients undergoing subdural grid implantation for invasive presurgical evaluation were instructed to name out loud objects presented on the computer screen every 5000 ms (e.g., living object such a rabbit or butterfly, or non-living such an airplane or guitar). **(B)** After removing epochs that included artifacts or interictal epileptic discharges within -2000 to +1000 ms at visual stimulus, reaction times for living (black) and non-living (gray) objects were computed. On each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers (within 1.5 times the height of the central box), and the outliers are plotted individually using the unfilled circle. Reaction times converted to z-scores for living and non-living stimuli across the patients were compared, showing statistical significance. * $p < 0.05$.

Figure 2. Neural activation during visual category recognition. **(A)** Electrodes selected for visual category recognition (used for the analysis of event-related causality, ERC). At the left, the filled yellow circles or pie charts (for lateral occipital [LO] in a red circle and ventral temporal lobe [VTL] in an orange circle) denote electrodes that ranked in the top 10% of elicited high-gamma activities (80-150 Hz) in each patient. All electrodes, from 12 patients, are depicted on the MNI standard brain. Electrodes from the right hemisphere were flipped into the left one. Posteriorly, the electrodes in LO and VTL are clustered compared to the yellow electrodes that are sparsely located. The electrodes in bad condition (black; baseline fluctuation, or severe artifacts that suggest wire breaking) and all the other recorded electrodes (blue square) were also

shown. The dotted white lines indicate the border of the anterior temporal lobe defined by Rice, et al (Rice *et al.* 2015). The electrodes anterior to the border were excluded for ERC analysis in advance, although only 5 electrodes were involved across the patients. At the right, an example of spectral representation of responses elicited by living (top) or non-living objects (middle) (†) in VTL. Z-scores of HG (white rectangle) in reference to prestimulus baseline (-2000 to 0 ms) were further shrunk/collapsed to the line plot (bottom). Z-clusters of HG, the area under the waveform satisfying $z > 3$ within 0-500 ms were used for HG indices as above. The relative magnitude of z-clusters of HG at each electrode (living [magenta] vs. non-living [green]) are shown using pie chart. Note that HG-wise, no clear demarcation of activities was found between the subregions in VTL. **(B)** The relative magnitude and the time course of mean HG in the posterior cortex (LO and VTL) during visual recognition of living (magenta) and non-living objects (green). Each colored line shows the mean of HG (LO - top, VTL - bottom) and their shaded areas show 1.96 x standard error of the mean at each time point. *: $p < 0.05$ after correction for multiple comparisons by Holm's method.

Figure 3. The examples of ERC during recognition of living (upper rows) and non-living objects (lower rows) in Pt. 6 and Pt. 8. The propagation patterns were calculated for magenta or green electrodes, respectively. In Pt. 6, The red asterisks are the sites of insertion of depth electrodes, which were excluded from this study. The magnitude of propagation is shown by the color and thickness. Note that relatively earlier propagation within the VTL is observed during recognition of living objects although the propagations that include LO or parietal areas are observed during recognition of non-living objects.

1

2 **Figure 4.** The time course of ERC in the posterior cortex (LO - red circle, VTL - orange circle)
3 during visual recognition of living vs non-living objects. *: $p < 0.05$ by permutation test for
4 cluster-level statistics. Note that HG propagation within VTL is significantly larger around 230-
5 270 ms during visual recognition of living objects as compared to non-living, suggesting higher
6 interdependency between nodes in this region. The other conventions are the same as in Figure
7 2.

8

9

Supplementary Information

Oct. 25th, 2022

**The dynamics of cortical interactions in visual recognition of object category:
living vs non-living**

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1 **Supplementary Table 1. A full list of living/non-living items**

Living		Non-Living	
bat	gorilla	cymbals	gun
cockerel	goat	shell	hammer
crab	horse	ski	harp
dragon	kangaroo	slide	helicopter
ladybird	lion	tractor	iron
tortoise	lobster	web	kite
whale	monkey	yo-yo	ladder
ant	mouse	airplane	mitten
butterfly	ostrich	anchor	motorbike
bear	owl	barrel	nut
bee	peacock	basket	piano
camel	penguin	bell	pram
cat	pig	cake	skirt
caterpillar	rabbit	cannon	sledge
cow	raccoon	chain	snowman
deer	rhinoceros	church	suitcase
dog	seahorse	cigar	swing
duck	sheep	clock	toaster
eagle	snail	crown	train
elephant	snake	dress	trumpet
fish	spider	drum	vase
fly	squirrel	fence	violin
fox	swan	flute	wheel
frog	tiger	glove	whistle
giraffe	zebra	guitar	windmill

2

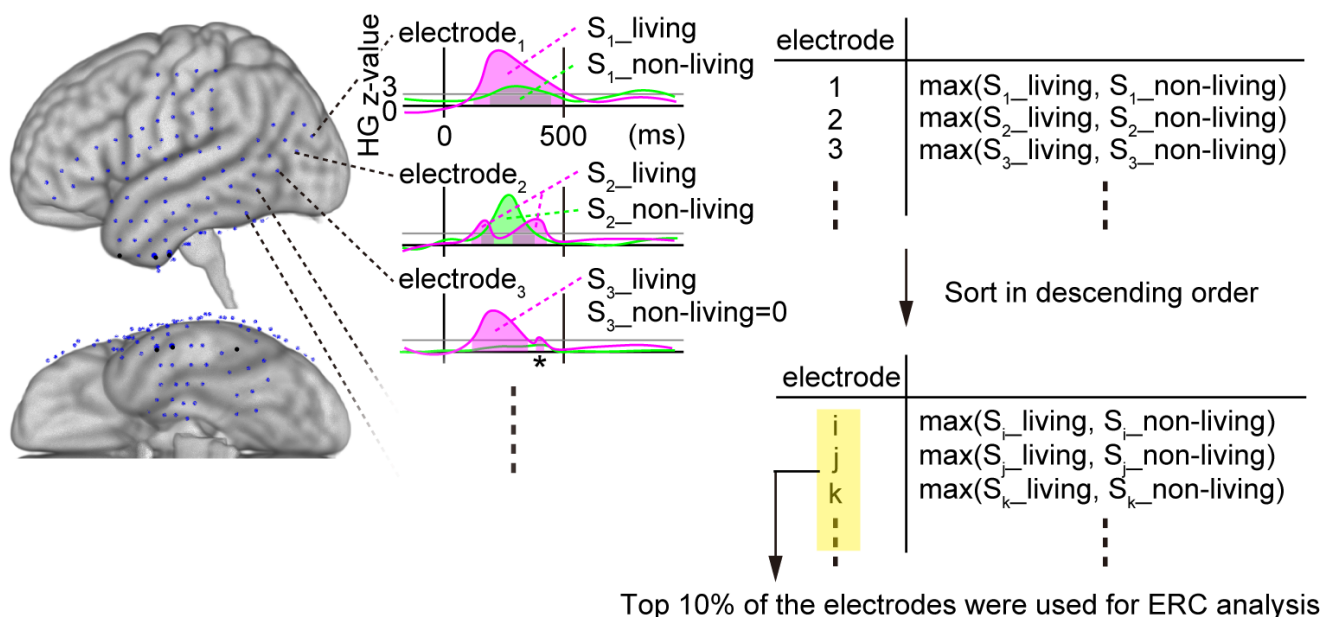
3

1 **Supplementary Table 2. A full list of MNI coordinates of the electrodes in LO (lateral**
2 **occipital) and VTL (ventral temporal lobe) areas selected for the analysis of living/non-**
3 **living objects**

Patient #	Area, the name of the electrode	Coordinate (x, y, z)	Patient #	Area, the name of the electrode	Coordinate (x, y, z)
1	LO, B01	-48, -72, -20	7	VTL, H01	-34, -54, -24
1	LO, C01	-64, -68, -2	7	VTL, H02	-38, -46, -28
1	LO, C06	-58, -74, 4	7	VTL, H03	-44, -38, -32
1	LO, C11	-54, -80, 10	8	LO, D01	-58, -70, 14
1	LO, C12	-58, -72, 16	8	LO, D02	-64, -62, 12
1	LO, C16	-46, -84, 16	8	VTL, C11	-24, -40, -22
1	LO, C17	-52, -78, 22	8	VTL, C12	-36, -38, -28
1	VTL, A18	-34, -28, -32	8	VTL, C16	-28, -50, -18
1	VTL, B02	-52, -60, -24	8	VTL, C17	-38, -48, -24
2	LO, B06	40, -86, 30	8	VTL, C18	-48, -46, -28
2	LO, B08	56, -72, 30	9	LO, H01	-64, -60, -6
2	LO, B12	50, -80, 18	9	VTL, E09	-26, -38, -24
2	LO, B13	56, -72, 18	9	VTL, E10	-32, -36, -28
2	LO, B16	46, -88, 4	9	VTL, E11	-42, -34, -34
2	LO, B17	52, -80, 6	9	VTL, E12	-54, -28, -36
3	VTL, B11	-24, -26, -28	10	LO, E01	-60, -66, -12
3	VTL, B16	-26, -36, -22	10	LO, F01	-62, -68, 8
3	VTL, C01	-32, -58, -20	10	LO, F06	-60, -68, 20
3	VTL, C02	-42, -52, -26	10	VTL, D10	-30, -30, -30
4	VTL, I17	-36, -28, -32	10	VTL, D11	-38, -32, -32
4	VTL, J01	-44, -44, -28	11	LO, E01	-50, -84, 8
4	VTL, J02	-50, -36, -30	11	LO, E02	-56, -76, 6
4	VTL, K01	-28, -74, -18	11	VTL, D09	-34, -40, -28
4	VTL, K02	-36, -66, -20	11	VTL, D10	-46, -42, -30
4	VTL, K03	-46, -56, -24	12	LO, D01	-44, -90, -8
4	VTL, K04	-58, -46, -28	12	LO, D02	-50, -82, -10
5	LO, H01	-48, -86, 20	12	LO, D03	-56, -72, -16
5	LO, H03	-60, -68, 2	12	LO, D06	-46, -90, 2
5	LO, H10	-58, -72, 18	12	LO, D07	-54, -80, 2
5	VTL, E01	-20, -46, -16	12	LO, D16	-48, -82, 26
5	VTL, E02	-30, -46, -24			
5	VTL, F02	-32, -54, -20			
5	VTL, F03	-44, -52, -26			
5	VTL, G02	-48, -60, -24			
5	VTL, G03	-58, -56, -24			
6	LO, H01	46, -86, -12			
6	LO, H02	52, -80, -6			
6	LO, H03	58, -72, -2			
6	VTL, F02	34, -46, -26			
6	VTL, F03	44, -44, -30			

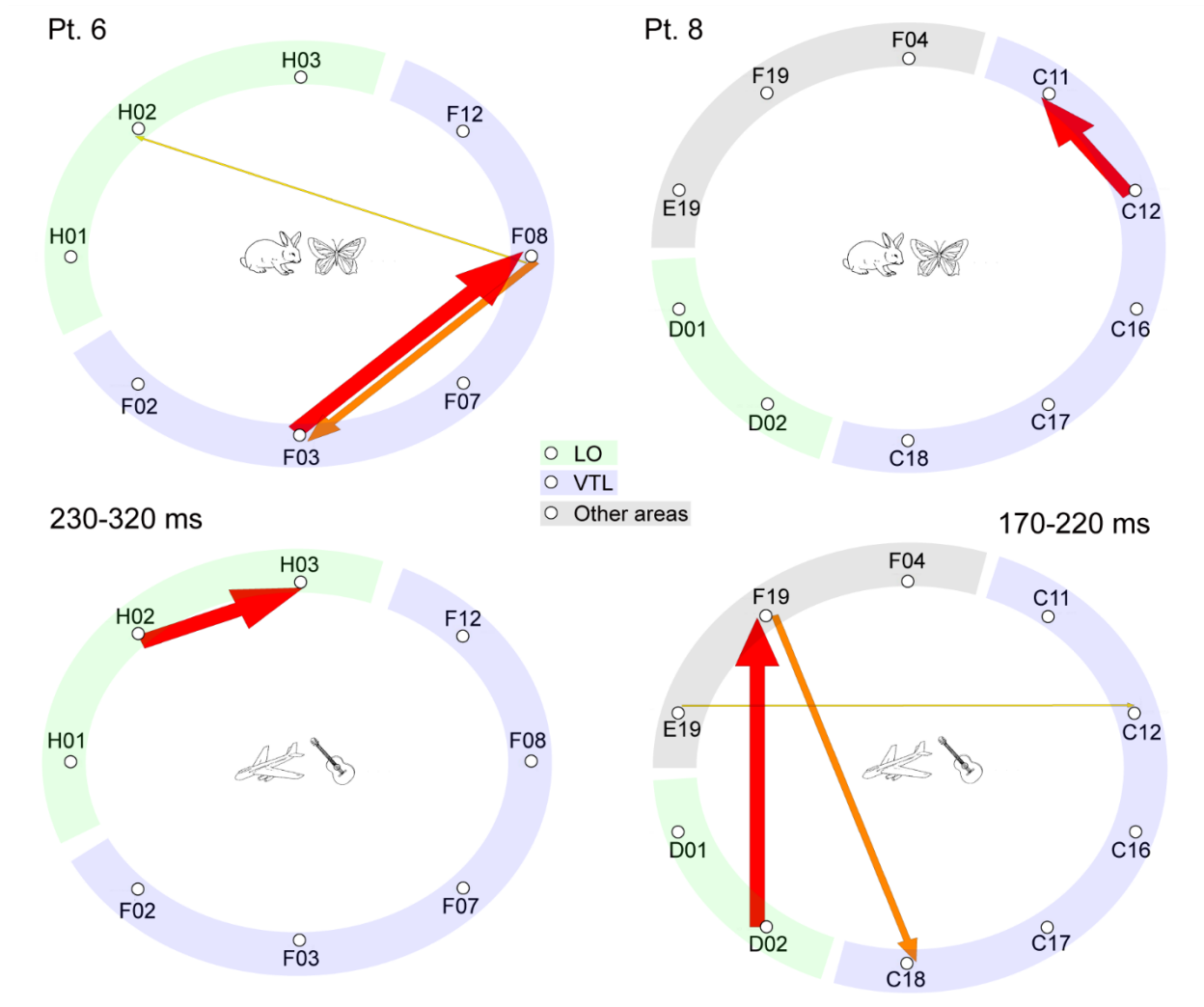
6	VTL, F07	32, -36, -28
6	VTL, F08	42, -34, -30
6	VTL, F12	30, -28, -30

1



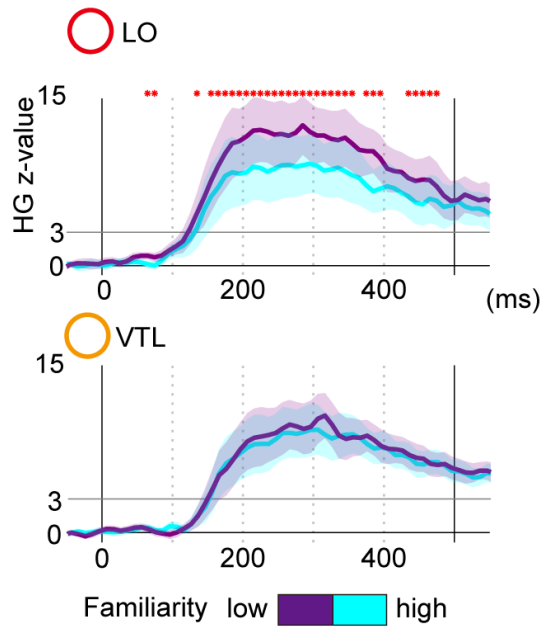
2 **Supplementary Figure 1.** The selection of electrodes used for ERC analysis (please see Figure
 3 2A). In each electrode, the z-scores of power changes between 0 to 500 ms were calculated
 4 separately for living (magenta) and non-living objects (green). Please note that all clusters lasting
 5 at least 50 ms were summed (S) in each category before the comparison between living and non-
 6 livings (ex. living in electrode₂), and clusters lasting less than 50 ms were not included in the
 7 sum (ex. a cluster marked by the asterisk (*) in the bottom plot).

1

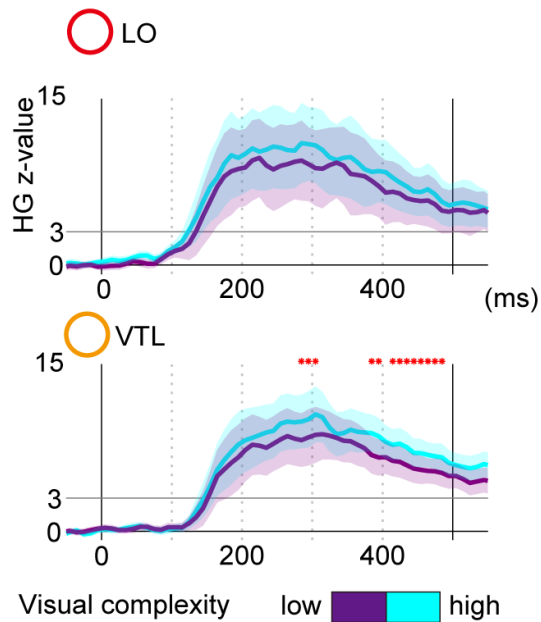


2 **Supplementary Figure 2.** Diagram representation of neural activity propagation depicted in
 3 Figure 3. The magnitude of propagation from one electrode to another is shown by the color and
 4 thickness of the arrow.

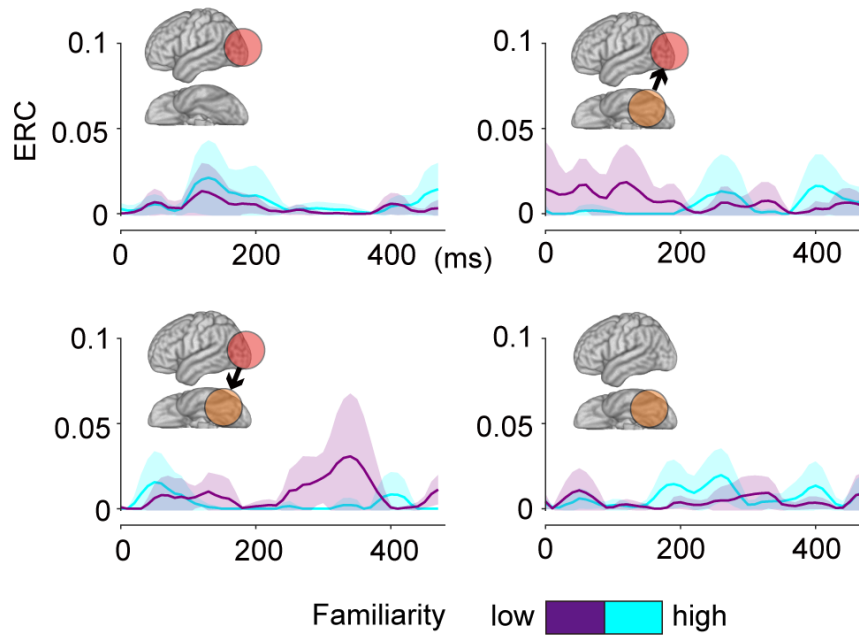
5



Supplementary Figure 3. Comparison of the time course of HG activation in the posterior cortex between trials of high (cyan) and low familiarity (purple) during visual recognition.



Supplementary Figure 4. Comparison of the time course of HG activation in posterior cortex between trials of high (cyan) and low visual complexity (purple) during visual recognition.



Supplementary Figure 5. Comparison of the time course of ERC in the posterior cortex between trials of high (cyan) and low familiarity (purple) during visual recognition.