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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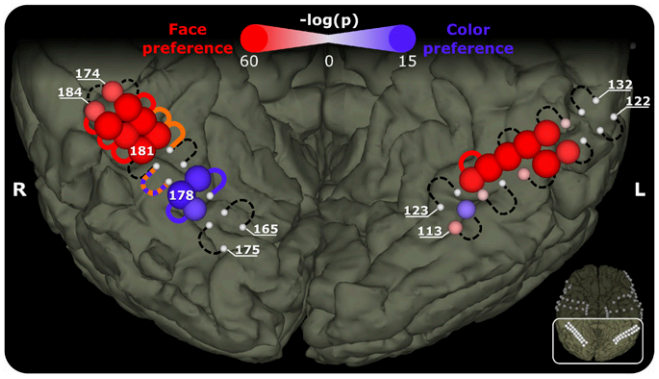

Fig. 1. Location and significance [in −log(p)] of preference for faces > objects (red) and color > grayscale (blue) of ventral electrodes. Arcs show electrode pairs that were stimulated, with arc color indicating resulting percepts: red for faces, orange for eyes, blue for colors, and dashed black for 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 greyscale. 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 V4α (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 × 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

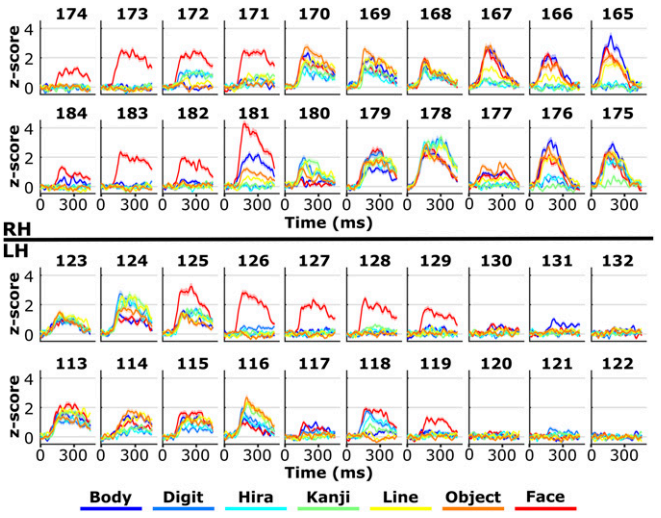

Fig. 2. Time course of ECoG broadband gamma responses for each category in each recording location. Response magnitude is given in z-scores that indicate single-trial response magnitude with respect to baseline. Solid lines give response mean; colored shading gives its SE. LH, left hemisphere; RH, right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

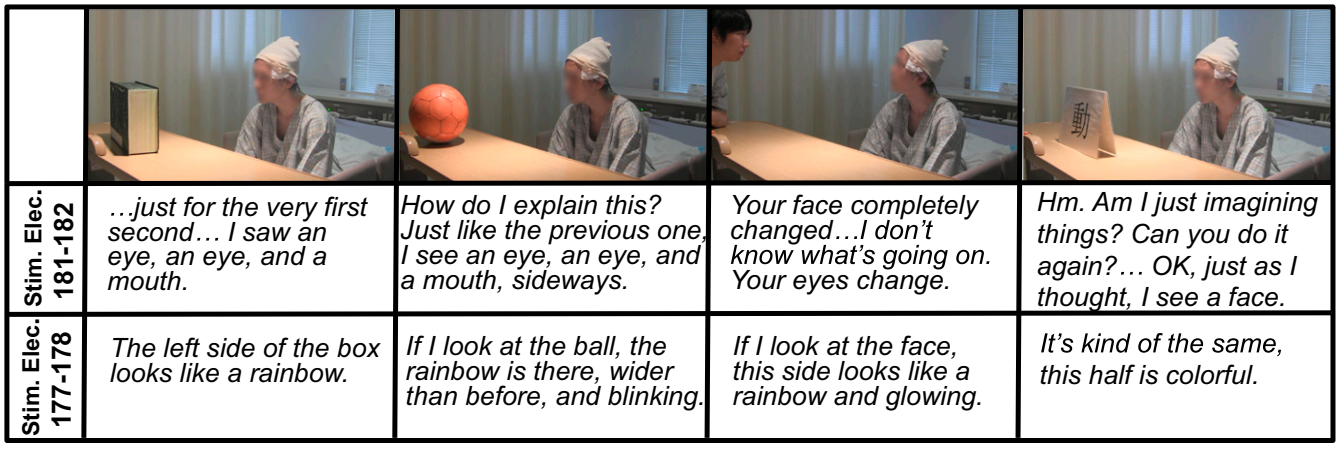

Fig. 3. Transcript excerpts from patient's report during electrical stimulation of electrodes 181–182 (FFA) and 177–178 (color-preferring site) while viewing a box, a ball, the experimenter's face, or a kanji character. For full transcript see *Transcript of Entire Stimulation Session*; for excerpted 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.HIamp 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.HIsys 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-μs 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 FAA 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 V4α (21). V4α is also known as "V8" (34), part of the VO complex (35), and the "central color" region (17).

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