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# The physiology of perception in human temporal lobe is specialized for contextual novelty

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**Miller KJ, Hermes D, Witthoft N, Rao RP, Ojemann JG.** The physiology of perception in human temporal lobe is specialized for contextual novelty. *J Neurophysiol* 114: 256–263, 2015. First published May 13, 2015; doi:10.1152/jn.00131.2015.—The human ventral temporal cortex has regions that are known to selectively process certain categories of visual inputs; they are specialized for the content ("faces," "places," "tools") and not the form ("line," "patch") of the image being seen. In our study, human patients with implanted electrocorticography (ECoG) electrode arrays were shown sequences of simple face and house pictures. We quantified neuronal population activity, finding robust face-selective sites on the fusiform gyrus and house-selective sites on the lingual/parahippocampal gyri. The magnitude and timing of single trials were compared between novel ("house-face") and repeated ("face-face") stimulus-type responses. More than half of the category-selective sites showed significantly greater total activity for novel stimulus class. Approximately half of the face-selective sites (and none of the house-selective sites) showed significantly faster latency to peak (~50 ms) for novel stimulus class. This establishes subregions within category-selective areas that are differentially tuned to novelty in sequential context, where novel stimuli are processed faster in some regions, and with increased activity in others.

adaptation; vision; face processing; temporal cortex; electrocorticography; broadband

TEMPORAL AND SPATIAL CONTEXT shape the neurophysiology of the visual stream at every level (Kandel and Schwartz 2000). Early visual areas adapt their firing thresholds in response to persistent simple image features such as orientation and contrast. Deep in the hierarchy of visual perceptual processing are regions that show selective responses to certain object classes, although how they are influenced by temporal context is not well-known (Ishai et al. 1999; Spiridon and Kanwisher 2002). The most well-described of these are the "place" and "face" loci of the ventral occipitotemporal cortex. In these regions, repeated presentation of the same faces, houses, and other familiar stimuli is associated with reduced metabolic expenditure (as measured by PET and fMRI) (Grill-Spector et al. 2006; Kanwisher et al. 1997; Koutstaal et al. 2001; Schacter et al. 2004).

The hemodynamic response acts as a low-pass filter, smearing neuronal activity over several seconds (Kim et al. 1997), but the perception of individual objects occurs at tens to hundreds of milliseconds (Keysers et al. 2001). Therefore, while fMRI has proved a valuable tool for studying sequential context in the human brain, its relatively low temporal resolution has necessarily left unanswered a number of important questions about the nature and mechanisms underlying adaptation. For example, some researchers have proposed that adaptation in fMRI reflects facilitated processing, meaning that information is accumulated more rapidly with repetition, resulting in a reduced response (James and Gauthier 2006). This hypothesis cannot be evaluated at the temporal resolution of fMRI. However, with the ability to look at faster cortical dynamics, one might address this and other questions, such as: how do ventral temporal dynamics change for repeat vs. novel presentation of a stimulus type? Is the single-trial response magnitude smaller? Is the neural processing slower? Is it more sustained? Can repetition effects be seen in less than a second? If present, are these universal properties of class-specific ventral temporal processing, or are they limited to a subset of class-selective regions?

To address these questions, we measured human electrocorticographic (ECoG) responses while patients were shown a rapid, random sequence of different pictures of faces and houses. Broadband ECoG potential change is thought to reveal averaged neural population activity with 20–40 ms resolution (Miller et al. 2009b). This time scale is propitious, because the speeds of perception, decision, and action are all of this order or slower. What we found was compelling: more than half of the category-selective loci showed significantly greater activity for novel than for repeated stimulus class. Approximately half of the face-selective sites showed that latency to peak activity was longer for repeat relative to novel stimuli (total activity and latency effects were uncorrelated), disproving the hypothesis that neural adaptation reflects faster processing of incoming stimuli. These observations show that ventral temporal physiology is differentially tuned to sequential context, with an emphasis on accentuating novelty.

## METHODS

*Subjects.* Cortical surface potentials were measured during simple visual tasks in 18 epileptic patients who underwent craniotomy and placement of intracranial subdural electrode for seizure localization (Harborview Hospital, Seattle, WA). Only the 11 that had at least one face- or house-selective site were included. Electrode placement location and implantation duration were determined by clinical criteria only (without consideration for this study). The arrays were typically placed for 5–7 days, with experiments on *days 3* to *5*. Participants gave informed consent for the study through a protocol approved by the University of Washington.

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*Recordings.* The platinum electrode arrays (Ad-Tech, Racine, WI) were configured as linear strips or grids. Linear platinum electrode strips (embedded in Silastic, 1 cm spacing, 4 mm diameter with 2.3 mm exposed) were placed along the inferotemporal subdural space via either burr holes or craniotomies (Fig. 1, *A* and *C*). In parallel with clinical amplifiers, ECoG signals were sampled at 1,000 Hz, band-passed from 0.3 to 200 Hz using Synamps2 amplifiers (Neuroscan, El Paso, TX), and then passed to BCI2000 software (Schalk et al. 2004). Postimplant CT was projected and resliced into preoperative axial-T1 MRI for determination of electrode location relative to gyral surface anatomy (Ashburner and Friston 2005; Hermes et al. 2010; Wells et al. 1996), and only ventral temporal electrodes were examined.

*Task.* Subjects were shown a random sequence of simple grayscale faces and houses (luminance and contrast matched) with blank inter-stimulus interval (ISI) (400 ms on/off, Fig. 1). At the bedside, 10-cm-wide pictures were displayed at ~1 meter away. There were three experimental runs, each with 50 different houses and 50 different faces. To maintain fixation on the stimuli, patients reported a simple upside down house target once each run (all subjects without reporting error).

*Data analysis.* After visual rejection of artifactual or epileptiform electrodes, the scalp-referenced ECoG potentials were rereferenced with respect to the common average (Fig. 1). From each electrode, samples of power spectral density (PSD) were calculated from 1-s epochs centered at the midpoint of each picture presentation or ISI and then decomposed using a singular value decomposition to find underlying spectral motifs (fully illustrated for this context in Miller et al. 2014, originally in Miller et al. 2009b). The first motif is reliably broadband in nature and has been shown to correlate with neuronal firing rate (Manning et al. 2009; Miller et al. 2009a). This first motif was projected to the normalized dynamic spectrum and smoothed (Gaussian envelope, SD 80 ms) to obtain the time course of broadband spectral change [in normalized units ("NU")].

Single-trial response magnitude [total activity ("TA")] is the average of the broadband time series from 100 to 400 ms into each stimulus or ISI. Latency to peak activity (in ms) is the time from stimulus onset until the highest peak of the broadband time series (within 800 ms, includes ISI). The response duration (in ms) is the sum of the broadband time series over the 800-ms interval following stimulus onset, divided by the magnitude of the peak broadband within that interval [commonly referred to as the "integration time" (Kraft et al. 1993)].

Individual distributions are initially compared by unpaired *t*-test. For identification of visually responsive and category-selective sites, TA was compared for face vs. ISI, house vs. ISI, and face vs. house trials, and Bonferroni-Holm corrected for multiple comparisons, adjusted for the total number of subtemporal sites in each subject. Additionally, only "robust" face vs. house cortical sites (TA squared-cross-correlation: $r^2 > 0.08$, which was roughly two times the threshold level met at minimum statistical significance) were deemed category selective. For total activity and latency, marked novel vs. repeat stimulus effects were present, with the same direction of effect

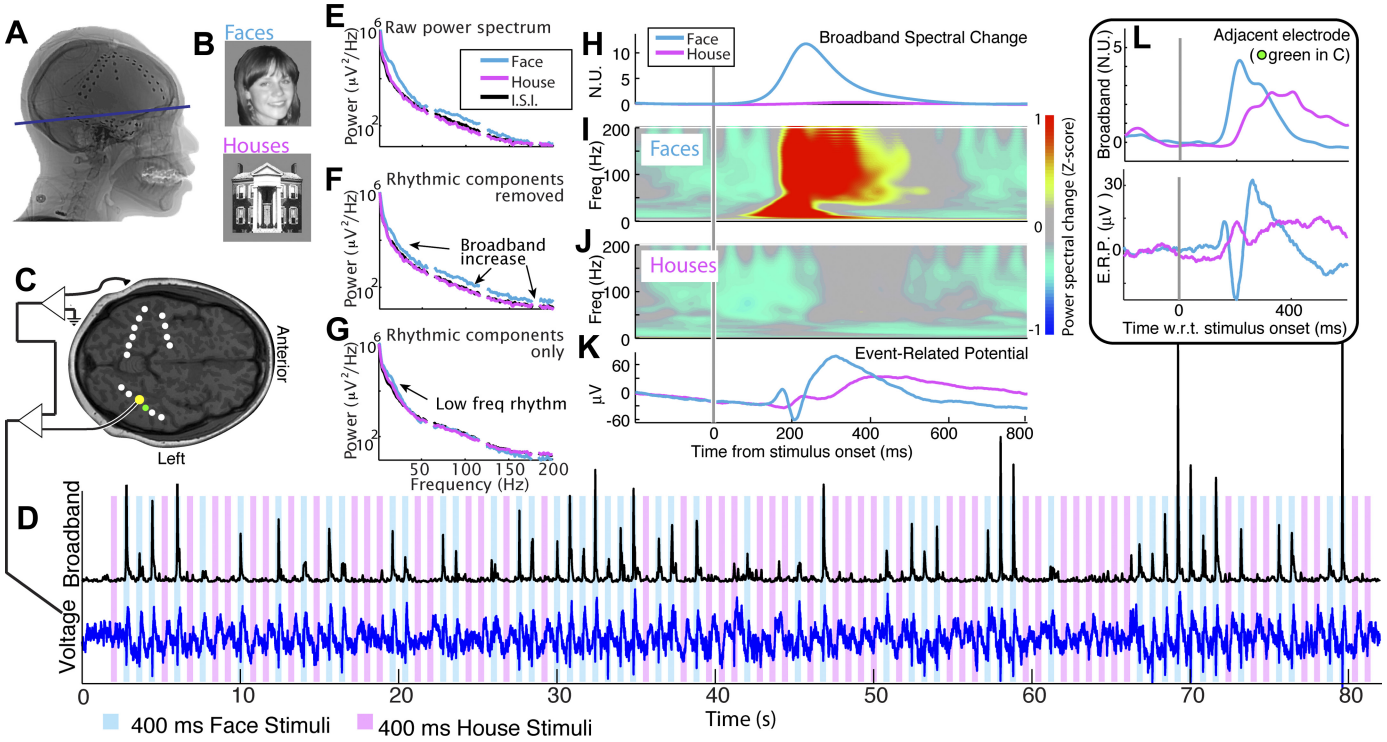


Fig. 1. Electrocorticographic (ECoG) measurement of category-selective ventral temporal visual response (*subject 1*). *A*: ECoG strips were slid inferotemporally via burr holes/craniotomies (here with coverage of other regions also). *B*: simple face/house pictures were shown in random order for 400 ms each (with 400 ms ISIs). *C*: an axial magnetic resonance image (MRI, at blue line in *A*) shows electrode sites with respect to ventral temporal gyral anatomy. *D*: a real-time extraction of broadband spectral change (black trace) from the raw potential (blue trace) at a fusiform electrode (yellow in *C*) is seen for an ~80-s period. There is a dramatic and robust response to face stimuli (blue background), and not house stimuli (pink). *E*: the averaged power spectral densities (PSD) from the voltage time series, for segments of time during face/house/ISI (blue/pink/black). *F*: PSDs from individual trials were decomposed using a singular value decomposition to reveal underlying motifs. When the 2nd to 4th (rhythmic) motifs are removed, face-specific broadband spectral increase is revealed across all frequencies. *G*: isolation of the 2nd to 4th motifs shows narrowband 4- to 20-Hz changes ($\theta$-/$\alpha$-/$\beta$-rhythms). *H*: stimulus-triggered average broadband time series in response to face (blue) and house (pink) stimuli reveals a robust face-selective response. *I*: face stimulus-triggered average dynamic spectra (spectrogram) showing the low-frequency spectral changes associated with the raw potential deflection, as well as strong, sustained, broadband spectral change. *J*: house stimulus-triggered average dynamic spectra, without significant change. *K*: stimulus-triggered average raw voltage time series [event-related potential (ERP)] in response to face and house stimuli revealing the classic N200 face response. *L*: the average broadband and ERP in a neighboring electrode demonstrating that the N200 response in the ERP does not guarantee face selectivity.

for >50% of category-selective sites so correction for multiple comparisons is not appropriate in that setting.

## RESULTS

*ECoG responses to simple face and house picture stimuli.* Electric potentials were measured from ventral-temporal ECoG sites while patients performed a simple task watching pictures of faces and houses, interleaved with ISI of equal length (400 ms, Fig. 1, *B–D*). PSD changes during face-picture presentations, in face-selective sites, show changes in low-frequency rhythms, as well as strong, sustained, broadband spectral change (example shown in Fig. 1, *E* and *I*). With the use of a principal component-type decomposition of the PSD, this broadband is shown to extend across all frequencies, and to be separable from low-frequency rhythmic elements (Fig. 1, *F* and *G*) (Miller et al. 2014; Miller et al. 2009b). Projection of the broadband motif into the dynamic PSD specifically captures the dynamics for processing of individual categories of visual stimuli with robust temporal fidelity (Figs. 1, *D* and *H*, and 2, *B*, *C*, and *F*). As in previous EEG, MEG, and ECoG studies (Allison et al. 1994; Ghuman et al. 2014; Harris and Nakayama 2007; Kadipasaoglu et al. 2014), we often observe a classic face-specific "N200" event-related potential (ERP) from the lateral occipitotemporal (fusiform) gyrus, although it was absent from many face-selective sites. Comparison with the broadband time course reveals that this face-specific N200 does not guarantee face selectivity (Fig. 1*L*). The biological interpretation of face-responsive ERPs is unclear, and recent ECoG work has shown that attenuation in this ERP is distinct from attenuation in overall neuronal activity (Privman et al. 2011). We therefore decided to focus exclusively on the broadband response, which has been directly linked to aggregate firing rate (Miller et al. 2014).

Of 258 total subtemporal electrodes in 11 subjects (Figs. 3*A* and 4*G*), 19 were face selective (multiple-comparison corrected $P < 0.05$ for both faces vs. ISI and faces vs. houses, and $r^2 > 0.08$ for faces vs. houses), 17 were house selective (same criteria), and 23 were visually responsive but nonselective

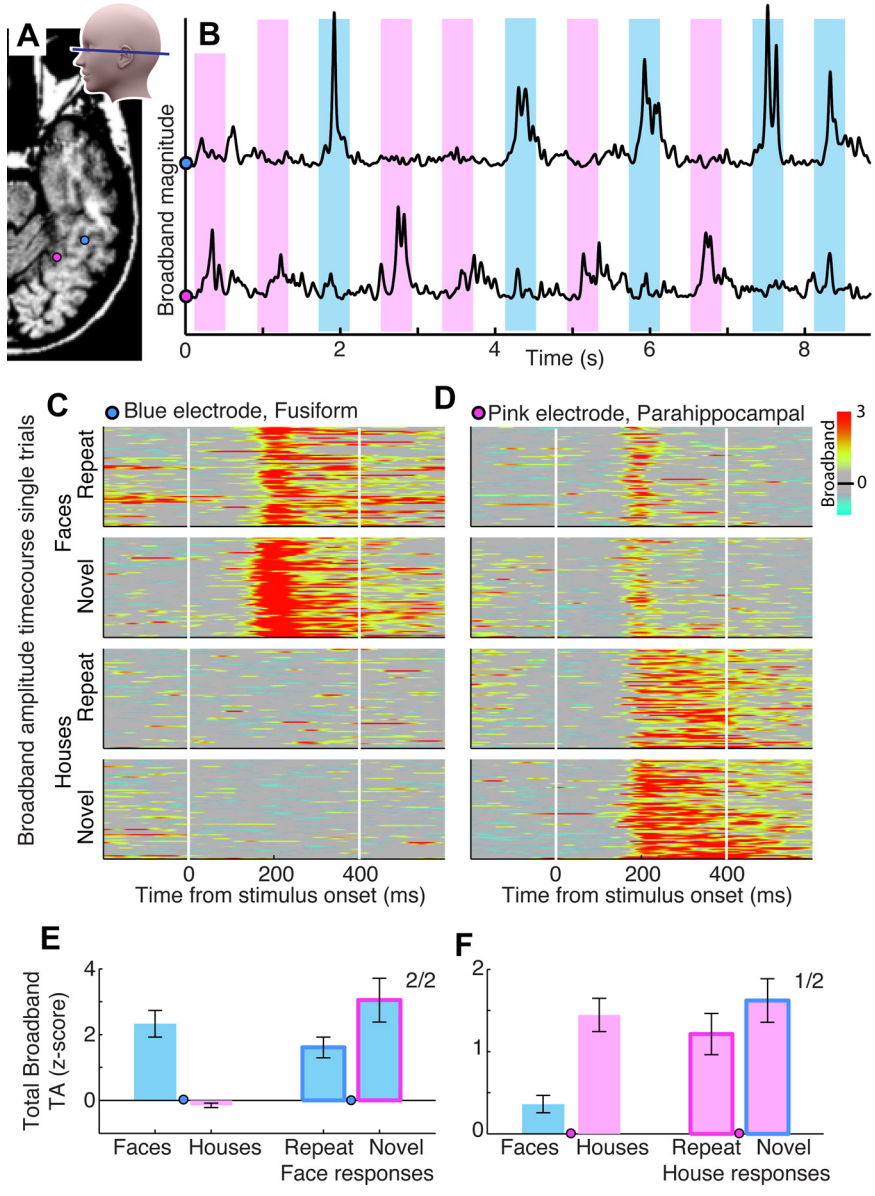


Fig. 2. Novelty effect in the category-specific response magnitude, *subject 2*. *A*: a medial, parahippocampal, electrode (pink) and a lateral, fusiform, electrode (blue) are shown in situ. *B*: broadband time series (black traces) from the sites in *A*, with 400-ms face (blue) and house (pink) picture presentation times. Note that the fusiform trace is face selective, and the parahippocampal site is house selective. *C*: single-trial rasters of all broadband responses from the fusiform site, sorted by prior stimulus [color scale truncated at normalized units (NU) = 3]. The four clusters, from *top* to *bottom* are faces following faces, faces following houses, houses following houses, and houses following faces. Vertical white lines indicate stimulus onset/offset. The novelty effect is visible by eye when comparing the top two rasters. *D*: as in *C*, for the parahippocampal electrode. *E*: bars on *left*, averaged fusiform site broadband responses from 100 to 400 ms following each stimulus for all face stimuli [blue bar on *left;* total broadband response activity (TA)] compared with all house stimuli (pink bar on *right*), error bars = 3 × SE. Faces significant vs. houses as well as ISI ($P < 10^{-6}$, after correction, for each, $r^2 = 0.75$ faces vs. houses). *Right*, face responses, sorted as novel (following previous house, bar on *right*/pink outline) or repeat (following previous face, bar on *left*/blue outline). The novelty effect is strong and significant ($P < 10^{-6}$, uncorrected, $r^2 = 0.20$ novel vs. repeat faces). The "2/2" indicates there are two face-selective sites for this patient, and both show the novelty effect (at least $P < 0.05$). *F*: as in *E*, for the parahippocampal site (class selective at $P < 10^{-6}$, corrected, $r^2 = 0.41$ faces vs. houses). Sorted house responses (bars on *right*) show a significant novelty effect ($P < 10^{-3}$, uncorrected, $r^2 = 0.07$ novel vs. repeat houses). The "1/2" indicates that only one of two house-selective sites shows the significant class-specific novelty effect at $P < 0.05$.

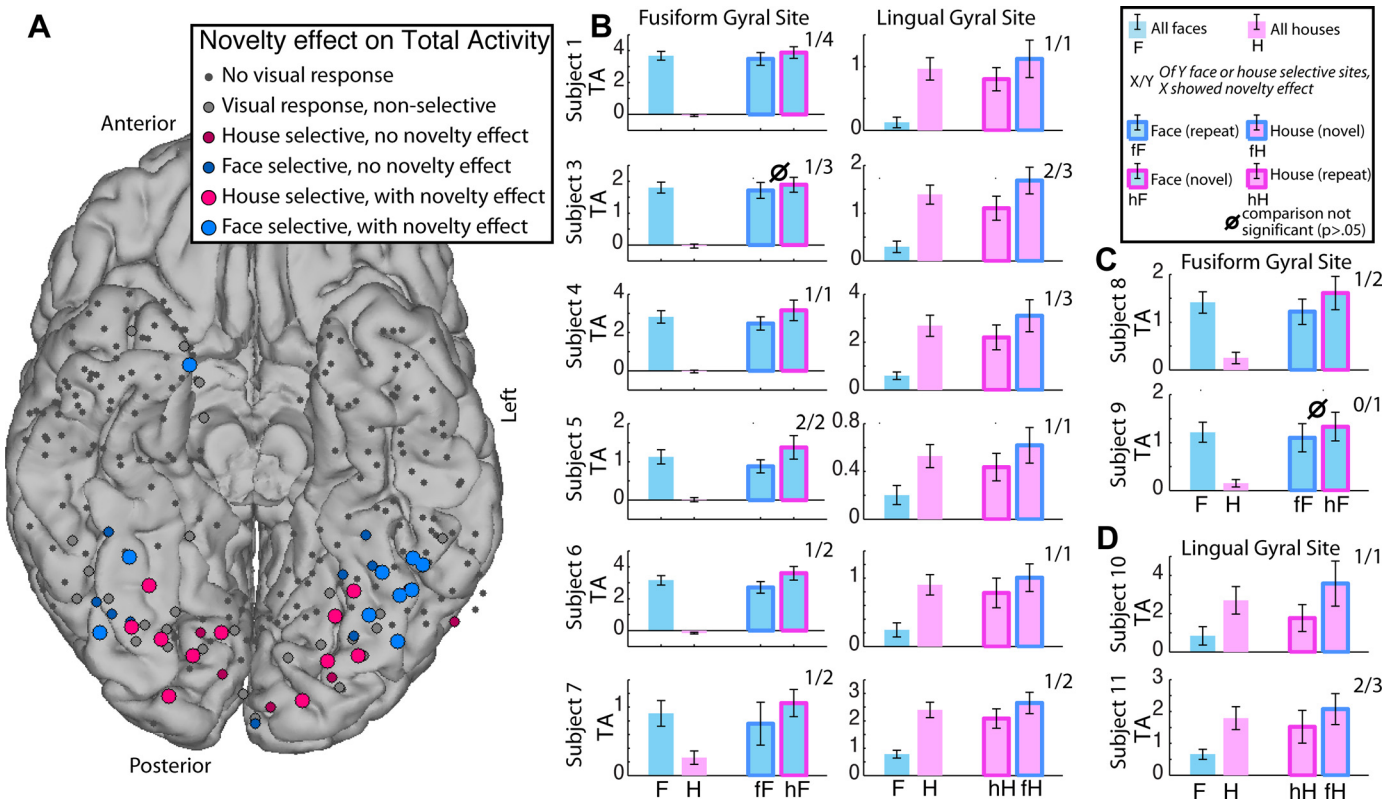


Fig. 3. Novelty effect on total activity, across subjects. *A*: electrode sites with selectivity and novelty (all plotted on MNI atlas here, but anatomy otherwise determined on actual MRI for each subject). Nearly all face- or house-responsive sites were on the posterior inferotemporal surface, and nonselective (face vs. house) electrodes were intermingled among category-selective sites. Although there was a general organization of faces lateral to houses, there was not a robust spatial relationship between sites with a novelty effect vs. those without. *B*: examples of face- and house-selective sites with significant novelty effect (*subjects 1* and *3-7*). As in Fig. 2, *bottom*, the two columns on the *left* show an example face-selective site from the fusiform gyrus, and the two columns on the *right* show an example house-selective lingual gyral site. Bar plots show broadband responses, clustered by stimulus type (F, all faces; H, all houses; fH, houses that follow faces, etc.). To the *top right* of the axes, the number pair separated by a forward slash indicates the number of sites that had the novelty effect out of the total number of selective sites for each type. The circle-slash indicates that the category-selective site did not have a significant novelty effect. *C*: face-selective fusiform gyral site (as in the column on the *left* in *B*) for *subjects 8* and *9*, where there were no house-selective sites. *D*: house-selective lingual gyrus site (as in the column on the *right* in *B*) for *subjects 10* and *11*, where there were no face-selective sites.

(corrected $P < 0.05$ vs. rest for each, and $r^2 < 0.08$ for faces vs. houses). Face-selective sites (mean $|x| = 34$ mm, $\pm$ SD 11 mm; mean $y = -55 \pm 19$ mm; MNI space) were consistently lateral ($P = 0.010$) and anterior ($P = 0.003$) to house-selective sites ($|x| = 23 \pm 13$ mm; $y = -72 \pm 10$ mm).

The subtemporal cortex was hand-parcellated into 7 gyral domains on each patient's magnetic resonance imaging (MRI), per Destrieux et al. 2010: of 47 total temporal pole sites, 1 was face selective and 1 was visually responsive but nonselective; of 21 middle temporal gyrus sites, 1 was visually responsive but nonselective; of 50 inferior temporal gyrus sites, 3 were visually responsive but nonselective, and 1 was house selective; of 8 inferior occipital gyrus sites, 1 was face selective, 1 was house selective, and 1 was visually responsive but nonselective; of 39 sites on the parahippocampal portion of the medial occipitotemporal gyrus, only 1 was house selective; of 44 sites on the lingual portion of the medial occipitotemporal gyrus, 9 were house selective, 1 was face selective, and 10 were visually responsive but nonselective; of 49 sites on the fusiform portion of the lateral occipitotemporal gyrus, 16 were face selective, 5 were house selective, and 7 were visually responsive but nonselective.

*Novel stimulus class augments total population activity.* As shown in Figs. 2 and 3, there is a significant effect of novelty on the category-specific response magnitude in roughly half of the face- and house-selective cortical sites. The aggregate neuronal activity, revealed by single-trial total integrated broadband ECoG power between 100 and 400 ms poststimulus onset (TA), was used to compare repeated within-class stimuli (face following previous face or house following house) vs. novel stimulus class (e.g., face following house or vice versa). What we discovered was a robust property of many category-selective sites. In 10 of 19 face-selective cortical sites, there was significantly less cortical activity for repeat stimulus class (face following face) than there was for novel stimulus class (face following house). For the 17 house-selective cortical sites, 11 showed less cortical activity for repeat stimulus class (house following house) than for novel stimulus class (house following face). A single site met significance criteria for an effect in the opposite direction (a house-selective site in *subject 11*). These results were unchanged if the whole 400-ms stimulus onset to offset is used, or if an 800-ms period from stimulus onset to the next stimulus onset, including the ISI, is used instead (data not shown).

There was no significant spatial clustering of sites that exhibited the novelty effect. The position of face-selective sites that had a significant effect of novelty on total activity (mean $|x| = 37$ mm, $\pm$ SD 8 mm; mean $y = -51 \pm 21$ mm; MNI

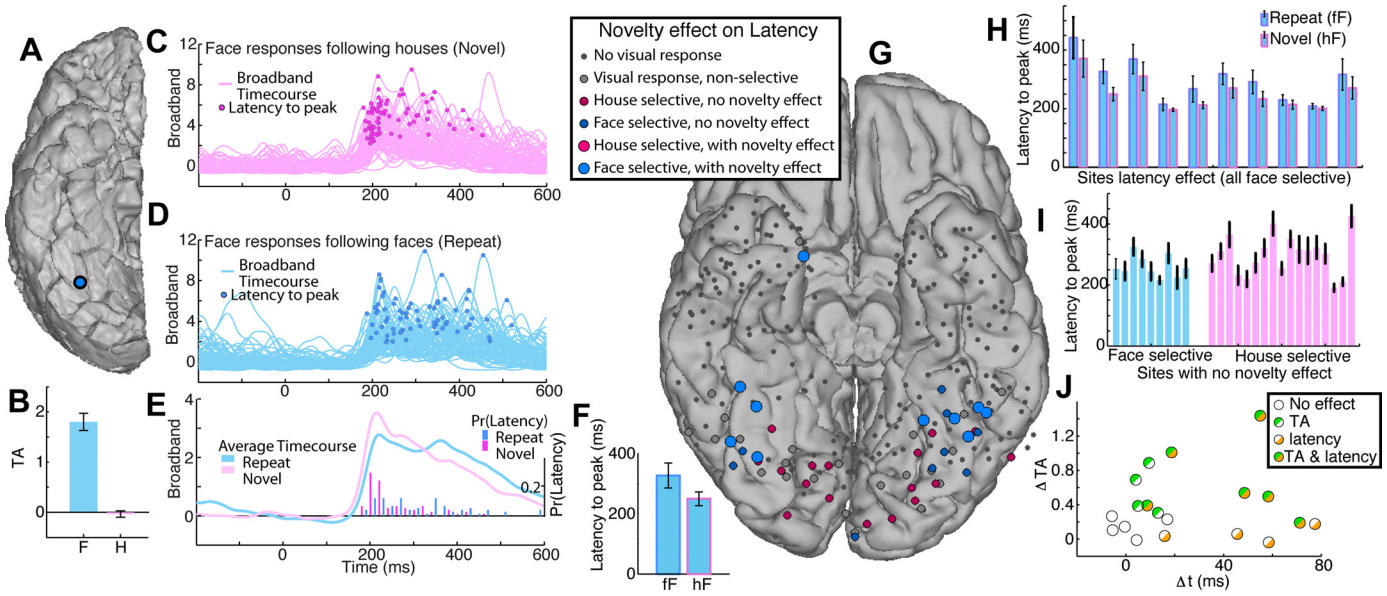


Fig. 4. Effect of previous stimulus on response timing. *A*: a fusiform site in *subject 3* is examined (*A–F*). *B*: this site is face selective, but it does not show novelty effect on total activity (data not shown). *C*: single-trial broadband traces to face stimuli that follow previous house stimuli. The time of peak activity from each single trial is shown with a pink dot. *D*: responses to repeated face stimuli (blue dot, peaks). *E*: averaged traces from *C* and *D*, with probability densities of peak times shown with bars beneath (20-ms bins). The novel responses are significantly quicker. *F*: average latencies to peak activity for repeat and novel class of stimuli (error bars 3 × SE), showing increase in latency for repeat stimulus class when compared with novel stimulus class ($P = 3 \times 10^{-6}$, uncorrected). *G*: topology of time to peak effect, all subjects (template brain, MNI atlas). There were novelty effects on latency to peak for 10 of the 19 face-selective sites but none for the house-selective sites. *H*: the latencies to peak for the 10 face-selective sites with significant novelty effect (error bars = 3 × SE). *I*: latencies for the remaining class-selective sites without significant novelty effect on latency. *J*: differences in TA vs. difference in latency, all face-selective sites, with coloring to indicate significant effect of previous stimulus for total activity or latency to peak. There is no simple correlation between the two.

space) and those that did not (mean $|x| = 30$ mm, ± SD 13 mm; mean $y = -60 \pm 16$ mm) was not significantly different in the $|x|$ or $y$ dimensions ($P = 0.16$ and 0.17, respectively). The position of house-selective sites that had a significant effect of novelty on total activity (mean $|x| = 22$ mm, ± SD 7 mm; mean $y = -71 \pm 10$ mm; MNI space) and those that did not (mean $|x| = 24$ mm, ± SD 20 mm; mean $y = -73 \pm 12$ mm) was not significantly different in the $|x|$ or $y$ dimensions ($P = 0.79$ and 0.17, respectively).

*Latency to peak activity is faster for novel stimulus class in some face-selective sites.* We measured how the class of previous stimulus affected the time to peak activity in the broadband response. Interestingly, there was a large discrepancy by stimulus class: in house-selective sites, there was no effect of previous class, but 10 of 19 face-selective sites showed longer latency to peak time if the face stimulus followed a face than if it followed a house ($P < 0.05$, Fig. 4). This effect was present within four of the nine subjects with face-selective electrodes (S1, 3/4 face-selective sites; S2, 2/2; S3, 3/3; and S5, 2/2). The mean difference between novel and repeat stimulus class responses in these 10 sites was 46 ms (SD ±24 ms; range 8–77 ms). The position of face-selective sites that had a significant effect of novelty on time to peak (mean $|x| = 36$ mm, ± SD 9 mm; mean $y = -47 \pm 19$ mm; MNI space) and those that did not (mean $|x| = 31$ mm, ± SD 13 mm; mean $y = -64 \pm 14$ mm) was not significantly different in the $|x|$ or $y$ dimensions ($P = 0.44$ and 0.49, respectively).

There is no straightforward explanation for why face-selective sites showed a latency effect and house-selective sites did not. Only 6 of these 10 sites were among the 10 face-selective sites with significant effect for total activity (with no correlation between magnitude of repetition effect between total activity and latency, Fig. 4*J*). There was no significant difference ($P = 0.14$) between latencies to peak for face-selective sites (269 ± 52 ms, range 205–406) compared with house-selective sites (299 ± 66 ms, 191–426). There was also no significant difference ($P = 0.30$) in the variance of the latency for face-selective vs. house-selective sites.

*Duration of response is occasionally affected by prior stimulus class.* A third parameter, the single-trial response duration, was estimated by dividing the total integrated activity from each trial by the peak activity in that trial (integration time). The average single-trial response durations within the 36 category-specific sites ranged from 61 to 170 ms (mean 117, SD 25) (no statistical difference in average response duration for face-selective vs. house-selective sites, $P = 0.84$). The response duration of the stimulus-averaged broadband time series is much longer than the average of single-trial response durations because the average broadband time series is more reflective of the probability distribution of peak responses than it is a scaling of the typical single-trial time course (an example of this can be seen by inspection of Fig. 4, *C* and *E*).

Of these 36 sites, 5 showed longer response duration for novel than repeat class of stimulus ($P < 0.05$, uncorrected, 4 house selective), and 2 showed longer response duration for repeat than novel stimulus class ($P < 0.05$, uncorrected, both face selective). Unlike total activity and latency to peak, the effect is not robust in one direction and is a rare event. As such, it should be subject to correction for multiple comparisons, after which only three of these sites remain significant (each by large margin, but these have no common thread).

Alternately, a different metric for response duration could be used, such as activity above a threshold fraction of the peak of the mean response (as in Rodriguez Merzagora et al. 2014). If

such an approach is applied to single trials, and compared for novel vs. repeat class of stimulus, findings are similarly sparse. Unlike our minimal effect findings, the work of Merzagora-Rodriguez and colleagues found that duration of suprathreshold activity (in averaged response) was found to be less for repeated than novel stimuli [during a letter-based working memory study (Rodriguez Merzagora et al. 2014)]. Because of the difference in experimental paradigm, and the use of averaged responses, with statistical comparison across electrodes, there is no direct explanation for the disparate findings.

## DISCUSSION

Measurement of broadband ECoG change revealed robust fusiform face-selective loci and parahippocampal/lingual place-selective loci across 11 human participants. More than half of these face- and place-selective loci showed significantly greater activity for novel than for repeated stimulus class type in the image sequence. Of all the face-selective sites, approximately half showed shorter latency to peak activity for the novel stimuli.

Experimental and modeling work has established a direct connection between neuronal population firing rate and broadband ECoG spectral change (Manning et al. 2009; Miller et al. 2009a). Because reliable methods have been developed for estimating the time series of this broadband, clinical ECoG measurement now sit in a middle ground ("Goldilocks zone") of experimental settings, making it ideal to study the physiology of perception. The timing of action potentials in single neurons in these cortical regions is stochastic and Poisson distributed (Dayan and Abbott 2001), and so averaging over units in an array or averaging over trials is necessary to determine the timing of responses. There are $\sim 5 \times 10^6$ neurons in the cortex beneath each clinical ECoG electrode, and the broadband measure may be loosely thought of as a real-time summation of this population's firing raster (i.e., intrinsically averaged). Because broadband reflects averaged neuronal population activity, the continuous signal is robust, and context-specific physiology can be resolved without averaging, on the subsecond time scale of single events, where conscious perception occurs (Miller et al. 2014). The spatial scale of cortical columns is not drastically smaller than the exposed ECoG electrode surface, so "local" physiology correlated with a particular brain function is not drowned by the uncorrelated cortex surrounding it, as is often the case for EEG or MEG. The fMRI BOLD response, a temporally smeared reflection of metabolic demand, cannot resolve cortical responses on subsecond time scales and requires averaging many perceptual events to overcome signal to noise issues. Some recent ECoG studies have measured a high-frequency approximation (>40 Hz) of this broadband during ventral temporal processing of face images and have found robust responses (fully separable from ERPs) that are invariant to individual faces (Ghuman et al. 2014; Privman et al. 2011; Vidal et al. 2010). Our work builds upon this by quantifying broadband responses to single trials, revealing how immediate sequential context influences the neuronal population dynamics while processing each image.

This simple experiment was tailored to capitalize on the unique properties of the ECoG spatiotemporal scale. The electrode size, placement, and spacing frequently revealed anatomically distinct face- and house-selective sites that correlate with known anatomic regions identified using fMRI. The simple grayscale picture sequence allowed for each cortical response to be described by three simple features: total activity, latency to peak, and response duration. Use of many different (nonrepeated) pictures minimized the influence of simple image features, assisted by a blank-screen ISI so images could not be directly compared during transition. Fixed timing was used to prevent confounding by temporal variation. It is a passive task, without choice, reward, or decision-making aspects. This task simplicity exposed stimulus-class novelty as a simple context to compare with measurement variation.

The finding of subsecond, within-category, attenuation to repeated stimuli suggests that at least some of the image-repetition adaptation in the fMRI metabolic response happens dynamically with individual percepts and is related to repeated stimulus type rather than repeat of single image. Adaptation effects have been shown to vary across regions of cortex. For example, longer adaptation times are required to produce a reduced fMRI response in V1 than in V4 (Fang et al. 2005). Differential effects of fMRI adaptation have also been observed between medial and lateral parts of the ventral temporal cortex (Weiner et al. 2010), using faces and houses as stimuli. Although using a very different paradigm, this corresponds to the anatomic locations of the place- and face-selective electrodes in this paper. Moreover, while the face and place electrodes are both defined using selectivity for a particular class of images, the underlying cortex is not the same in all other respects. For example, place- and face-selective responses are known to fall on parts of a large-scale eccentricity representation, with face responses aligned with foveally preferring responses and place-selective responses falling on peripherally preferring responses (Levy et al. 2001).

Cortical surface electrodes are more likely in the middle of centroids for face representation (which is in the crown of the gyrus) and more likely to be at the periphery of centroids for house representation (which are more likely to fall in the sulcus) (Grill-Spector and Weiner 2014). This may explain the lack of latency timing effect in house-selective sites. Furthermore, electrode position on the cortical surface is sparse because of the clinical placement, and so the relative clustering we see of timing effect within four subjects is likely due to difference in placement rather than interindividual variation.

The rapidity of the observed adaptation is too fast for synaptic depression, facilitation, or long-term depression, which have all been suggested as mechanistic explanations (Grill-Spector et al. 2006). Hyperpolarization across a neuronal population has been shown to be a mechanism for cortical adaptation to stimulus contrast in primary visual cortex (Carandini and Ferster 1997). Our finding that repeat stimulus class results in later (~50-ms) response suggests that this may be true for the class-selective adaptation we observe in the ventral temporal cortex. Much of our data also seem to be inconsistent with an "accumulation model" (James and Gauthier 2006), which predicts that less information needs to be accumulated for repeated stimuli and they will thus be processed faster. Our experiments demonstrate the opposite: in many ventral temporal face-selective sites, the time to peak activity is increased for repeated stimulus class (but we never saw the converse), and there were almost no findings of effect on response duration. This suggests that ventral temporal response attenuation to

repeated faces is about accentuating novelty in stimuli rather than optimizing efficiency in stimulus representation.

Interestingly, class-specific adaptation is only present in a subset of category-selective sites within each subject. In many face-selective fusiform sites, the time to peak processing of a face stimulus was found to be faster if preceded by a house stimulus, but the converse was never observed: it is unclear why this timing effect should be seen in the case of face-selective fusiform cortex, but not the house-selective sites. One might posit that the difference in significance between faces and houses in latency to peak could be explained by more drawn out responses for house stimuli and more variable times to peak within the prolonged responses. However, there were no differences in response duration, or latency to peak, between face-selective and house-selective sites. Increase in total activity and shortened latency to peak with novel stimulus class are clearly common effects, seen across many subjects, but they are not a universal property of these cortical regions: within each subject, a subset of cortical sites exhibit each effect, but an equal amount do not. Furthermore, the magnitude and timing novelty effects did not correlate with one another (Fig. 4*J*). This implies that category-selective regions are differentially specialized to process novelty and that one effect cannot serve as an explanation for the other. Rather than single regions, homogenous in purpose, category-selective ventral loci must have specialized subdomains, together creating a rich description of the perceived object and the context in which it is observed. It has been established that decisions and actions favor novelty in human experience, but our findings show that the basic physiology of perception has evolved to process contextual novelty.

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

## AUTHOR CONTRIBUTIONS

Author contributions: K.J.M., D.H., R.P.N.R., and J.G.O. conception and design of research; K.J.M. performed experiments; K.J.M. and D.H. analyzed data; K.J.M., D.H., N.W., and J.G.O. interpreted results of experiments; K.J.M. prepared figures; K.J.M. drafted manuscript; K.J.M., D.H., N.W., R.P.N.R., and J.G.O. edited and revised manuscript; K.J.M., D.H., N.W., R.P.N.R., and J.G.O. approved final version of manuscript.

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