

# Facephenes and rainbows: Causal evidence for functional and anatomical specificity of face and color processing in the human brain

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Neuroscientists have long debated whether some regions of the human brain are exclusively engaged in a single specific mental process. Consistent with this view, fMRI has revealed cortical regions that respond selectively to certain stimulus classes such as faces. However, results from multivoxel pattern analyses (MVPA) challenge this view by demonstrating that category-selective regions often contain information about “nonpreferred” stimulus dimensions. But is this nonpreferred information causally relevant to behavior? Here we report a rare opportunity to test this question in a neurosurgical patient implanted for clinical reasons with strips of electrodes along his fusiform gyri. Broadband gamma electrocorticographic responses in multiple adjacent electrodes showed strong selectivity for faces in a region corresponding to the fusiform face area (FFA), and preferential responses to color in a nearby site, replicating earlier reports. To test the causal role of these regions in the perception of nonpreferred dimensions, we then electrically stimulated individual sites while the patient viewed various objects. When stimulated in the FFA, the patient reported seeing an illusory face (or “facephene”), independent of the object viewed. Similarly, stimulation of color-preferring sites produced illusory “rainbows.” Crucially, the patient reported no change in the object viewed, apart from the facephenes and rainbows apparently superimposed on them. The functional and anatomical specificity of these effects indicate that some cortical regions are exclusively causally engaged in a single specific mental process, and prompt caution about the widespread assumption that any information scientists can decode from the brain is causally relevant to behavior.

fusiform face area | electrical stimulation | cortical specificity

Ever since Gall, Flourens, and Broca, neuroscientists have debated, often heatedly, whether each region of the brain is broadly engaged in a wide variety of mental functions or whether some regions are narrowly engaged in a single specific mental process (1–3). Functional neuroimaging has provided compelling evidence for functional specificity by revealing that some cortical regions respond selectively to certain stimulus classes such as faces (2, 4). On the other hand, multivoxel pattern analyses (MVPA) have provided an important challenge to this view by demonstrating that category-selective regions often contain information about “nonpreferred” stimulus dimensions (4–6). For example, MVPA studies have shown that the pattern of responses across voxels in the fusiform face area (FFA) contains information about multiple nonface stimulus dimensions (7), such as the ability to discriminate chairs from cars (5, 6). However, these correlational findings alone do not demonstrate that the FFA is causally involved in the perception of nonface stimuli: The fact that scientists can extract information of a particular type from the neural response patterns in a given region in no way implies that the rest of the brain is reading this information from that region (8, 9). Indeed, it is likely that many of the discriminative abilities we detect

with neural decoding methods are epiphenomenal, because representations sufficient to support one type of object discrimination will support many other object discriminations as well. The critical question for testing the functional specificity of a region or cortex, therefore, is whether the discriminative information about nonpreferred stimuli in that region is epiphenomenal or whether it plays a causal role in behavior. Here we test that question using electrocorticography (ECoG) and electrical stimulation in a neurosurgical patient implanted for clinical reasons with strips of electrodes along his fusiform gyri (Fig. 1).

Prior work in humans has provided compelling but not definitive evidence that face-selective regions are causally engaged in face perception only. Classic evidence comes from neurological cases of prosopagnosia, but pure deficits (10) are rare, perhaps because brain lesions need not respect the borders of functionally distinct regions. Similarly, transcranial magnetic stimulation (TMS) studies have reported striking evidence that stimulation of face-selective regions disrupts only face perception, and stimulation of body-selective regions disrupts only body perception (11), although the small effect size of TMS disruption leaves open the possibility that stronger manipulations of face-selective regions might still impair the perception of nonface stimuli.

## Significance

Are some regions of the human brain exclusively engaged in a single specific mental process? Here we test this question in a neurosurgery patient implanted with electrodes for clinical reasons. When electrically stimulated in the fusiform face area while viewing objects, the patient reported illusory faces while the objects remained unchanged. When stimulated in nearby color-preferring sites, he reported seeing rainbows. The fact that stimulation of face-selective sites affected only face percepts and stimulation of color-preferring sites affected only color percepts, in both cases independent of the object being viewed, supports the view that some regions of cortex are indeed exclusively causally engaged in a single mental process and highlights the risks entailed in standard interpretations of neural decoding results.

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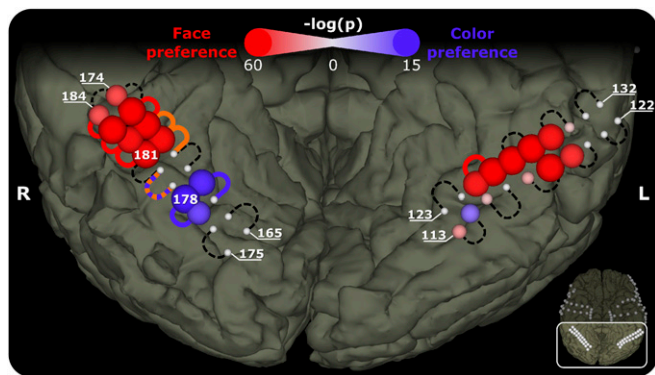
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**Fig. 1.** Location and significance [in  $-\log(p)$ ] of preference for faces > objects (red) and color > grayscale (blue) of ventral electrodes. Arcs show electrode pairs that were stimulated, with arc color indicating resulting percepts: red for faces, orange for eyes, blue for colors, and dashed black for no consistent change in color or shape (see [Supporting Information](#) for details). The effects (or lack thereof) from electrical stimulation shown here are based on the main experiment (see [Transcript of Entire Stimulation Session](#)) and clinical mapping conducted on the previous day.

Studies in monkeys have found that direct disruption of face-selective sites alters performance on face detection (12, 13) and discrimination (14) tasks, as expected, but evidence is conflicting on the critical question of whether this stimulation affects the perception of nonfaces. In one study, pharmacological inactivation of face-selective patch ML (middle lateral) did not disrupt detection of nonface objects (12). However, in another study, monkeys were more likely to report incorrectly that two identical nonface objects were different when they were electrically stimulated in face-selective patches (including ML) during the presentation of one of these objects (15). Nonetheless, this finding could have arisen if the perceptual effect of the electrical stimulation was to place an illusory face percept on top of the object the monkey was viewing (15), a result that would still be consistent with the exclusive role of the region in face perception. It is hard to know if this explanation is correct, because it is difficult for a monkey to tell us exactly what he sees. We therefore decided to ask a human.

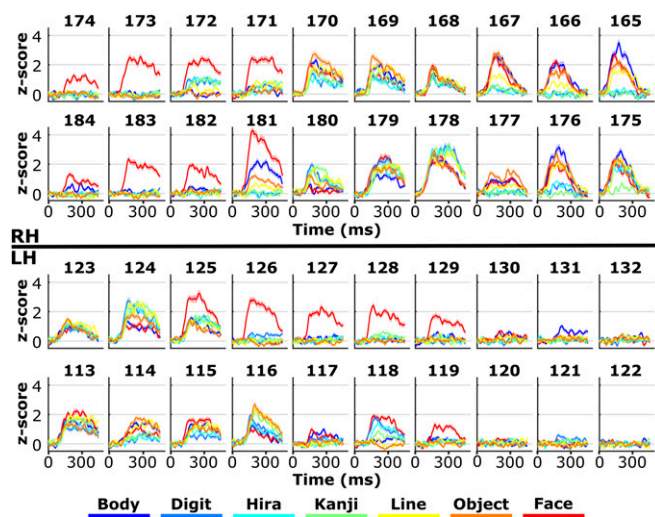
First, we measured broadband gamma responses at each fusiform electrode to a variety of visual stimuli from seven categories including faces, objects, words, and digit strings, each presented either in color or in grayscale. These recordings enabled us to replicate previous findings from fMRI and ECoG of strongly selective responses to faces in some electrodes and preferential responses to color in others (4, 16, 17). Second, we electrically stimulated pairs of adjacent electrodes while the patient viewed each of four different stimuli placed physically in front of him: a face (of the experimenter), a square object (a box), a round object (a ball), and a large printed word (in kanji). We presumed that we would replicate prior findings that stimulation of face-selective sites distorts the perception of a face (18, 19). The key question for our study was what, if any, effect stimulation of the FFA would have on perception of a nonface stimulus. One prior study reported that any such effects were subtle but did not systematically test this question (20). If neural responses within the FFA constitute part of the representation of nonface objects (5), then stimulation of this region should alter the appearance of the nonface object being viewed. However, if responses in the FFA are exclusively causally engaged in face perception, then stimulation of this region should affect only face percepts, and, similarly, stimulation of color-preferring sites should affect only color percepts. Our data provide striking evidence for the latter hypothesis and suggest that the FFA is causally involved in face percepts only and that nearby color-preferring regions are causally involved in color percepts only.

## Results

**ECoG Responses.** Fig. 1 shows the location of the fusiform electrodes in our patient, and Fig. 2 shows the time course of ECoG broadband gamma responses from each of these electrodes for each category (pooled across color and grayscale). We first determined whether the average response of each electrode between 100 and 400 ms after stimulus onset showed a preference for faces and/or color. This analysis revealed multiple electrodes (indicated in Fig. 1) that responded selectively to faces in locations corresponding to the right and left FFA (18, 19) and multiple electrodes responding preferentially to color (Wilcoxon rank-sum tests contrasting faces vs. object photographs and all colored vs. all grayscale stimuli, respectively,  $P < 0.05$  Bonferroni-corrected by the number of electrodes). The three color-preferring electrodes (168, 177, and 178 in Fig. 1) were posterior and medial to the right FFA, in the neighborhood of two regions previously implicated in color processing, hV4 (16) and V4 $\alpha$  (21). The time courses corresponding to the faces vs. object and color vs. grayscale contrasts are shown in Fig. S1. They reveal a highly robust face selectivity in individual trials in many electrodes and a weaker but significant color preference in other electrodes.

We also tested for an interaction between category and color preferences. Specifically, we conducted a two-way ANOVA on the average broadband gamma responses between 100 and 400 ms after stimulus onset of each electrode individually, with factors of color/grayscale  $\times$  stimulus category. In addition to revealing multiple sites showing a main effect of category and of color (consistent with the previous analyses), this analysis revealed that ECoG responses in two electrodes (124 and 179) showed an interaction of color and category (Fig. S2). The form of this interaction is apparent in the time course of the ECoG response in these electrodes to each of the 14 stimulus conditions, revealing a color preference only for the photograph stimuli (body, face, object) but a higher response to the black-and-white than to the color versions of the symbol/line drawing stimuli (Fig. S3).

**Effects of Electrical Stimulation.** To test the causal role of these sites on perception, we then electrically stimulated pairs of adjacent fusiform electrodes (Fig. 1) while the patient viewed four different real objects placed in front of him (Fig. 3) and asked him to report any change in his percept. Although careful two-alternative forced



**Fig. 2.** Time course of ECoG broadband gamma responses for each category in each recording location. Response magnitude is given in z-scores that indicate single-trial response magnitude with respect to baseline. Solid lines give response mean; colored shading gives its SE. LH, left hemisphere; RH, right hemisphere.

choice (2AFC) psychophysical testing might have enabled us to test the causal role of each site on specific dimensions of shape perception more precisely, for clinical reasons only a few stimulation trials could be conducted at each site, rendering such tasks ineffective. In contrast, simply asking the patient if he observed any change during the stimulation enabled us to test the causal role of each pair of sites on essentially all dimensions of visual perceptual experience at once. [Further, as discussed by Jazayeri and Afraz (22), the high-dimensional response space entailed in this open-ended task reduces the ambiguities inherent in “off-manifold” neural manipulations.] Thus, we asked if the patient observed any change while viewing each of four different real objects placed in front of him: a face (of one of the experimenters), and three nonface stimuli: a round object (an orange soccer ball), a rectangular object (achromatic box), and a word (a large kanji character printed on a piece of paper).

A full transcript of the patient’s reports is provided in *Transcript of Entire Stimulation Session* along with video excerpts from stimulation of sites 181–182 and 177–178. For many of the sites that were stimulated, the patient reported “no change” or simple visual changes such as “blinking” or motion toward the visual field contralateral to the stimulation site. For sham stimulation, the patient reported “no change” (see transcript). However, when face- and color-preferring sites were stimulated, the results were very different, as described next.

**Stimulation of face-selective sites.** Each of the three times the patient was stimulated in the right FFA (electrodes 181 and 182) while viewing the face of one of the experimenters (Fig. 3), the patient reported that the appearance of the face changed (see *Transcript of Entire Stimulation Session* and *Movie S1*). For example, in one case the patient reported: “Your face completely changed . . . I don’t know what’s going on . . . Your hair stays the same, but your eyes and nose . . . I can’t describe it with words” (Fig. 3, *Supporting Information*, and *Movies S1* and *S2*). This finding, which was repeated 20 min later, replicates prior results showing that stimulation of the FFA produces distortions in face percepts (18, 20, 23, 24) and supports the hypothesis that the FFA is causally involved in the perception of faces.

However, our key question was what, if any, role the FFA plays in the perception of stimuli that are not faces. While viewing the box, the patient said: “It doesn’t change much . . . But, for the first second, just for the very first second after it started, I saw an eye, an eye, and a mouth. I started thinking ‘what is this?’, but the next thing I noticed, I was just looking at this box.” Such “facephenes” occurred each of the six times the patient was stimulated at this site while viewing a nonface object

(twice for each of the three nonface objects tested) (Fig. 3, *Supporting Information*, and *Movies S1* and *S2*). Thus, stimulation of the FFA does affect the perception of other stimuli beyond faces (15), but it does so by adding a face percept. These facephenes are apparently superimposed on, rather than replacing, the percept of the object the patient is looking at: On two occasions, the patient reported that despite the facephene, “the shape does not change” (see also *Supporting Information*). Further, during conversations after the experiment, the patient further explained that the facephene always appeared on top of the stimulus he was viewing rather than in the periphery and that it tended to appear on particular salient parts of the stimulus (e.g., in the location of the logo on the ball), but that the percept of the stimulus itself was otherwise unchanged. These findings support a selective causal role of the FFA in face percepts only.

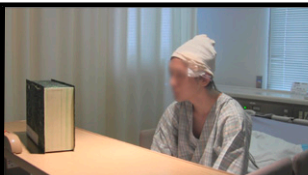



Several electrodes adjacent to this site also produced facephenes when stimulated (Fig. 1 and *Supporting Information*). All electrodes that produced facephenes when stimulated responded selectively to faces in ECoG, but not vice versa. For example, some strongly face-selective sites in the left fusiform gyrus did not produce facephenes when stimulated, consistent with one prior report (24), although one left-hemisphere site (electrodes 125–126) did (Fig. 1).

Interestingly, stimulation of one site immediately posterior to the FFA that did not respond selectively to faces in ECoG elicited percepts of eyes (see Fig. 1 and *Transcript of Entire Stimulation Session*) (25).

**Stimulation of color-preferring sites.** Each time the two most color-preferring pairs of electrodes (electrode pairs 177–178 and 167–168 in Fig. 1) were stimulated, the patient reported that he saw a “rainbow” or that his percept “became colorful.” This happened in eight out of eight trials (one stimulation trial for each of the four objects at each of these two sites). He did not report any other perceptual changes, except that the rainbow moved to the left (presumably because this right hemisphere site has a left visual field bias), and the patient was “chasing” the percept with saccades (as one does with a retinal afterimage). No other sites produced strong color percepts when stimulated, although the patient did report occasional weak color percepts during stimulation of electrode 179, which responded preferentially to color only in photograph stimuli (Fig. S3).

## Discussion

Decades of evidence from fMRI and intracranial recordings have revealed that some cortical regions respond very specifically to certain classes of stimuli. However, the strong hypothesis that

				
Stim. Elec. 181-182	<i>... just for the very first second... I saw an eye, an eye, and a mouth.</i>	<i>How do I explain this? Just like the previous one, I see an eye, an eye, and a mouth, sideways.</i>	<i>Your face completely changed... I don't know what's going on. Your eyes change.</i>	<i>Hm. Am I just imagining things? Can you do it again?... OK, just as I thought, I see a face.</i>
Stim. Elec. 177-178	<i>The left side of the box looks like a rainbow.</i>	<i>If I look at the ball, the rainbow is there, wider than before, and blinking.</i>	<i>If I look at the face, this side looks like a rainbow and glowing.</i>	<i>It's kind of the same, this half is colorful.</i>

**Fig. 3.** Transcript excerpts from patient’s report during electrical stimulation of electrodes 181–182 (FFA) and 177–178 (color-preferring site) while viewing a box, a ball, the experimenter’s face, or a kanji character. For full transcript see *Transcript of Entire Stimulation Session*; for excerpted videos see *Movies S1* and *S2*.

these regions are exclusively engaged in processing their preferred stimulus classes has been challenged by demonstrations that even these very selectively responding regions contain information about nonpreferred stimuli in the pattern of responses across their voxels (5). On the other hand, neither the univariate evidence for functional specificity nor the multivariate evidence challenging it tests the actual causal role of that neural response in perception. The only way to do this is to directly intervene on the region and ask what happens perceptually. Prior efforts from studies of neurological patients, TMS in normal subjects, and focal cortical stimulation or disruption in monkeys have all offered compelling evidence for functional specificity, but all of these findings have left room for alternative accounts (see Introduction). Here we used direct electrical stimulation of focal regions along the fusiform gyrus in a neurosurgery patient to ask whether the FFA is exclusively involved in processing face information or whether it plays some causal role in the perception of other nonface stimuli. We find that electrical stimulation of the FFA during viewing of nonface objects did not affect the percept of those objects themselves but instead produced only illusory face percepts, or facephenes. Similarly, electrical stimulation of nearby color-preferring sites did not affect the appearance of objects or faces themselves but instead resulted in illusory rainbow percepts. These findings support the selective, perhaps exclusive, causal role of these regions in processing only their preferred dimensions.

In particular, we first replicated prior findings of (i) selective broadband gamma responses to faces in the left and right FFA and (ii) distortion of face percepts when this region was stimulated during face viewing (18, 20, 23, 24). On three occasions, the patient reported such distortions, remarking that, “Your face completely changed” (see Fig. 3, *Transcript of Entire Stimulation Session*, and *Movies S1* and *S2*). These findings accord with extensive prior evidence that the FFA is causally involved in the perception of faces. However, our key question was whether the FFA is also causally involved in the perception of other nonface perceptual dimensions. Each of the six times that the patient was stimulated in the most face-selective right FFA site while viewing a nonface object (two stimulations each for the box, ball, and kanji character), he reported seeing a face apparently superimposed upon the object being viewed. Importantly, he did not report other changes in his experience, and on several occasions he noted that the object being viewed did not change in shape. Other face-selective sites also produced face percepts when stimulated (*Results*), but clear face percepts never resulted from stimulation of sites that had not responded selectively to faces. These results provide striking evidence that the FFA is selectively causally engaged in representing faces.

This conclusion is consistent with prior causal tests in humans and monkeys, with one possible exception. Moeller et al. (15) showed that monkeys were more likely to judge two nonface shapes as different when they were stimulated in a face-selective region during the presentation of one of those shapes. However, as the authors noted, this result might have arisen if the monkey perceived the nonface shape veridically but perceived an illusory face on top of it. This is apparently what happened to the human in our study, and it seems plausible that this is also what happened to the monkeys in the Moeller study. Thus, all the prior causal evidence is consistent with the strong conclusion that face-selective regions are exclusively causally engaged only in face percepts.

We also showed that stimulation of color-preferring sites, adjacent to the face-selective site, produces illusory rainbows. These rainbow percepts may have resulted from stimulation of multiple adjacent columns, each of which is tuned to a specific color and retinotopic location, as described previously for posterior inferior temporal regions in macaques (26, 27). Only sites that produced selective ECoG responses to faces produced clear

face percepts when stimulated, and only color-preferring sites produced color percepts when stimulated.

Several factors lend credence to the patient’s reports. First, the patient had no knowledge of which sites were being stimulated and no way to predict what perceptual changes might result from each. Second, the patient evinces surprise at the percepts he experiences and asks on multiple occasions for the stimulation to be repeated so that he can report more accurately (see *Transcript of Entire Stimulation Session* and *Movies S1* and *S2*). Third, he reported “no change” on many occasions when other fusiform sites were stimulated. The data reported here come from a single subject and include a relatively small number of trials and testing conditions. If we had had the opportunity to conduct extensive psychophysical testing on many perceptual tasks and stimuli, with and without stimulation, we might have found a subtle effect of FFA stimulation on the perception of nonface objects. However, any such effect would have to be very small to escape the notice of this careful and attentive patient (*Movies S1* and *S2*). Thus, our findings provide striking evidence for a selective causal role of the FFA only in the representation of face information and a selective causal role of the color-preferring site only in the representation of color.

One might object to this conclusion by arguing that on logical grounds alone, the mean response of the FFA must entail information about nonface categories, if only by indicating the probability that the stimulus is a nonface. For example, a high FFA response would imply that the stimulus is not a car. However, this inference would be valid only if the neural code were known to represent only a single object at a time. Conversely, a very low response in the FFA would constitute evidence that a nonface object was present only if it was independently known that an object was present at all. The question of whether and how the visual system represents such “objecthood,” including which visual features pertain to which object (aka the “binding problem”) is an important and classic question in its own right (28, 29). The fact that our patient did not report that objects “turned into” faces but instead reported that the objects “did not change,” despite the face percept, suggests that the illusory face was perceived as a visual object distinct from the physically present object. In turn, this conclusion would further suggest that the number of objects in a scene is inferred from the neural representations of the features and categories that are active and is not represented separately in the brain. If so, then the strength of activation in the FFA could inform only whether a face is present, not whether a nonface is present. These speculations and their implications for the perceptual construction of objecthood could be further tested in a future electrical stimulation study if patients were specifically asked how many objects/faces are perceived at a time and whether the face percept appears to replace or exist in parallel with the object percept.

A further concern is that the electrical stimulation used here likely produced neural response patterns that differ at a finer grain from anything likely to occur naturally [i.e., an “off-manifold” perturbation (22)], and surely these responses would not be expected to precisely duplicate any of the specific patterns of responses across neurons that have been shown to be (weakly) diagnostic of nonface objects such as cars or shoes. Nonetheless, the electrical stimulation produced here would be expected to drastically disrupt such patterns, and evidently this neural disruption did not distort the percept of the nonface objects the patient was viewing. These considerations suggest that it is not simply the overall mean response magnitude of the FFA, but also the fine-grained spatial profile of response across the FFA that is not causally related to the perception of nonface stimuli.

It is worth distinguishing the functional specificity hypothesis defended here from other ideas with which it is often conflated. First, our hypothesis that some cortical regions are functionally very specific for a single mental process in no way implies that all

regions of cortex are functionally specific to a similar degree, and indeed extensive evidence indicates that many cortical regions are not (30, 31). Second, by arguing that a particular region of cortex is functionally very specific, we do not mean to imply that this region acts alone; no region of cortex can function without extensive connectivity to, and interaction with, other brain regions. Third, the functional specificity of a region of cortex need not imply the innateness of that region or of its selectivity, as shown most strikingly with the case of the visual word-form area (32, 33). Fourth, demonstrating that a region of cortex is functionally specific for a given mental process in no way constitutes an explanation of that mental process. Instead, demonstrations of functional specificity aid the grander enterprise of human cognitive neuroscience by revealing the fundamental components of the mind and brain and thereby providing a roadmap for future cognitive, computational, and mechanistic investigations into how each of these things actually work.

In sum, the fact that electrical stimulation of the FFA did not disrupt the percept of nonface objects but merely added a face on top argues that the neural code in this region is causally engaged in face percepts only. Similarly, the fact that stimulation of the color-preferring region did not distort the percept of objects but simply added rainbow colors indicates that the neural code in this region is causally engaged in color percepts only. Thus, these findings offer striking support for the longstanding view that some cortical regions are very specifically engaged in a single mental process. They also suggest that some of the pattern information about nonpreferred stimuli that has been shown with neural decoding methods may be epiphenomenal and that the causal role of a cortical region in behavior may be more accurately revealed by its univariate response selectivity.

## Methods

**Participant.** The subject in this study was a 26-y-old man with intractable epilepsy who was temporarily implanted with 188 subdural electrodes to localize seizure foci at Asahikawa Medical University. The platinum-iridium electrodes had an exposed diameter of 1.5–3.0 mm and an interelectrode distance of 5–10 mm. The subject had postoperative computerized tomography imaging to identify electrode locations and preoperative MRI to define the cortical anatomy. The subject was right-handed with left-sided language lateralization. The study was approved by the Institutional Review Board of Asahikawa Medical University (No. 146). The subject gave informed consent for the study and permission for publication of the video excerpts.

**ECoG Recording Procedure and Analysis.** The subject was asked to look at a video screen that displayed visual stimuli from seven stimulus categories: photographs of bodies, faces, and objects; line drawings of objects; kanji characters; hiragana characters; and digit strings. There were 20 stimuli per category, and each stimulus was presented once in color and once in black and white for a total of 280 stimuli and trials ( $20 \times 7 \times 2$ ). Each stimulus was presented for 200 ms, followed by a rest period of 600–800 ms during which the screen was blank. The subject did not receive particular instructions other than to observe the stimuli.

ECoG signals were recorded at the bedside with a DC-coupled g.Hlmp biosignal amplifier (g.tec medical engineering GmbH). Data were digitized with

24 bits at 2,400 Hz, synchronized with stimulus presentation with a photo diode, and acquired using the g.Hlms real-time processing library (g.tec medical engineering), which also controlled the experimental paradigm and stimulus presentation. We used electrodes in dorsal parietal locations (i.e., distant from the areas of interest in this study) as ground. We then extracted ECoG signals in the broadband gamma range, i.e., signals widely recognized to represent local cortical population activity. To do this, we first removed signal drifts (2 Hz high-pass, Butterworth, order 4), rereferenced the signals with a common-average-reference montage, band-pass filtered the results (110–140 Hz, Butterworth, order 4), applied the Hilbert transform, extracted the analytic amplitude, down-sampled (to 400 Hz) and square-root transformed the results, and finally normalized them by z-scoring with respect to all baseline periods (the 300 ms immediately preceding stimulus presentation). For each location, we then determined whether its average broadband gamma responses between 100 and 400 ms after stimulus presentation were selective to faces or colors by using unpaired/paired Wilcoxon rank-sum tests (faces vs. objects/colored vs. grayscale contrasts, respectively,  $P < 0.05$  Bonferroni-corrected by the number of electrodes). In Fig. 1, all electrodes that were face- or color-selective were colored in red and blue, respectively; color intensity and electrode diameter were both scaled by the corresponding  $-\log(p)$  value resulting from the statistical test.

**Electrical Stimulation Methods.** The electrical cortical stimulation mapping procedure was separated into 2 days. Because we used all four stimuli (face, box, ball, kanji characters) only on day 2, we report only those data here. A g. Estim electrical stimulator (g.tec medical engineering) applied trains of 8-mA biphasic pulses (300- $\mu$ s phase duration, 50 Hz) for 3–6 s. The subject was asked to report any change or feeling while looking at the target object. The subject did not know which site was stimulated. At the same time, we performed multiple stimulation trials, and so in later trials he may have anticipated that some aspect of the appearance of objects or faces might change. An integrated stimulation buzzer indicated ongoing stimulation that might have been heard by the subject, although he was not informed about the buzzer before the mappings. We also performed sham stimulation with announced but not connected electrodes to confirm the correct and true explanation of the subject.

## Identification of the FFA and Color-Preferring Regions.

**Face-selective sites.** The FFA was identified as the site with a strongly face-selective broadband gamma response in the midfusiform gyrus (electrodes 181–182; see Fig. 1). This location accords well with the location of the FFA as identified in prior fMRI and ECoG studies. Adjacent electrode sites also responded selectively to faces but with weaker absolute response magnitudes (Fig. 2 and Fig. S1).

**Color-preferring sites.** The color-preferring region stimulated here (electrodes 168, 177, and 178 in Fig. 1) is in the neighborhood of two regions previously implicated in color processing, hv4 (16) and V4 $\alpha$  (21). V4 $\alpha$  is also known as “V8” (34), part of the VO complex (35), and the “central color” region (17).

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# Supporting Information

Schalk et al. 10.1073/pnas.1713447114

## Supplementary Data: No Strong Evidence for Selectivity for Other Visual Categories

The time course of response of each electrode to each category (Fig. 2) reveals that none of the sites that were stimulated in our experiments responded specifically to just digit strings or to just words (kanji or kana), although two electrodes (124 and 180) showed some preference for both. Several other electrodes (131, 165, and 176) showed weak preferences for bodies. Finally, three electrodes responded more strongly to photographic stimuli (faces, bodies, and objects), a response profile that could reflect a preference for 3D shape information, texture/materials or surface properties, or simply the more complete retinotopic coverage of the photographic stimuli compared with line-based stimuli.

### Transcript of Entire Stimulation Session

Note: As part of clinical mapping, multiple pairs of fusiform electrodes were stimulated on the day before this experiment was run, although only while the patient was viewing faces or kanji characters (not the box or ball). For several of these pairs the patient reported illusory percepts of eyes, faces, or colors; these are indicated in Fig. 1. Below we report the transcript from the main testing session.

#### Electrodes 173–174.

**Box.**  
Experimenter (E): “Did anything change?”  
Subject (S): “No ... I’m ok.”  
E: “Nothing really changes?” (tells other experimenter: “No change.”)  
S: “Can you do it again?”  
E: “How is it?”  
S: “Ahh, when I blink and reset it just looks like a box, but when it began for the first 3 s, how do I say this ...?”  
E: “Do you see a face? Or no? Does it look distorted? The color changes?”  
S: “No, the color doesn’t change but, for example, the pattern right here ... it’s kind of forcing me to see an eye ... to see an eye ... how do I say this? Maybe it’s forcing me to see a face.”  
E: “The pattern’s impression changes?”  
S: “For a brief moment it changes, but when I blink it just looks like a box.”  
E: “Ok. Once again.” (Repositions box.)  
E: “How is it?”  
E: “Are you ok?”  
S: “I’m ok.”

**Ball.**  
E: “How is it?”  
S: “The shape doesn’t change at all.”

**Face.**  
E: “How is it? Does it change?”  
S: “Ahh ...”  
E: “Does it look like cartoonish like before?”  
S: “For a brief moment his impression changed.”  
E: “But not a huge change?”  
S: “Right.”  
S: “The features of his face doesn’t [sic] change, but the impression changed for a brief moment.”  
E: “Ok if it’s just a brief moment, that’s ok” (as if he doesn’t care). “Only if it stays for a while.”  
E: (English explanation)

**Kanji character.**  
E: “Let’s start the kanji character.”  
S: “Ok.”

E: “Any change?”  
S: “No ... no cha...” (cut off by experimenter)  
E: “If it doesn’t change, you can say it doesn’t change.”  
S: “For a brief second at the very beginning, I felt like it was going to start changing, but after seconds, nothing had really changed.”

**Electrodes 171–172.** The video camera battery ran out during stimulation of electrodes 171–172. Thus, the video and the verbatim text of the patient’s report from the stimulation of these electrodes were lost. However, notes taken at the time indicate that the patient reported for each of the four stimuli viewed that he saw eyes or a face.

**Electrodes 169–170.**

**Box.**  
E: “Did it change?”  
S: “What is this, you see the small patterns here looked like a landscape scenery painting.”  
E: (explains in English)  
E: “Not a face?”  
S: “No, not a face.”  
E: “The shape doesn’t change?”  
S: “The shape doesn’t change.”  
(English conversation)  
E: “The color?”  
S: “The color changed a bit. Not like rainbow colors, how would I say it ... what color was it ...?”  
E: “White?”  
S: “No.”  
S: “Can you do it again?”  
E: “Again?”  
(stimulation)  
S: “The color didn’t change.”  
E: “Green black?”  
S: (nods)  
E: “Landscape colors?”  
S: “Landscape ... this time it was more like a pattern ... pattern ... landscape ... not like a landscape, more like patterns. How do I explain ...?”  
E: (English explanation)

**Ball.**  
S: “There’s a familiar ... like a pattern I’ve seen before right here. The color doesn’t change much.”  
E: “Not a face?”  
S: “No, not like a face.”  
E: (in English) “Not face?”  
S: “Like a pattern.”  
E: “Like colored dots?”  
S: “Yea, kind of like those put together.”  
E: (English explanation)

**Face.**  
S: “How do I explain ... it changed. Just the eye changed ... the eye changed ... picture? Like a picture or like a drawing. The shape of the eye didn’t change, but it just looked different.”  
E: “Like a cartoon character?”  
S: “Maybe it’s like that.”  
E: “Both eyes?”  
S: “No, just that side.”  
E: (English explanation)

**Kanji character.**  
S: “What is this ... I can’t put it in words at all. Can you do it again?”  
E: “Again.”  
S: “This part and the lines right here. The shape doesn’t change, and the color doesn’t change, but how do I say this ...? It almost looks

like it was written by hand. It changed like that just around here. The way I see it changes. The shape and color doesn't [sic] change."

E: "Like the font changed?"

S: "Yea, kind of like that ... maybe."

E: (English explanation.)

(Note: "Shodo" is Japanese calligraphy.)

#### **Electrodes 167–168.**

##### **Box.**

E: "How is it?"

S: "Just like before, part of it looks like there's rainbow colors, but once I start focusing on it, the colors shift to the left."

E: (English explanation)

##### **Ball.**

E: "How is it?"

S: "Kind of like before, when I start focusing on the rainbow colors, it starts shifting to the left. It moves like this."

##### **Face.**

S: "Same as before. When I focus on the colors, it starts moving gradually."

E: (starts English explanation)

E: "This way, right?"

S: "Yes."

E: (English explanation)

##### **Kanji character.**

S: "Same as before. The rainbow colors move."

#### **Electrodes 165–166.**

##### **Box.**

S: "Totally different from before."

E: "Different."

S: "There's something blinking ... What does it look like? ... Like really shiny blinking flashes, and it starts moving upwards."

E: "Do you feel nauseous?"

S: "It's still continuing."

E: "Getting better?"

S: "Just now, its going away."

E: "Feels weird?"

S: "Yea, blinking flashes."

E: "Do you feel nauseous?"

S: "No, feeling-wise, it's fine."

E: (English explanation)

##### **Ball.**

S: "So if I keep following it, it gradually moves to the left."

E: "Blinking like boom, boom, boom?"

S: "If I look at the ball, it's shining over here, but if I look at it, it keeps moving."

E: (English explanation)

E: "Are you ok?"

S: "I'm ok."

E: (English)

##### **Face.**

S: "So if I look at your eyes, your forehead is flashing."

E: "Like right here?"

S: "Over there, above your eye is flashing when I look at your eyes. And if I try to look at the blinking light, it starts moving up again."

##### **Kanji character.**

S: "Yup. The same. Just like before, if I look at the middle, there's [sic] blinking lights in the upper left, and if I look at it, it starts moving up."

E: (English explanation)

#### **Electrodes 175–176.**

##### **Box.**

S: "Similar to before. You know how I said the light moves to the upper left? Like a flashing light. It's like that, but a smaller light, but it moves similarly. If I chase it, it keeps moving toward the left."

E: (English explanation)

E: "How big?"

S: "One ... the one before was like this size, but this time was like this size."

E: "So, like half the size?"

S: "Yes, probably about this size."

##### **Ball.**

E: "Same?"

S: "Same."

E: "Haha same?"

S: "Like it moves."

##### **Face.**

S: "You know how I said the size was half of what it was before on the last one? Well, looking at your face, it hasn't changed much. The size."

E: (English explanation that the light was the same large size as with the previous electrode stimulation)

##### **Kanji character.**

S: "For the kanji, the size (of the light) hasn't changed much from before. Yea ... its the same as before."

E: (English explanation)

#### **Electrodes 177–178.**

##### **Box.**

S: "So ... if I stare at the center of the box, this half over here is brightly lit rainbow colors."

E: "So the color changes over here."

S: "Yes."

E: (English explanations)

##### **Ball.**

S: "So if I stare at the lights and chase it, it feels like it starts moving to the left."

E: "What about the color?"

S: "So when I look at the ball, there's [sic] flashing rainbow lights that expands [sic] wider than the ball."

E: "Did it not blink before?"

S: "No, it blinked before too. Like that box right?"

E: "When this side was rainbow colors?"

S: "Yes, it was blinking."

E: "Was it moving?"

S: "Last time I was only staring at the center, but now over here (the ball) when I stared at the center, I saw the blinking and chased it with my eyes, and it started moving to the left."

E: (English explanation)

##### **Face.**

S: "I was staring right around your nose, and again that side of the face is flashing rainbow colors, and if I chase it, it moves to the left. Like this size of rainbow flashes moved gradually."

E: (English explanations)

##### **Kanji character.**

S: "Similar as before. This half."

E: "Colorful this side."

S: "And if I chase it, it moved to the left gradually."

#### **Electrodes 179–180.**

##### **Box.**

E: "How is it?"

S: "I can't say it changed much."

E: "No change?"

S: "Can you do it again? I kind of blinked at a bad timing. Can you do it again?"

E: "How is it?"

S: "What kind of picture is this ...? very faint, but I saw a familiar-looking weird picture that I can't put in words. Sort of comes out right here."

E: (English explanation)

##### **Ball.**

E: "How is it?"

S: "Similar to the box. I see an unexplainable picture right around here, about this size."



E: (English explanation)  
E: "What kind of picture?"  
S: "What ... what kind of ... How do I say it ...? I can't put it in words."  
E: "Stripes? Dots?"  
S: "Can you do it again?"  
E: "How is it?"  
S: "It's like a small eye that appears several times over here."  
E: (English explanation)

**Face.**

S: "Slightly flashing rainbow colors and again those little eyes I saw with the ball ... um ... not cartoons, but really small ... um ..."  
E: "Like right here?"  
S: "Yes. There's [sic] eyes. Like two or three of them like this."  
E: "What about the color? Over here?"  
S: "Yea, kind of rainbow colors ..."  
E: (English explanation)

**Kanji character.**

E: "How is it?"  
S: "Like before, there's [sic] those small eyes, but when I chase them they moved up."  
E: "Could you read the kanji?"  
S: "Yes."  
E: "Color?"  
S: "Very slightly rainbow like."  
E: "Around here?"  
S: "The eyes here and rainbow ..." (points to left)  
E: (English explanations)

**Electrodes 181–182.**

**Box.**

S: "It doesn't change much. But for the first second, just for the very first second after it started I saw an eye, and eye, and a mouth for a bit but I started thinking 'what is this?' but the next thing I noticed was just looking at this box."

**Ball.**

S: "How do I explain this ... just like the previous one, I see an eye, an eye and a mouth, sideways."  
E: "What kind of face was it?"  
S: "Just now? What's that cartoon character? ... Not sure what, but some sort of cartoon character."

**Face.**

S: "Your face completely changed."  
E: "Oh, how did it change?"  
S: "I don't know what's going on. Your eyes change."  
E: "Everything?"  
S: "Yes."  
E: "I change into a completely different person?"  
S: "Your hair stays the same, but your eyes and your nose ... I can't describe it with words. Can you do it again?"  
(second stimulation)  
"Just this area of your face. Your face turns into a cartoon character that I might see in an anime."  
E: "What about my mouth?"  
S: "Your mouth doesn't really change, but the nose and eyes, this area changed."

**Kanji character.**

S: "Hmm ... am I just imagining things? Can you do it again?"  
(second stimulation)  
"Ok. Just as I thought, I see a face. An eye, an eye, and mouth around here. I don't really know, but something that looks kind of like an anime character."  
E: "Was there color?"  
S: "Just a bit, I saw a purplish color."

**Electrodes 183–184.**

**Box.**

No change

**Ball.**

S: "Why is this? The letter (character) right here appeared to have eyes, but after two seconds I couldn't see it anymore."

(Note: the soccer ball has some letters on it)

E: "Ok. Maybe not the letters." (Switches the direction of the ball to where there are no letters)

(Second stimulation)

S: "For a second I see an eye an eye, and I think that's a mouth."

E: "Like an anime character?"

S: "Yes, the shape is just in the shape of this ball with an eye, an eye, and a mouth."

E: "What about the color?"

S: "The color doesn't change."

**Face.**

S: "Your facial expression changed."

E: "What changes?"

S: "From your eyes to your mouth, your face kind of changes into an anime character."

**Kanji character.**

(First stimulation)

"Can you do it again?"

(Second stimulation)

"Oh ... this area felt like a face for a bit. It's not that I could see the eyes, nose, and mouth or anything, but it just felt like that was a face right there, and I felt like there was a hand there."

E: "Like an anime?"

S: "Yea, something like that."

**Electrodes 127–128.**

**Box.**

E: "How was it?"

S: "Didn't change much."

**Ball.**

S: "Doesn't really change."

E: "Doesn't change?"

**Face.**

E: "No change?"

S: "So your face and the color doesn't [sic] change, but for a brief moment, like very brief ... even for the box and the ball, and this time with your face, I saw a flash of a face right next to it, and disappeared."

E: "A face right here?"

S: "A brief moment."

E: "Like a picture?"

S: "Well ... it just appeared ... how can I explain it? ... A face ... I mean, not a big change."

E: (English explanation)

**Kanji character.**

E: "How is it?"

S: "The face is ... (inaudible). I see an upper body faintly right over here on the right for a brief moment."

E: "Can you read the kanji character?"

S: "Yes, I can totally read the character."

E: (English explanation)

E: "Just the upper body, right?"

S: "Yes."

**Electrodes 125–126.**

**Box.**

E: "Are you ok?"

S: "Yes."

E: "How is it?"

S: "For a second it seemed blurry."

E: "It hurts? Can't bear it anymore?"

S: "No, it's not like that, but it hurt a bit at the beginning. But I'm ok."

E: "No big change?"

S: "How can I say this? It got blurry right here and moved toward the right."

E: "The shape."

S: "The shape doesn't change."

**Ball.**

S: "It wasn't very clear, but very faintly I saw a picture. Not sure who's pictured, but some picture appeared right there."

E: "A face?"

S: "Upper body. Couldn't see the face clearly. It was just very faint."

E: "In the middle?"

S: "Over here."

E: (English explanation)

E: "Color?"

S: "Blackish, especially the person in it."

E: (English explanations)

**Face.**

S: "Your face doesn't really change, but over here around your right ear, I don't know who it is, but I see an upper body and face."

E: (English explanation)

E: "Right here?"

S: "Yes."

E: "In my ear?"

S: "Well ... just around your ear."

E: (English explanation)

S: "The face was the size of your ear."

**Kanji character.**

S: "I see a face that I just saw right next to your ear. I don't know who it is but just right here. One person is facing the other way, and there's a person next to it facing this way."

E: "Two people?"

S: "Yes, it actually kind of looks like someone similar to you."

E: "Could you read the character?"

S: "Yes, I could read it."

(English conversation)

E: "Is it always the same picture?"

S: "Yes."

**Electrodes 123–124.**

**Box.**

S: "I faintly saw some blinking lights, and then it moved."

E: (English explanation)

**Ball.**

S: "Just like before, very faintly I see blinking lights that move."

E: (English explanation)

**Face.**

S: "So when I chase it, it moves."

E: (English explanation)

**Kanji character.**

S: "Over here."

E: "Can you read it?"

S: "Yes."

E: (English explanation)

**Electrodes 115–116.**

**Box.**

E: "How is it?"

S: "This doesn't change."

E: (English explanation)

**Ball.**

E: "How is it?"

S: "No change."

E: (English explanation)

**Face.**

S: "Doesn't change at all."

E: (English explanation)

**Kanji character.**

S: "Doesn't change at all."

E: (English explanation)

**Electrodes 117–118.**

**Box.**

E: "How is it?"

S: "No change."

E: (English explanation)

**Ball.**

E: "How is it?"

S: "No change."

E: (English explanation)

**Face.**

S: "Doesn't change at all."

E: (English explanation)

**Kanji character.**

S: "This doesn't change either."

E: (English explanation)

**Electrodes 113–114.**

**Box.**

E: "How is it?"

S: "No change."

E: (English explanation)

**Ball.**

S: "No change again."

E: (English explanation)

**Face.**

S: "Doesn't change at all."

E: (English explanation)

**Kanji character.**

S: "No change again."

E: (English explanation)

**Electrodes 181–182.**

**Box.**

E: "How is it?"

S: "Can you do it again?"

S: "What is this? ... I see something cartoon-like character with an eye, an eye, and mouth ... what kind of character is this ...?"

E: (English explanation)

E: "The shape doesn't change?"

S: "No, the shape doesn't change."

E: (English explanation)

**Ball.**

E: "How is it?"

S: "Similar to the box before ... where the shape and color doesn't [sic] change, but the patterns inside start looking like eyes."

E: "A face?"

S: "Yea, like a face."

E: "Like a cartoon?"

S: "What is it? ... Every direction I look at ... I start seeing eyes over here, but if I look over here, I see eyes over here."

S: "Every direction I look, there's always ..."

E: "Always in the middle, right?"

E: (English explanation)

**Face.**

S: "It no longer looks like your face."

E: "Everything changed?"

S: "The shape of your face doesn't change, but your eyes ..."

E: "This area?"

S: "Yea, that area I can no longer tell who it is."

E: (English explanation)

Another experimenter: "Was it like a picture or a line drawing?"

S: "I guess like a drawing. It's no longer a human face, almost like a cartoon character."

**Kanji character.**

E: "How is it?"

S: "I see a weird face."

E: "Around here?"

S: "You see this here? These kind of look like eyes."  
 E: (English explanation)  
 S: "I couldn't see a real face shape."

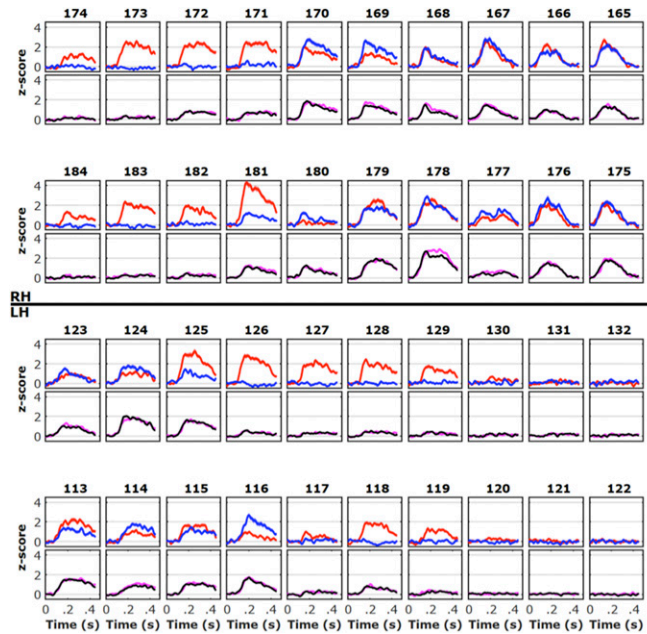
**Ball.**  
 S: "No change."  
 E: (English explanation)

**Electrodes: Sham stimulation.**

**Box.**  
 E: "How is it?"  
 S: "No change."  
 E: (English explanation)

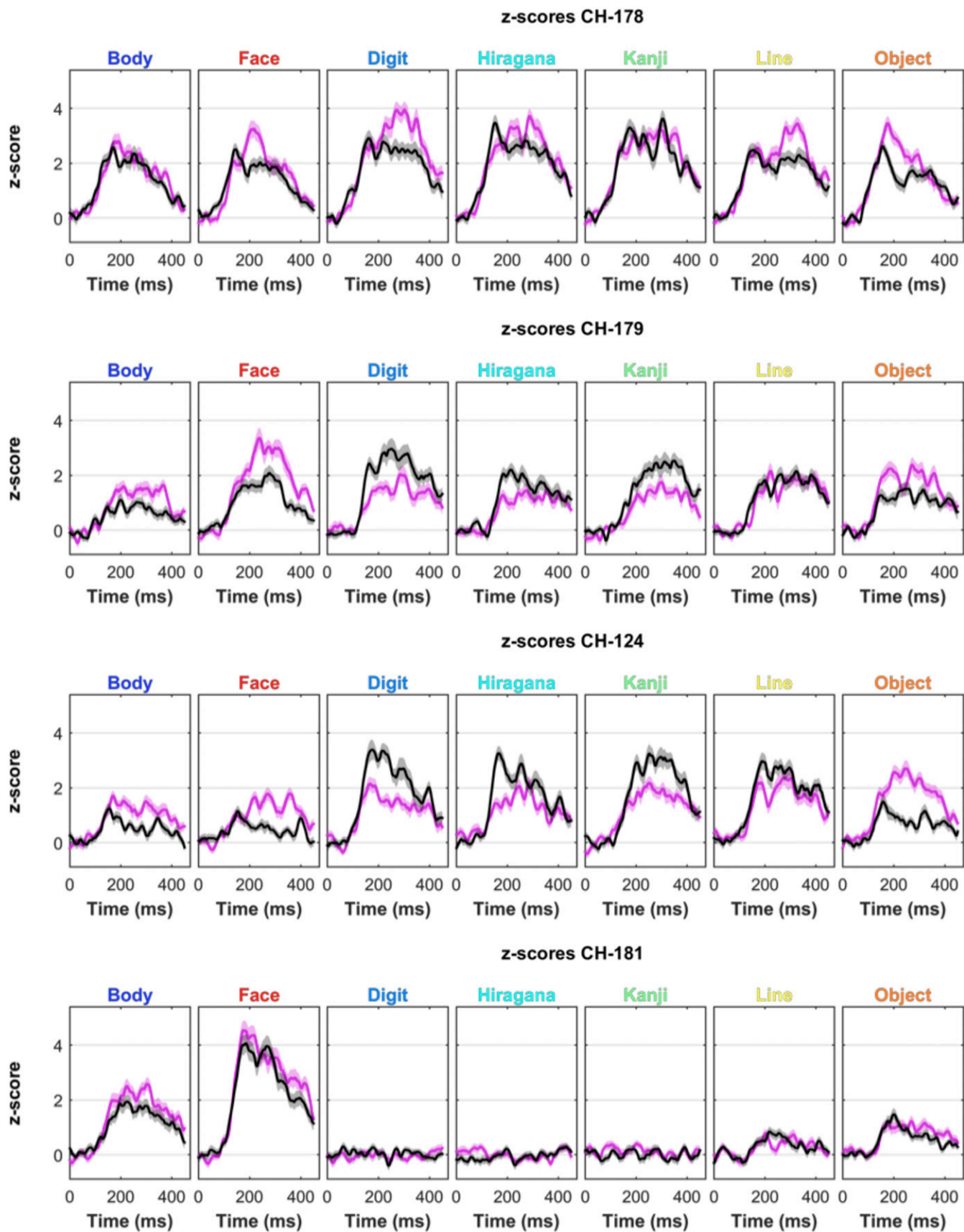
**Face.**  
 S: "No change."  
 E: (English explanation)

**Kanji character.**  
 S: "No change at all."  
 E: (English explanation)



**Fig. S1.** Time course of ECoG broadband gamma responses for each fusiform electrode for faces (red traces), objects (blue traces), colored stimuli (purple traces), and black/white stimuli (black traces). Response magnitude is the average across trials of the z-score calculated separately for each trial with respect to the prestimulus baseline from all trials. Solid lines give response mean; colored shading gives its SE across trials. LH, left hemisphere; RH, right hemisphere.





**Fig. S3.** Time course of broadband gamma power for color (purple) and grayscale (black) conditions for each of the stimulus categories for the two electrodes that showed a significant interaction of color  $\times$  category (electrodes 124 and 179) and (for comparison) for a face-selective electrode (181) and a color-prefering electrode (178) that did not show a significant interaction of color  $\times$  category. Interestingly, the interaction in electrodes 124 and 179 reflects a color preference only for the photograph stimuli (body, face, object), not for the symbol/line drawing stimuli, for which the response is higher for the black and white than color versions. Also note that stimulation of electrode 179 produced weak color percepts.

