Diverse temporal dynamics of repetition suppression revealed by intracranial recordings in human ventral temporal cortex

Vinitha Rangarajan[1], Corentin Jacques[2], Robert T. Knight[1,3], Kevin S. Weiner[1,3*], and Kalanit Grill-Spector[4,5,6*]

1. Department of Psychology, University of California, Berkeley, USA
2. Psychological Sciences Research Institute (IPSY), Université Catholique de Louvain, Belgium
3. Helen Wills Neuroscience Institute, University of California, Berkeley, USA
4. Department of Psychology, Stanford University, California, USA
5. Neurosciences Program, Stanford University, Stanford, CA
6. Wu Tsai Neurosciences Institute, Stanford University, Stanford, CA

*Co-Senior Authors

Abstract (186/200)

Repeated stimulus presentations commonly produce decreased neural responses - a phenomenon known as repetition suppression (RS) or adaptation – in ventral temporal cortex (VTC) in humans and nonhuman primates. However, the temporal features of RS in human VTC are not well understood. To fill this gap in knowledge, we utilized the precise spatial localization and high temporal resolution of electrocorticography (ECoG) from 9 human subjects implanted with intracranial electrodes in VTC. Subjects viewed non-repeated and repeated images of faces with (long-lagged) intervening stimuli between repeats. We report three main findings: (i) robust RS occurs for VTC activity in high-frequency broadband (HFB), but not lower frequency bands, (ii) RS is associated with lower peak magnitude, lower total responses of the HFB signal, and earlier peak responses, and (iii) RS effects occur early within initial stimulus processing and persist for the entire stimulus duration. We discuss these findings in the context of early and late components of visual perception, as well as theoretical models of RS in which these ECoG data empirically support timing predictions stemming from the facilitation model of RS in human VTC for the first time.

Keywords (5/5)

Repetition Suppression; Electrocorticography; Perception; Temporal Dynamics; Adaptation

Introduction

Repeated exposures to sensory stimuli produce decreased neural responses, a phenomenon known as repetition suppression (RS), habituation, or adaptation. RS is common across sensory modalities in humans (Buckner RL et al. 1995; Grill-Spector K et al. 1999; Henson R et al. 2000; Alink A et al. 2018) and non-human primates (Gross CG et al. 1969; Gross CG et al. 1979; Miller EK et al. 1991; Lueschow A et al. 1994; McMahon DB and CR Olson 2007). RS is also considered a simple form of sensory learning (Thorpe W 1956; Groves PM and RF Thompson 1970; Miller EK *et al.* 1991) and a critical mechanism for perception (Grill-Spector K et al. 2006). Despite the ubiquity and proposed role of RS in perception, a surprising dearth of studies have examined RS using human intracranial measurements.

To our knowledge, the few studies that have examined RS in human VTC using intracranial electrophysiology implemented experimental designs in which the inter-stimulus intervals (ISIs) were short (largely between 275 and 500 milliseconds (Puce A et al. 1999; McDonald CR et al. 2010; Engell AD and G McCarthy 2014; Rodriguez Merzagora A et al. 2014; Miller KJ et al. 2015). These experimental designs were motivated by a) seminal findings showing that RS decreases with increasing ISIs, and is ablated once the ISI reached 20 seconds (Miller EK *et al.* 1991), and b) recent studies examining RS in macaque VTC, which continue to use short ISIs to maximize RS (McMahon DB and CR Olson 2007; Verhoef BE et al. 2008; De Baene W and R Vogels 2010; Kaliukhovich DA and R Vogels 2011; Kuravi P and R Vogels 2017). Interestingly, functional magnetic resonance imaging (fMRI) experiments have replicated and extended the characterization of repetition effects in human VTC. These studies illustrated that RS: a) occurs even with just a single stimulus repetition (Sayres R and K Grill-Spector 2006), b) transpires across many intervening stimuli between image repetitions (Chao LL et al.

1999; Henson R *et al.* 2000; Sayres R and K Grill-Spector 2006; Weiner KS et al. 2010), and c) is larger for repetitions with no intervening stimuli and shorter time lags (Chao LL *et al.* 1999; Sayres R and K Grill-Spector 2006; Weiner KS *et al.* 2010).

Despite these findings across species and methodologies, the temporal characteristics of RS in human VTC remain largely unknown, especially for long-lagged repetitions in which the repeated image occurs after multiple other images and typically after intervals of 10 seconds and longer. Long-lagged repetitions are particularly interesting as they reflect an implicit memory trace and cannot be explained by refractory periods that may dampen the generation of action potentials (Grill-Spector K *et al.* 2006). Thus, advancements in measuring high-frequency broadband (HFB) signals in the awake human brain, which are thought to be related to neuronal firing and local field potentials (Ray S and JH Maunsell 2011), offer a unique opportunity to determine the temporal features of RS.

To study the temporal characteristics of long-lagged RS, we conducted an electrocorticography (ECoG) experiment in 9 participants in which we measured electrical signals from VTC to novel and repeated images of faces. We used faces due to the large body of research documenting both face-selective responses in VTC with ECoG (Allison T et al. 1999; McCarthy G et al. 1999; Parvizi J et al. 2012; Davidesco I et al. 2013; Rangarajan V et al. 2014; Jonas J et al. 2016), as well as robust RS for faces in VTC observed with fMRI (Grill-Spector K and R Malach 2001; Sayres R and K Grill-Spector 2006; Weiner KS *et al.* 2010; Engell AD and G McCarthy 2011). Here, repetitions occurred after many intervening images and tens of seconds (average of 20.1 – 31.7 s between repetitions; **Figure 1**). We discuss our findings in the context of bottom-up and top-down components of visual perception, as well as theoretical models (Grill-Spector K *et al.* 2006 2006). In particular, we consider our findings with respect to

the facilitation model, which uniquely makes temporal predictions about RS (Henson RN and MD Rugg 2003; Henson RN 2012).

Methods

Participants: 9 subjects (3 female) were implanted with intracranial electrodes for neurosurgical evaluation for the treatment of refractory epilepsy. Electrode locations were chosen exclusively for clinical reasons by the subjects' neurologist (JP) and neurosurgeons. The electrodes (AdTech) were implanted in the right and left hemispheres in 4 and 4 subjects, respectively, with 1 bilateral strip implantation. Electrodes had either 5 or 10 mm inter-electrode spacing (center to center) with an exposed recording surface diameter of 2.3 mm. All subjects gave informed written consent to participate in research studies at Stanford Medical Center as approved by the Stanford University Internal Review Board. All electrodes clinically implicated in the epileptogenic zone were excluded from analysis. In order to localize electrodes, high-resolution MRIs were acquired on a 3-tesla GE scanner as previously described (Rangarajan V *et al.* 2014). Post-implantation computed tomography (CT) images were co-registered to the MRIs to visualize electrode locations in the subjects' native head-space (Hermes D et al. 2010).

Experimental paradigm (**Figure 1**)*:* Subjects participated in an experimental visual paradigm. Subjects viewed images of faces, body parts (limbs), cars, and houses that were presented foveally at a visual angle of approximately 10° by 10°. Each stimulus was presented for a duration of 1000 ms with a randomized inter-stimulus interval varying between 600-1400 ms. Some of the images were shown only once and some of the images were shown repeatedly (up to 6 times) during the experiment. However, only the first and second presentations of an image

were analyzed in the present study to maximize the RS effects. On average, there were 8±1 intervening stimuli and 27.5±8.6 seconds between the first and second presentations of the same image. Images were equally likely to be repeated or nonrepeated throughout the course of the experiment. Images of all presented categories were included in both the nonrepeated and repeated conditions. The nonrepeated stimuli served two purposes (1) they were used as independent trials to assess the category selectivity of each electrode and (2) they were used as intervening stimuli between repetitions of the same image.

Task: Participants were instructed to fixate on a central fixation and to indicate when its color changed by pressing a button on an external keypad Each subject participated in 5-10 runs of the experiment resulting in an average of 16 repeated face exemplars and 46 repeated non-face exemplars.

[INSERT Figure 1]

Data Acquisition: Intracranial electrode activity was recorded on a Tucker Davis Technologies recording system sampled at 3052 Hz (subjects S1-7) and 1526 (S8-9). Signals were referenced online to a silent intracranial electrode and digitally bandpass filtered from 0.5 to 300 Hz. Pathological channels, as identified clinically, and noisy channels were removed before data processing. Additionally, channels containing voltage greater than five times the mean variance in voltage were also removed. The remaining channels (mean: 68 ± 26 electrodes/subject) were notch filtered at 60 Hz harmonics and then re-referenced to the common average to remove shared noise. The onsets of stimulus presentations were marked with a photodiode, time-locked to the neural data, and sampled at 24.4 kHz to maintain high temporal fidelity.

Time-Frequency Data Processing: The data were filtered for canonical frequency bands: theta (Θ: 4-8 Hz), alpha (α: 8-13 Hz), beta (β: 16-30 Hz), and high frequency broadband (HFB: 70-150 Hz). β and HFB data were obtained by bandpass filtering the original signal using 5 Hz non-overlapping frequency bins (e.g., 70-75, 75-80…145-150 Hz). The time-varying power in each 5 Hz bin was estimated by applying a Hilbert transform (analytic amplitude squared). Each power time series was log transformed and the mean for the entire log power time series was subtracted. The transformed power times series were then averaged per canonical frequency band and downsampled to 100 Hz. This resulted in time series activity for Θ, α, β, and HFB activity corrected for the 1/frequency power decay in each frequency range. All analyses were done using custom MATLAB (Mathworks Inc) analysis scripts. All data were normalized (z-scored) with respect to the average of the 150 ms prestimulus baseline period per stimulus.

Localization of face-selective electrodes: In each subject, we identified face-selective electrodes using independent data from trials containing images that appeared only once during the long-lagged experiment, as in our prior studies (Parvizi J *et al.* 2012; Rangarajan V *et al.* 2014; Jacques C et al. 2016). In each electrode, we calculated the mean HFB power over a 0–900 ms window after stimulus onset averaged across all images from each category that were shown once. Then, we conducted paired two-sided *t* tests to test if responses were significantly higher to images of faces compared to images of non-faces ($p < 0.05$). A false discovery rate procedure (FDR; Benjamini-Hochberg procedure; (Benjamini Y et al. 2001) for multiple-comparison correction was applied ($\alpha = 0.05$) across electrodes within each subject. Importantly, the stimuli used for electrode-selectivity identification were excluded from all further analyses. Thus, all repetition suppression analyses were conducted with independent data.

To visualize the location of face-selective electrodes on a common MNI brain, the 3D whole brain anatomical images and electrode coordinates for each subject were converted to the MNI space and displayed over the mean cortical surface of the MNI brain (Hermes D *et al.* 2010) as in our prior studies (Rangarajan V *et al.*). On the MNI brain, we displayed all recorded electrodes across subjects as well as the subset of face-selective electrodes, as illustrated in **Figure 2**.

[INSERT Figure 2]

Analyses of neural responses to the first and second presentation of images across frequency bands: Because different frequency bands are thought to represent varied features of electrocortical activity (Ray S and JH Maunsell 2011; Miller KJ et al. 2014), we examined in each electrode responses to first and second stimulus presentations separately for each of the canonical frequency bands: theta (Θ: 4-8 Hz), alpha (α: 8-13 Hz), beta (β: 16-30 Hz), and high frequency broadband (HFB: 70-150 Hz). A two-way analysis of variance (ANOVA) was performed on the total response using as factors stimulus presentation number (1st and 2nd face presentations, which resulted in 1 degree of freedom) and frequency bands (Θ, α, β, and HFB, which resulted in 3 degrees of freedom) in the long-lagged task across all 9 subjects. Post-hoc paired t-tests comparing the total response to 1st versus 2nd face presentations were performed for each frequency band in three time-windows: 100-350 ms (reflecting early visually evoked responses), 350-900 ms (reflecting the response after the evoked response) and 100-900 ms (reflecting the total response duration).

Determining significant repetition suppression effects: Subsequent analyses focused on HFB activity because HFB responses showed differences between the 1st and 2nd presentations.

Additionally, HFB activity is thought to reflect population spiking activity (Manning JR et al. 2009) and local post-synaptic activity (Logothetis NK et al. 2001; Miller KJ et al. 2010), which correlates with BOLD responses (Hermes D et al. 2012; Jacques C *et al.* 2016). To determine if RS was significant ($p < 0.05$), in each face-selective electrode we conducted a paired two-sided *t* test of the response to the 1st versus 2nd face presentations in the 0-900 ms time window. A false discovery rate procedure (FDR: Benjamini-Hochberg procedure (Benjamini Y *et al.* 2001) for multiple-comparison correction was applied ($\alpha = 0.05$).

Movie 1: To visualize the temporal dynamics of neural responses to stimulus repetition in VTC, we implemented a two-fold procedure. First, for each electrode, we computed a paired *t* statistic comparing HFB responses for the first versus second face presentation. These values were calculated in an interval between 0-900 ms after stimulus onset, in 10 ms bins and plotted as the static electrode size. Second, we generated a movie of these values by visualizing the t-value of each electrode on the MNI surface across 10 ms time bins. This enabled visualizing the spatial and temporal effects of stimulus repetition across face-selective electrodes. For display purposes, the additive spatial distribution of t-values across electrodes were scaled to the same maximum and minimum (-2 (blue) and 2 (red), respectively), and corrected for the spatial distribution and overlap of included electrodes. This controls for varied electrode coverage and prevents areas with higher spatial overlap of electrodes from appearing more task-active. The video is slowed down 10 times such that 900 ms is displayed for 9 seconds. We tested if the average values for each 10 ms time window were significantly different using a paired t-test (1st versus 2nd presentation, $p<0.05$) to identify the rough onsets of RS or repetition enhancement effects at the group level.

Quantifying stimulus repetition: In all face-selective electrodes, we quantified the effect of stimulus repetition on HFB responses from single trials (e.g. one stimulus) separately for each experiment using four metrics that capture the features of the HFB temporal response as well as its overall response amplitude:

1. Area under the response curve (AUC) is a measure of the total neural response. It was measured separately for each stimulus for the first (non-repeated) and second (repeated) stimulus presentation. AUC was calculated for each trial using a trapezoidal numerical integration, which reflects a sum of all responses in the HFB band between 0 to 900 milliseconds time window in 10 ms steps per trial.
2. Peak Magnitude (PM) was calculated by finding the peak (maximum) HFB z-score value separately for the first and second presentation of each stimulus and then measuring the average response across a 10 ms window surrounding the peak. The 10 ms time-window based provides an estimate of the peak response that is less susceptible to noise-related fluctuations.
3. Response Onset Latency (ROL) of the neural signal was calculated by adapting the approach of Flinker A et al. (2010). We first identified the trials that showed a response to the stimuli. Responsive trials were trials that significantly deviated from noise. These trials significantly exceeded a null distribution of 1000 mean HFB epochs with random sampling. For these trials, we measured ROL during a 0–500 ms time window after stimulus presentation. The ROL was defined as the first time-point during the 0–500 ms time window in which the response passed the HFB z-score threshold ($p<0.05$) for a

duration of least 50 ms. This criterion was to ensure that we did not consider a momentary fluctuation as the response onset.

4. Peak Timing (PT) was calculated as the timing of maximal (peak) response for a given trial. Peak response was defined as the maximal HFB z-score value. PM and PT were calculated separately for the first and second presentation of each image. This trial-by-trial resolution enabled to assess temporal variability between trials. All peaks >500 ms were excluded as noise for a conservative estimate of peak timing.

Statistical testing: AUC, PM, ROL, and PT values were calculated at the single trial level, then averaged across trials per electrode. We examined the mean difference values (2nd – 1st presentation) for each electrode as well as the overall mean for each of these metrics for first and second presentations of each stimulus. We tested if the average values for each metric were significantly different using a paired t-test (1st versus 2nd presentation) was done to identify whether each metric showed a positive or negative shift ($p<0.05$) and a false discovery rate procedure (FDR: Benjamini-Hochberg procedure (Benjamini Y *et al.* 2001)) for multiple-comparison correction was applied ($\alpha = 0.05$) across electrodes.

Results

Stimulus repetition produces reduced neural responses (repetition suppression, RS) in high-frequency broadband, but not other frequency bands

We first examined the effect of long-lagged image repetitions on ECoG responses by comparing ECoG signals for the 1st and 2nd presentation of faces in each of the canonical Θ, α, β, and HFB frequency bands. **Figure 3** shows the mean response across all 48 face-selective

electrodes, which were localized with independent data (**Figure 2**) for each of these frequency bands during the 1st (red) and 2nd (blue) presentation of face images (S1= 9, S2= 11, S3= 3, S4= 10, S5= 2, S6= 2, S7= 1, S8= 8, S9= 2 face-selective electrodes). Notably, we observed reduced responses for the second compared to the first presentation (or repetition suppression, RS) in the HFB, but not other frequency bands.

We assessed the significance of our observations using a two-way analysis of variance (ANOVA) on the total HFB response integrated over a 0-900 ms time window after the stimulus onset using as factors presentation number (1st/ 2nd) and frequency band (Θ, α, β, and HFB). Across all subjects (S1-9), we found a significant effect of frequency band [$F(3, 376)=95.96$, $p<10^{-46}$], but no significant main effect of repetition ($p>0.05$) or significant interaction ($p>0.05$).

[INSERT Figure 3]

Given the significant main effect of frequency band, we conducted post-hoc analyses in three separate time windows: 100-900 ms (stimulus duration), 100-350 ms (evoked response), and the remainder of the stimulus duration after the evoked response (350-900 ms). Examination of the time course of neural responses revealed significant RS in HFB (Figure 3) which was significant over the entire window (paired t-test, 100-900 ms; $t(47)=4.14$, $p<10^{-4}$, FDR corrected). This HFB RS effect was already evident in the HFB in the early (100-350 ms) portion of the trial (paired t-test, $t(47)=3.75$, $p<10^{-4}$, df=47 n-1 electrodes, FDR corrected). This 100-350 ms temporal period is associated with the synchronized evoked visual response that is prominent in low frequencies. Notably, RS in the HFB persisted beyond the evoked response window, as significant RS was also observed after the evoked response (paired t-test, 350-900 ms; $t(47)=4.12$, $p<10^{-4}$, FDR corrected).

In comparison to neural responses in the HFB, responses in Θ, α, and β frequency bands were more transient. Specifically, responses in these frequency bands increased from baseline during a 100-350 ms time-window after stimulus onset, and then returned to baseline. Interestingly, there was no significant RS in Θ and α frequency bands not only across the entire stimulus duration (100-900 ms, $p>0.05$) but also not during the evoked response (100-350 ms, $p>0.05$) or later period (350-900 ms, $p>0.05$). Altogether, these results indicate that RS largely occurs in HFB, but not lower frequency bands.

Spatio-temporal dynamics of RS in the VTC

We visualized the spatiotemporal dynamics of RS in human VTC. To do so, we generated **Movie 1** that illustrates the average difference in HFB response (t-values) between the 1st and 2nd presentation of each face image at 10 ms time bins for each electrode. Consistent with our subsequent analyses and statistical quantification, **Movie 1** shows that the most pervasive effect of stimulus repetition is reduced HFB responses to the 2nd compared to the 1st presentation. Spatially, this reduction, illustrated in the warm colors in **Movie 1** occurs primarily in the lateral fusiform gyrus (FG). Interestingly, RS is evident early in the response, and appears within the first 100-200 ms after stimulus onset in several electrodes. The average first significant 10 ms window across all electrodes showing RS was 153.75 ± 145.27 ms. RS persists throughout the duration of the stimulus and the effect size increases over time, and spreads both more posteriorly and anteriorly, particularly in the right hemisphere. Nevertheless, since there are only 3 left hemisphere electrodes with significant RS time windows, we did not directly compare lateralization effects. We also note that 3 electrodes show a weak enhanced response to the 2nd versus 1st presentation. Two electrodes were located in the right inferior temporal gyrus (ITG),

and one in the anterior and medial aspect of the right FG. Notably, the first time point showing this significant enhancement appeared later in the trial, on average 376.25 ± 313.59 ms after stimulus onset. These spatial and temporal dynamics of RS are further quantified in the sections below.

[INSERT Movie 1 here]

Robust RS in single electrodes: Reduced total and peak responses in HFB for repetitions

The analyses in the previous section examined the integration of neural responses over the entire trial duration and across electrodes, which may obscure finer temporal characteristics of RS visible in **Movie 1.** Thus, we next examined the spatial and temporal dynamics of HFB responses in each electrode. As RS effects in the HFB persisted throughout the trial, all subsequent analyses were done in a 100-900 ms time window. To characterize responses over time, we calculated and compared four metrics of the HFB response for first and second face presentations (Methods, **Figure 4A**): (1) total response (area under the response curve, AUC), (2) peak magnitude (PM), (3) response onset latency (ROL), and (4) peak timing (PT). Each metric was calculated at the single trial level and then averaged across all trials for each electrode.

[INSERT Figure 4]

We analyzed the effect of repetition on (a) the total HFB response (AUC) and (b) the peak magnitude (PM), revealing two main findings.

First, the total HFB response was reduced for 2nd versus 1st presentation of faces at the fine-spatial scale of a single electrode (**Figure 4B**). The mean AUC for the first presentation was 3.4 ± 2.1 versus 2.5 ± 1.6 for the second presentation. 77.1% (37/48) of electrodes in all (9/9) subjects showed lower AUC values for the 2nd versus 1st presentation leading to a negative difference in the AUC between presentations (blue dots in **Figure 4B**). Statistical comparisons of the 1st versus 2nd presentations showed a significant reduction in the total AUC of HFB responses (**Figure 4B**, paired t-test $t(47)= 4.16$, $p<10^{-4}$, FDR corrected). Additionally, 22.9% (11/48, 6/9 subjects) of electrodes showed a change in AUC that is either equal to zero or enhanced (2nd > 1st), while only 3 electrodes showed significant repetition enhancement reflected by substantial increase in AUC (RE: paired t-test $p<0.05$, FDR corrected). It is, however, noted that enhancement occurs in smaller time-windows throughout the trial, but not over the complete trial (**Movie 1)**.

Second, we examined the effect of repetition on peak magnitude (PM) responses of each electrode. As HFB responses were converted to z-scores relative to the baseline response, PM metrics are reported in units of z-score (see Methods). This analysis revealed that PM for the 2nd presentation of a face was smaller compared to its 1st presentation. Indeed, the mean PM for the first presentation was 7.5 ± 3.0 standard deviations away from the baseline, mean pre-stimulus response, while the 2nd presentation was only 6.3 ± 2.6 standard deviations away from the baseline. Similar to the analysis of the AUC, the majority of electrodes (64.6%, 31/48, 8/9 subjects) showed a negative PM difference between the 2nd versus 1st presentation (**Figure 4C,** paired $t(47)=3.39$, $p=0.001$, FDR corrected).

Together these analyses indicate that both the total HFB response (AUC) and peak HFB response are lower for the 2nd versus 1st presentation of a face, illustrating significant RS in face-selective electrodes for long-lagged stimulus repetitions.

Peak timing is faster for the second compared to the first image presentation in a majority of electrodes

Next, we quantified the temporal profile of neural responses to face repetitions using two metrics: (1) the response onset latency (ROL) of HFB responses and (2) peak timing (PT) of HFB response.

The mean response onsets to the 1st and 2nd presentations were 101.8 ± 38 ms and 100.2 ± 31.4 ms respectively, which were not significantly different. Examination of the differences in ROL for the 2nd versus 1st presentations of faces showed a delayed onset in 27/48 (56.3%, 8/9 subjects) for 2nd versus 1st presentations of faces, while the remaining electrodes (43.7%, 21/48, 8/9 subjects) showed the opposite effect (**Figure 4D**). Consequently, across electrodes, there was no significant difference in the ROL (paired t-test, $p>0.05$) between the 1st and 2nd presentations. Additionally, the difference in ROL was not significantly different than zero ($p>0.05$).

It is interesting that while there were no differences in ROL, PT was significantly earlier for the 2nd compared to the 1st presentation of a face in the majority of face-selective electrodes (64.6%, 31/48, 8/9 subjects). Indeed, the mean PT for the first presentation of a face was 275.9 ± 39 ms and for the 2nd presentation it was about 20 ms earlier, averaging at 258.7 ± 51 ms. Statistical comparisons of the 1st versus 2nd presentations showed a significant earlier PT (paired t-test: $t(47)=2.8939$, $p=0.005$, FDR corrected) and was on average 17 ms ± 4 ms faster during the

second presentation. Additionally, a minority of electrodes (n=5) showed the converse pattern and a significantly delayed PT ($p<0.05$) during second compared to first stimulus presentations.

Taken together, analyses of the temporal dynamics illustrate that HFB responses are overall lower, have a smaller peak magnitude, as well as an earlier time to peak for the 2nd compared to the 1st presentation of faces.

Discussion

Using intracranial recordings, we characterized the effect of stimulus repetition in human ventral temporal cortex (VTC) for long-lagged stimulus repetitions (an average of 20.1 – 31.7 s between repetitions). We found that RS occurs for high-frequency broadband (HFB) activity, but not lower frequency bands. Furthermore, we found that RS reduces the total neural response and peak magnitude; these effects are more robust in the latter compared to the former. These RS effects occur early (~150 ms) in the neural response and persist for the stimulus duration. Interestingly, HFB responses had different temporal characteristics for face repetitions: neural responses were faster to peak for second versus first presentations while there were no differences in response onset timing. In the sections below, we further discuss RS effects across frequency bands, as well as theoretical models of RS.

Repetition Suppression in HFB, but not Lower Frequency Bands

Our data reveal RS in HFB (>70Hz), but not lower frequency bands (<30Hz). These findings are consistent with ECoG data from Engell AD and G McCarthy (2014) who showed that for immediate repetitions of faces (8 repetitions of the same face, 2s ISI, and no intervening stimuli) there were decreases in low (30-60Hz) and high gamma (60-100Hz), with no significant

changes in the α (8-12Hz) or β (15–30Hz) bands. As lower frequency activity is closely tied to visual evoked potentials (VEP) (Allison T *et al.* 1999; Rossion B 2014), and VEP and HFB responses are often dissociated in face-selective regions (Engell AD and G McCarthy 2011; Rangarajan V *et al.* 2014), our data explain why prior studies have failed to find RS to faces (Puce A *et al.* 1999) in visual areas. Specifically, the lack of RS in lower frequencies in the present study and the coupling between VEP and low frequency activities is consistent with the lack of RS in the VEP observed in prior studies. We cannot rule out other effects of repetition that may be present in synchronous or phase-locked features of low frequency responses (Gilbert JR et al. 2010; Engell AD and G McCarthy 2014), simply because we have not measured them in the current study. Nonetheless, we find robust RS in the HFB and in the majority of face-selective electrodes indicating that future studies of stimulus repetition should quantify HFB responses.

Our finding of RS in HFB activity is also consistent with prior studies showing RS in gamma and high-gamma bands of local field potentials (LFP) for repetitions of faces (Engell AD and G McCarthy 2014), letters (Rodriguez Merzagora A *et al.*), and objects (McMahon DB and CR Olson 2007; De Baene W and R Vogels 2010; Friese U et al. 2012; Engell AD and G McCarthy 2014) in both human VTC as well as macaque VTC. Additionally, RS occurs within 100-350 ms of stimulus onset and persists for the remainder of the image duration. As HFB activity is correlated with local neuronal firing (Logothetis NK *et al.* 2001; Nir Y et al. 2007; Miller KJ *et al.* 2010), our results suggest that RS in HFB is due to reduced neuronal firing rate to repeated stimuli, which is consistent with reports of RS in single neurons of macaque VTC (Miller EK *et al.* 1991; Li L et al. 1993; McMahon DB and CR Olson 2007; De Baene W and R Vogels 2010).

Theoretical implications

Several theories have been proposed to account for RS in high-level visual cortex such as scaling, sharpening, facilitation, synchrony, and prediction error, and combinations therein (Grill-Spector K *et al.* 2006; Summerfield C et al. 2008; De Baene W and R Vogels 2010; Weiner KS *et al.* 2010; Gotts SJ et al. 2012; Henson RN 2016; Vogels R 2016; Alink A *et al.* 2018). To date, most empirical data testing these theories have largely examined the effect of repetition on the magnitude of responses, as the prevalent scaling and sharpening models make specific predictions about the amplitude, rather than timing of RS. Consistent with both the scaling and facilitation models, we find lower PM and AUC for the second versus the first presentation of a face.

As the facilitation model is the only model that makes specific predictions about the time course of repetition effects, we leveraged the millisecond temporal precision of intracranial recordings to examine the time course of neural responses to repeated images. In doing so, we could consider how our findings relate to temporal dynamics associated with the facilitation model, different variants of which predict (a) a faster (Henson RN and MD Rugg 2003; James TW and I Gauthier 2006) response onset latency (ROL), (b) an equal (Henson RN 2012, 2016) ROL, (c) an earlier peak timing (Henson RN and MD Rugg 2003; Henson RN 2016), or (d) a shorter response duration (Henson RN 2016) for repeated presentations irrespective of the repetition paradigm. Intriguingly, our results provide the first empirical support for the timing predictions of the facilitation model during long-lagged stimulus repetitions. Specifically, our data showed features consistent with predictions of Henson and Rugg (2003): (i) repetition of

faces produced neural responses that were faster to peak and (ii) the area under the neural response curve was smaller for repeated compared to non-repeated stimulus presentations.

We also note that 3 electrodes show a weak enhanced response to the 2nd versus 1st presentation. Notably, the first time point showing significant enhancement appeared later in the trial (on average ~375 ms) as compared to significant RS electrodes (on average ~150 ms) after stimulus onset. These varied temporal profiles of repetition suppression versus enhancement may suggest different mechanisms such as bottom-up implicit memory signals in RS compared to top-down feedback signals driving enhancement (Cheal M et al. 1991; Pinto Y et al. 2013).

While some studies have suggested that the predictability of repetition is a key feature driving RS especially for faces (Summerfield C *et al.* 2008), we believe that predictability is an unlikely explanation underlying the different temporal features of neural responses during repeated compared to non-repeated conditions for three main reasons. First, participants were unaware when repetitions were going to occur in our paradigm and there was an equal occurrence of repeated and non-repeated images throughout the experiment, thereby controlling for repetition likelihood. Second, subjects participated in an orthogonal fixation task, which did not require top-down attention on the face images. Third, reported effects of stimulus predictability on the magnitude of RS are inconsistent across studies, stimuli, and measurements (Kaliukhovich DA and R Vogels 2011; Kovacs G et al. 2013; Tang MF et al. 2018; Vinken K et al. 2018). Thus, while the prediction error account for RS is an appealing hypothesis, it does explain the presence of RS during our long-lagged paradigm.

A theoretical implication resulting from comparing our findings to previous work is that different experimental paradigms may affect different features of the temporal dynamics of neural responses in VTC. For example, while we found no effect of repetition for ROL, previous

intracranial studies recording from VTC in humans (Rodriguez Merzagora A *et al.* 2014) Engell & McCarthy, 2014) and non-human primates (McMahon DB and CR Olson 2007; Anderson B et al. 2008; De Baene W and R Vogels 2010; Engell AD and G McCarthy 2014) have shown delayed ROL. As such, future modeling work should take into consideration how the nature of stimulus repetition may affect the temporal properties of the response such as ROL and PT. For instance, previous work has shown delayed ROLs in VTC for immediate stimulus repetitions with no intervening stimuli and less than 2 seconds between repetitions implemented in short-lagged paradigms (Anderson B *et al.* 2008; De Baene W and R Vogels 2010; Engell AD and G McCarthy 2014). This suggests that immediate repetitions and long-lagged repetitions with intervening stimuli (as in the present study) may have different temporal characteristics. This implies the possibility that different neural mechanisms may lead to the differential temporal effects across repetitions given varied stimulus timing parameters. Future studies can test this hypothesis by systematically varying the interval between repetitions of the same stimuli, measuring how timing properties affect the temporal characteristics of the neural response, and using computational encoding models to understand the temporal features of stimulus repetitions (Stigliani A et al. 2019). Additionally, as RS effects vary across brain regions (Verhoef BE *et al.* 2008; Weiner KS *et al.* 2010), future studies are needed to a) determine if the facilitation of the PT observed here is prevalent across other regions or is specific to human VTC and b) explore the dynamics of repetition effects using other visual categories and for non-visual domains.

Conclusion

In sum, neural RS is a pervasive effect across high-level visual regions in cortical sensory systems. Understanding and characterizing RS dynamics – across temporal and neuroanatomical

spatial scales – serves as a window to understand how cortical responses depend on the history of a stimulus, which has direct implications for modeling neural systems subserving mechanisms of learning, memory, and perception. Here, we leveraged the precise spatial localization and high temporal resolution of ECoG from 9 human subjects implanted with intracranial electrodes in VTC to measure the effects of stimulus repetition after tens of seconds. Our approach revealed that RS (a) occurs in VTC activity in HFB range, but not lower frequency bands, (b) is associated with lower peak magnitude, lower total responses of the HFB signal, and earlier peak responses, and (c) RS effects occur early (~150 ms) and persist for the entire stimulus duration. Together, these data empirically support predictions of the facilitation model of RS and motivate future empirical and theoretical work examining the effects of stimulus repetition on neural responses not only within VTC, but also throughout the brain and in other sensory and non-sensory domains.

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Figure Legends

Figure 1: Design of repetition suppression (RS) long-lagged experiment. All 9 participants viewed images of cars, body parts, faces, and houses. Images were presented for 1 second with a randomized inter-stimulus-interval (ISI) ranging between 600-1400 ms. The average time between repeats was 27.5 ± 8.59 seconds. *Task:* participants were instructed to press a button on a keypad when the central fixation cross changed color from white to red. Example image sequences are shown below each experiment with colored letters indicating the stimulus category (F: faces; B: body parts; C: cars; H: houses) and numbers indicating the exemplar identity (e.g., F1 is face, exemplar number 1).

Figure 2. Face-selective electrodes in ventral temporal cortex. (A) All electrodes from the ventral temporal cortex (VTC) were projected into MNI space and illustrated on the Colin Brain cortical surface. The color and size of the electrode indicate their degree of face-selectivity, measured in the high frequency broadband (HFB, 70-150Hz) range. That is, larger size and brighter color indicates larger face selectivity (see colorbar). Face-selectivity was determined in each electrode by comparing the average magnitude of HFB response for faces versus non-faces during a time interval of 0 to 0.5 s. This selectivity was determined using independent trials during the long-lagged experiment which contained stimuli that appeared only once during the experiment. *Yellow electrodes* showed significantly higher HFB responses to faces than nonfaces (t-value, FDR corrected $p<0.05$). *Black electrodes* did not show significant selectivity to faces. We identified a total of 48 face-selective electrodes in VTC, which were anatomically positioned on the fusiform gyrus (FG) and occipito-temporal sulcus (OTS) across the 9 subjects. On average, there were 6 ± 4 face-selective electrodes per subject. All subjects had at least 1 face-selective electrode (B) Average HFB responses across items of a category in an example

electrode (green outline in A) located near the mid-fusiform sulcus (MFS). Dashed vertical lines indicate onset and offset of the stimulus.

Figure 3. Repetition suppression (RS) in human VTC occurs in HFB, but not lower frequency bands, for repetitions between images. Average responses to first (red) versus second (blue) face presentations across frequency bands. From top to bottom, frequencies are theta (Θ: 4-8 Hz), alpha (α: 8-13 Hz), beta (β: 16-30 Hz), and high frequency broadband (HFB: 70-150 Hz). Shaded error indicates standard error across 48 face-selective electrodes.

Figure 4: Quantifying the effect of repetition on the magnitude and timing of HFB responses

(A) Schematic illustration of four metrics of the HFB signal that were calculated or each of the 48 face-selective electrodes*:* (1) Total HFB response, which is the area under the response curve (AUC) from 0-900 ms (light red), (2) peak magnitude (PM), (3) response onset latency (ROL), and (4) peak timing (PT).

(B) Difference in Total Response (AUC) (2nd presentation – 1st presentation) for faces.

(C) Peak Magnitude (PM) difference (2nd presentation – 1st presentation) averaged over a 10 ms window surrounding the peak.

(D) Response Onset Latency (ROL) difference (2nd presentation – 1st presentation).

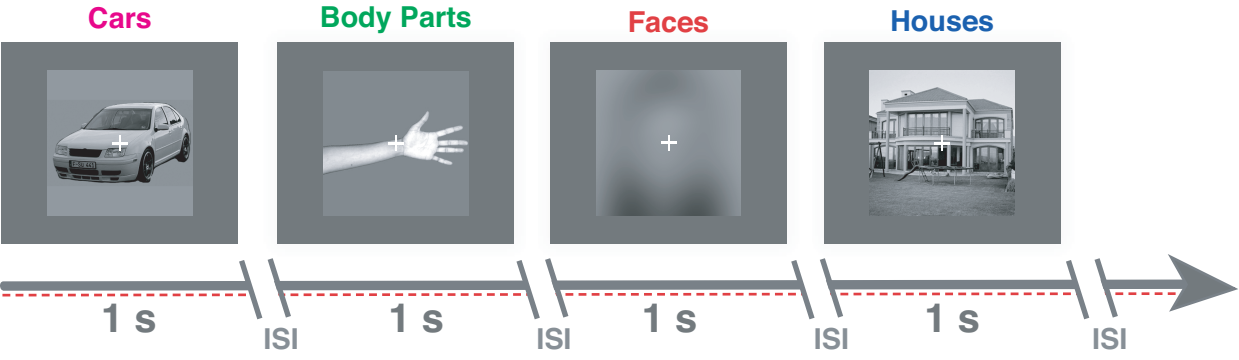
(E) Peak Timing (PM) difference (2nd presentation – 1st presentation).

In B-E, each point is an electrode. Negative values (blue) indicate decrements, while positive values (red) indicate increments. Vertical line indicates mean across electrodes.

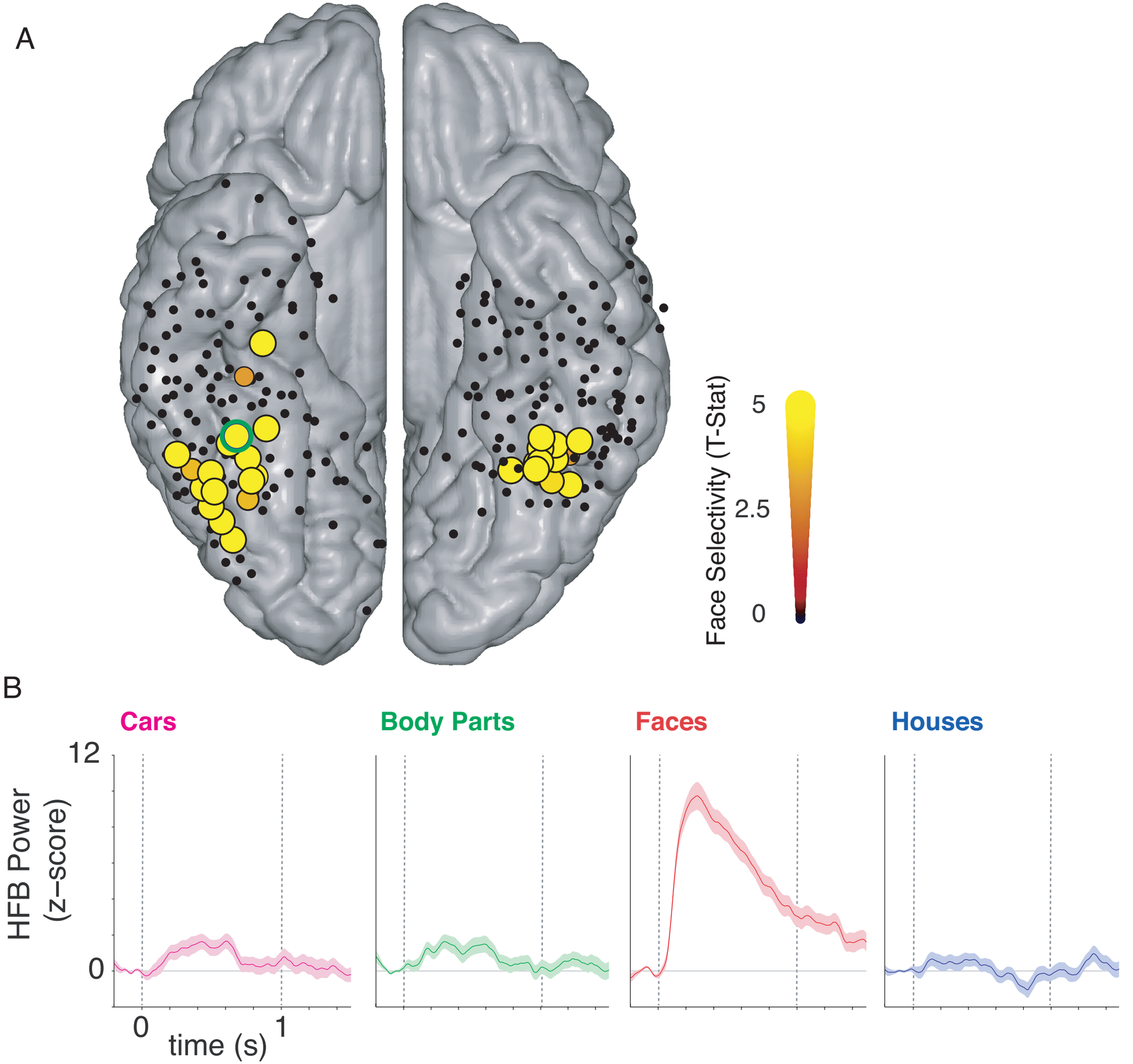
Movie 1: The temporal dynamics of average RS in each of the 49 face-selective electrodes are presented on the MNI averaged brain. The spatial-temporal distribution of RS is visualized and corrected for electrode overlap density. For display purposes, the additive spatial

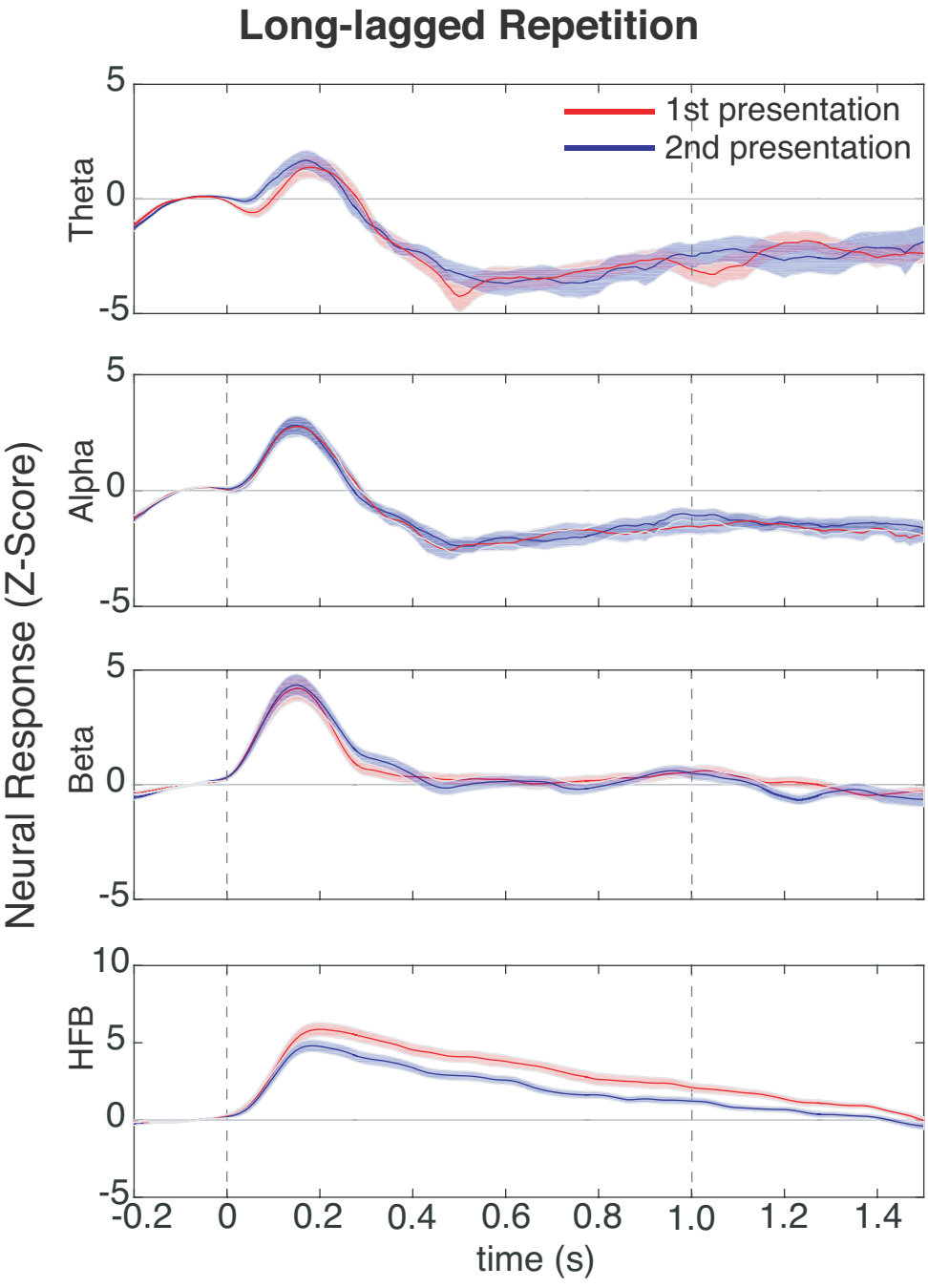
distribution of t-values are scaled to the same maximum (2, red) and minimum (-2, blue), as well as corrected for the spatial distribution of included electrodes. Electrode locations for all subjects are overlaid to display the temporal evolution of RS. The video is slowed down 10 times for ease of viewing.

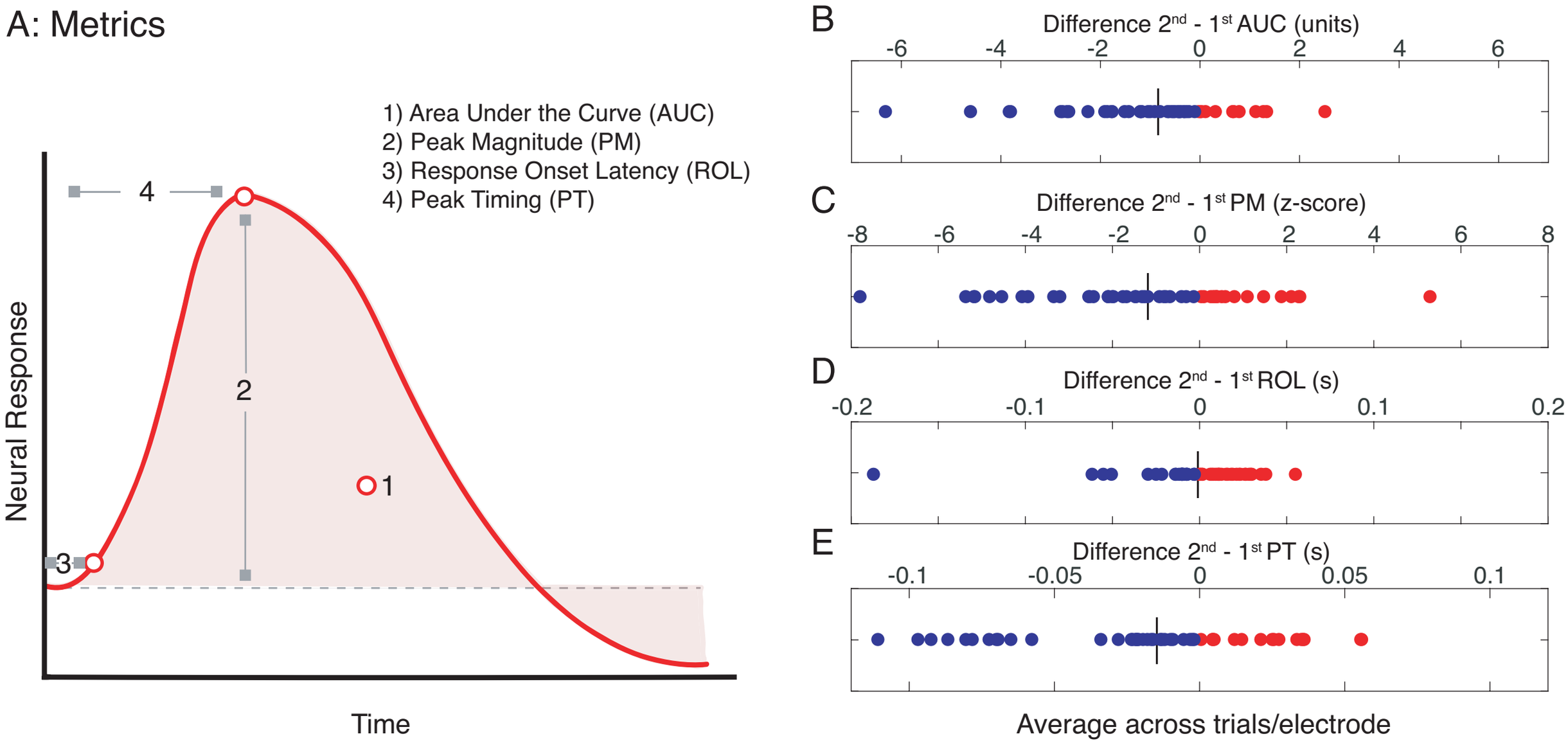
Long-lagged Repetition (27.5 sec avg ISI)



Sequence: C1 B1 F1 H1 B1 C1 B2 F1 H1 F2 B2 F2 B3 H2 F3


A
Face Selectivity (T-Stat)
5
2.5
0
B
Cars
Body Parts
Faces
Houses
12
0
HFB Power
(z–score)
0
1
time (s)


Long-lagged Repetition
1st presentation
2nd presentation
Theta
Alpha
Beta
HFB
Neural Response (Z-Score)
5
0
-5
10
-0.2
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
time (s)


A: Metrics
1) Area Under the Curve (AUC)
2) Peak Magnitude (PM)
3) Response Onset Latency (ROL)
4) Peak Timing (PT)
Neural Response
Time
B
Difference 2nd - 1st AUC (units)
C
Difference 2nd - 1st PM (z-score)
D
Difference 2nd - 1st ROL (s)
E
Difference 2nd - 1st PT (s)
Average across trials/electrode