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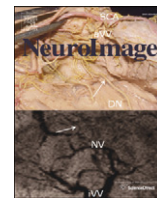
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## Interaction between the electrical stimulation of a face-selective area and the perception of face stimuli

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### ABSTRACT

We electrically stimulated the face-selective area in epileptic patients while they were performing a face-categorization task. Face categorization was interfered by electrical stimulation but was restored by increasing the visual signal. More importantly, face-categorization interference by electrical stimulation was confined to face-selective electrodes, and the amount of interference was positively correlated with the sensitivity of the face-selective electrodes. These results strongly support the hypothesis that the face-selective area has a direct causal link to face perception.

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### Introduction

Face recognition is an important ability for humans as social animals (Adolphs, 2003). Faces convey information about the species, gender, age, identity, intentions, and mood of an individual. Owing to the importance of face recognition, a large number of studies have investigated the underlying neural mechanisms. Wide networks of brain areas in the ventral stream (Allison et al., 1994; Haxby et al., 1994; Kanwisher and Yovel, 2006) and in the frontal lobe (Tsao et al., 2008) have been associated with face processing. However, relatively few attempts have been made to investigate how selective these areas are for faces. Moreover, no study investigated how changes in the activity of a face-selective region due to electrical stimulation interact with the strength of face stimuli and the perception of these stimuli.

Although the interaction between electrical stimulation and the strength of stimuli has not been investigated, direct modulation of activity in the face-selective region showed a strong relationship between the brain region and face perception. Stimulating the right occipital area of normal participants with transcranial magnetic stimulation has been shown to disrupt the discrimination of face parts (Pitcher et al., 2007). Moreover, electrical stimulation of the fusiform

gyrus in epileptic patients disrupted face naming (Allison et al., 1994; Jonas et al., 2012) and face discrimination (Mundel et al., 2003). In monkeys, microstimulation on small patches of the inferotemporal cortex facilitated face categorization, and this effect was positively correlated with the face selectivity of the stimulated patches (Afraz et al., 2006). Although the relationship between the selectivity of face responses and the effect of stimulation on face perception has been parametrically investigated in monkeys (Afraz et al., 2006), no attempt has been made to investigate this relationship in humans. Moreover, how the modulation of neural activity by direct electrical stimulation interacts with the strength of physical stimuli has not been investigated previously. In addition, it is important to stimulate a face-selective region while participants view actual stimuli. Murphey et al. (2009) electrically stimulated higher visual areas without presenting stimuli. They found that it was difficult to evoke complex percepts such as faces by electrical stimulation. Therefore, we presented faces and varied their strength when a face-selective region was electrically stimulated.

To investigate the effect of electrical stimulation on a face-selective region, we defined this region using both the anatomical location based on previous studies (Supplemental references) and the neurophysiological criterion of the N200. We considered the fusiform gyrus as the most likely candidate of a face-selective region based on previous studies (Supplemental references). Moreover, we measured intracranial field potentials (Liu et al., 2009) to define face-selective electrodes neurophysiologically. Specifically, we measured the N200 component, which is known for its selectivity to faces over other stimuli (Engell and McCarthy, 2010, 2011; Liu et al., 2009; McCarthy et al., 1999;

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Rosburg et al., 2010). The amplitude of the N200 is known to indicate how selective an electrode is for faces over other stimuli (Engell and McCarthy, 2010, 2011; McCarthy et al., 1999). Therefore, we used the amplitude differences of the N200 between faces and scenes to define the degree of face selectivity.

In this study, we electrically stimulated a face-selective region while participants were performing a face categorization task. To test whether there is a direct relationship between the degree of face selectivity and face perception, we used patients with drug-intractable partial epilepsy. These patients gave us a rare chance to modulate a specific brain region while they were performing a visual task. We found that electrical stimulation interfered with face categorization and that the amount of this interference was correlated with the degree of face selectivity. In addition, this interference was reduced by increasing the face signal.

## Materials and methods

### Participants

Eight patients with drug-intractable partial epilepsy (4 females and 4 males; 14–52 years old; all right-handed) participated in the study after signing written informed consent forms. They had subdural electrodes placed around the fusiform gyrus to localize seizure origins before epilepsy surgery. For 2 minor patients, written informed consent was obtained from themselves as well as from their parents. The clinical characteristics of the patients are shown in Table 1. Four patients had electrodes on the right hemisphere. All tests conformed to the guidelines of the Institutional Review Board at Samsung Medical Center (Seoul, Korea). During the experiment, the patients were sitting or leaning against pillows on a bed facing a CRT monitor with a viewing distance of approximately 50 cm.

The stainless steel electrodes had a diameter of 5 mm and were implanted with an inter-electrode distance of 10 mm (Lee et al., 2000). Electrodes were arranged in grids or strips. The number of electrodes and their positions were determined by a neurologist (SBH) and a neurosurgeon (SCH) after reviewing all of the presurgical evaluation results, including a detailed clinical history of seizures, electroencephalogram (EEG) readings, brain magnetic resonance images (MRI), brain single-photon emission computed tomography (SPECT) results, brain 18F-fluorodeoxyglucose positron emission tomography (FDG-PET) readings, Wada test results, and neuropsychological evaluation results, to localize an epileptic focus and map brain functions over that region.

### Anatomical localization of electrodes

To localize the cortical positions of intracranial subdural electrodes, brain CT images showing the electrodes were co-registered with brain MR images for each patient. MR images were obtained with a GenesisSigna 1.5 T unit (GE Medical Systems, Milwaukee, WI, USA), and CT images were obtained with a LightSpeed CT scanner (GE Medical

Systems). Spoiled gradient-recalled 3-dimensional volumetric MR images were acquired in 124 coronal slices (matrix size = 256 × 265; slice spacing = 1.6; slice thickness = 1.6; TR = 30 s; TE = 7 s; FOV = 22 cm). Thirty to 65 CT images were acquired in axial slices. The tube current was 220 mA, and voltage was 120 kVp (matrix size = 512 × 512; No-gap; slice thickness = 3 mm; FOV = 21 cm).

The locations of the electrodes in the CT images were transformed onto MR images using both 3D Slicer (<http://www.slicer.org>) and FMRIB's Linear Image Registration Tool (FLIRT, Jenkinson and Smith, 2001). MR images with electrode locations were transformed into MNI coordinates by FLIRT and then to Talairach coordinates (Talairach and Tournoux, 1988) using the algorithm of Lancaster et al. (2007). We evaluated the acquired Talairach coordinates to determine whether the electrodes were within the face-selective areas as defined by previous research. We used reported fusiform face area (FFA) coordinates from 32 studies that localized human FFA using neuroimaging techniques, including subdural electrodes (Allison et al., 1994; Haxby et al., 1994; see the complete list in Supplemental references).

### Neurophysiological localization of electrodes

We recorded intracranial field potentials to measure the face selectivity of the electrodes using SynAmps amplifiers and Neuroscan software (Compumedics, Charlotte, NC, USA). A Stim2 visual stimulator (Compumedics) was used for the visual presentation of the stimuli. Four categories of images (faces, scenes, scrambled images, and butterfly images) were presented to the patients while recording the intracranial field potentials. Faces were viewed frontally with neutral expressions, and scene images were landscapes with both natural and artificial objects. Scrambled images were composed of both face and scene images by dividing the original images into one hundred cells (each cell 30 × 30 pixels) and randomly shuffling them. All of the images were 300 × 300 pixels (8.94° by 8.94°) and gray-scaled with a RMS contrast of 30%.

Intracranial field potentials were obtained in 2 successive recording sessions for each patient. Each session consisted of either 100 or 200 trials. The number of trials varied depending on the patients' availability. The stimulus duration was 250 ms and the inter-stimulus intervals varied randomly from 1.8 to 2.2 s (Allison et al., 1994). Patients were instructed to press a button when they saw a butterfly, which infrequently appeared (10% of the trials) in order to draw the patients' attention. Intracranial field potentials were acquired from electrodes using a gain of 10,000 and a bandpass filter of 0.1–100 Hz. Recordings were referenced to the vertex and digitized at a sampling rate of 250 Hz.

The recorded intracranial field potentials were pre-processed using baseline correction, linear detrending and a band pass-filter (1–30 Hz; 24 dB/oct; zero phase shift). The intracranial field potentials were segmented into 700 ms epochs, from 200 ms before the onset of stimuli to 500 ms after the onset. The epochs were analyzed by repeated-measures ANOVA to compare the averaged potentials of

**Table 1**  
Clinical characteristics of the patients.

No	Sex	Age (years)	Handedness	Epilepsy type	Epileptic focus	MRI findings	Epileptic discharges in FSA
1	Male	52	R	R TLE, symptomatic	R mesial temporal	R HS	No
2	Female	20	R	R FLE, cryptogenic	R orbitofrontal	Normal	No
3	Female	32	R	R TLE, symptomatic	R mesial temporal	R HS	No
4	Female	44	R	R PLE, cryptogenic	R parietal	L HS	No
5	Male	17	R	L TLE, symptomatic	L mesial temporal	L DNET in anterior temporal	No
6	Male	14	R	L TLE, symptomatic	L mesial temporal	L DNET in mesial temporo-occipital	No
7	Female	34	R	L TLE, symptomatic	L mesial temporal	B HS	No
8	Male	32	R	L TLE, symptomatic	L lateral temporal	R CD	No

R, right; L, left; B, bilateral; TLE, temporal lobe epilepsy; FLE, frontal lobe epilepsy; PLE, parietal lobe epilepsy; HS, hippocampal sclerosis; FSA, face-selective area; DNET, dysembryoplastic neuroepithelial tumor; CD, cortical dysplasia.

each electrode between 150 ms and 250 ms after the onset of the stimulus. When the N200 component to face images was significantly more negative than that to scene images ( $p < 0.05$ ), we categorized that electrode as face-selective. To quantify the degree of selectivity for face versus scene images, we defined the  $d'$  index (Afraz et al., 2006) of each electrode by applying the following formula:

$$d' = \frac{M(f) - M(s)}{\sqrt{\frac{\sigma^2(f) + \sigma^2(s)}{2}}}$$

Here,  $M(f)$  and  $M(s)$  indicate the mean amplitude averaged within the time window of 100 ms (between 150 ms and 250 ms post-stimulus) to face and scene images, respectively, and  $\sigma^2(f)$  and  $\sigma^2(s)$  indicate the variances of the mean amplitude across trials of face and scene images, respectively. The higher the  $d'$  index of an electrode, the more selective it was for faces compared with scenes.

*Electrical stimulation experiment*

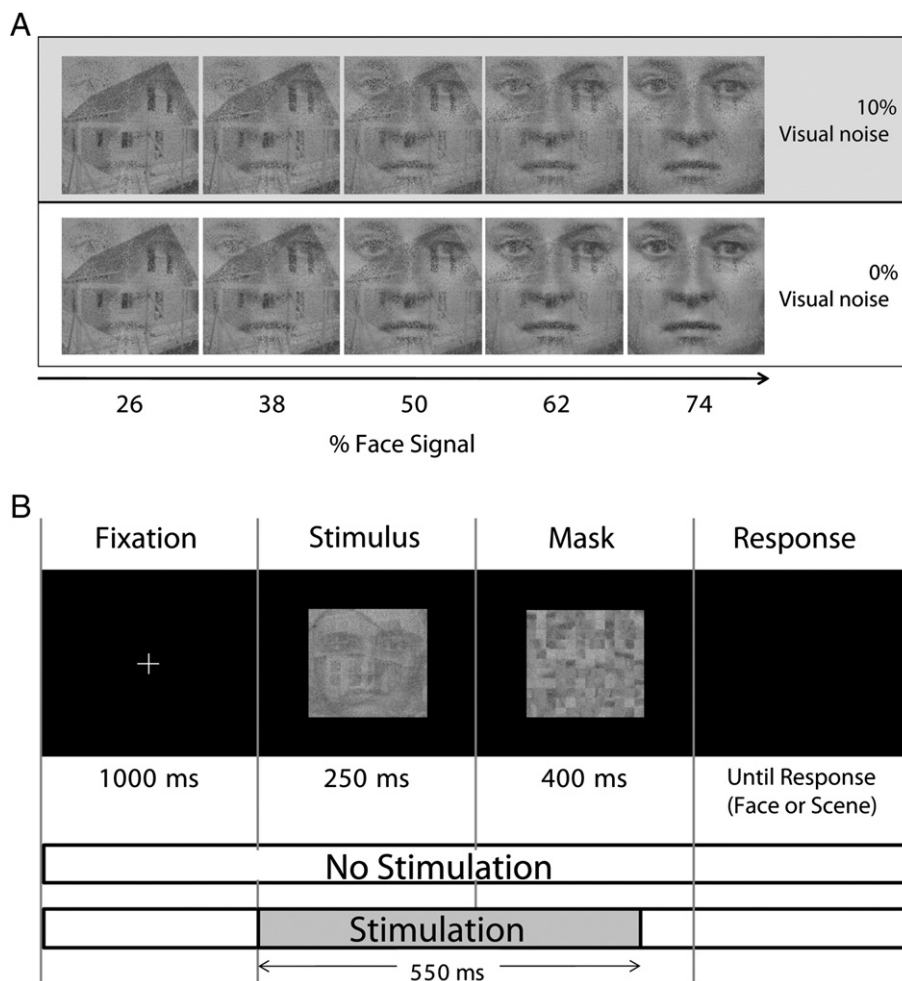
Electrical stimulation was controlled by a PC using the psychophysics toolbox (Brainard, 1997). Visual stimuli were presented on a 17-inch Samsung monitor at a refresh rate of 75 Hz. Patients categorized the stimuli with a response box. A Grass S12 Isolated Biphasic Stimulator (Grass Instrument Co., Quincy, MA, USA) was used for the electrical stimulations. The stimulator was triggered by a custom-built electric circuit, which was controlled by the same computer.

Electrical stimulation was done using 2 electrodes as a pair because the electric potential differences between two electrodes were necessary to generate electric currents.

Electrical stimulation was given while patients were categorizing visual stimuli as faces or scenes (Fig. 1B). Compound images were used in this categorization task (Fig. 1A). The compound images were generated by mixing a certain percentage of a face image with a certain percentage of a scene image. For example, 60% of pixels randomly selected from a face image replaced 60% of a scene image at the corresponding locations, generating a compound image with 60% of a face signal. Note that it became easier for participants to categorize stimuli as faces as the face signal percentage increased. A set of compound images for each patient had 5 or 7 levels of face signal percentages depending on the patients' availability. In addition, we added visual noise to the compound images by randomly rearranging 10% of the pixels in each stimulus, thus making the categorization task more difficult.

We used the compound images without additional noise for 4 out of 8 patients. This was done to determine how the strength of the face stimuli interacts with electrical stimulation. Without the noise, the visibility of the stimuli increased such that the images were easier to categorize as faces at the same face signal percentage. Every aspect of this condition was identical to those in the stimulation except that we used compound images without visual noise.

After the presentation of a compound image, a mask was presented to control the duration of the display and to prevent the formation of afterimages. The mask was generated by randomly scrambling the positions of the cells (each cell:  $30 \times 30$  pixels) of



**Fig. 1.** (A) Examples of compound images. The upper panel shows images with 10% visual noise and the lower panel shows images without visual noise. (B) The sequence of stimulus presentation and the time window of electrical stimulation.



the original compound images. Each trial started with a fixation cross (0.298° by 0.298°) on a black background that lasted for 1000 ms (Fig. 1B). The compound images were presented for 250 ms after the fixation cross, followed by a mask for 400 ms.

Electrical stimulation was in the form of a single train with bipolar current pulses, given for 550 ms from the onset of the compound images. The pulse duration was 0.3 ms and the pulse interval was 50 Hz. The current of the pulse for most of the patients was 2.5 mA. (In some sessions, we increased the current pulses to 5.5 or 7.5 mA for patients 3 and 4.)

An experimental block consisted of 10 or 14 trials (stimulation or no stimulation × 5 or 7 face signal levels). A session comprised 30 blocks, and the trial sequence was always re-randomized after a block. Each patient performed 4 to 7 sessions depending on his or her availability.

We plotted the percentage of “face” responses against the percentage of the face signal level depending on the stimulation conditions (Fig. 2A). The range of the face signal level for each patient was varied to acquire a precise point of subjective equality (PSE). We then fitted a Weibull function to the data with 1999 iterations using the Psignifit toolbox version 2.5.6 for Matlab (see <http://bootstrap-software.org/psignifit/>), which implemented the maximum-likelihood method described by Wichmann and Hill (2001). The PSE was defined as the face signal percentage necessary to reach the criterion of 50% “face” responses on the fitted function. The PSE indicates the point at which a participant subjectively perceived stimuli as a face in 50% of the trials. We considered non-overlapping 95% confidence intervals as significant differences.

#### Control experiment

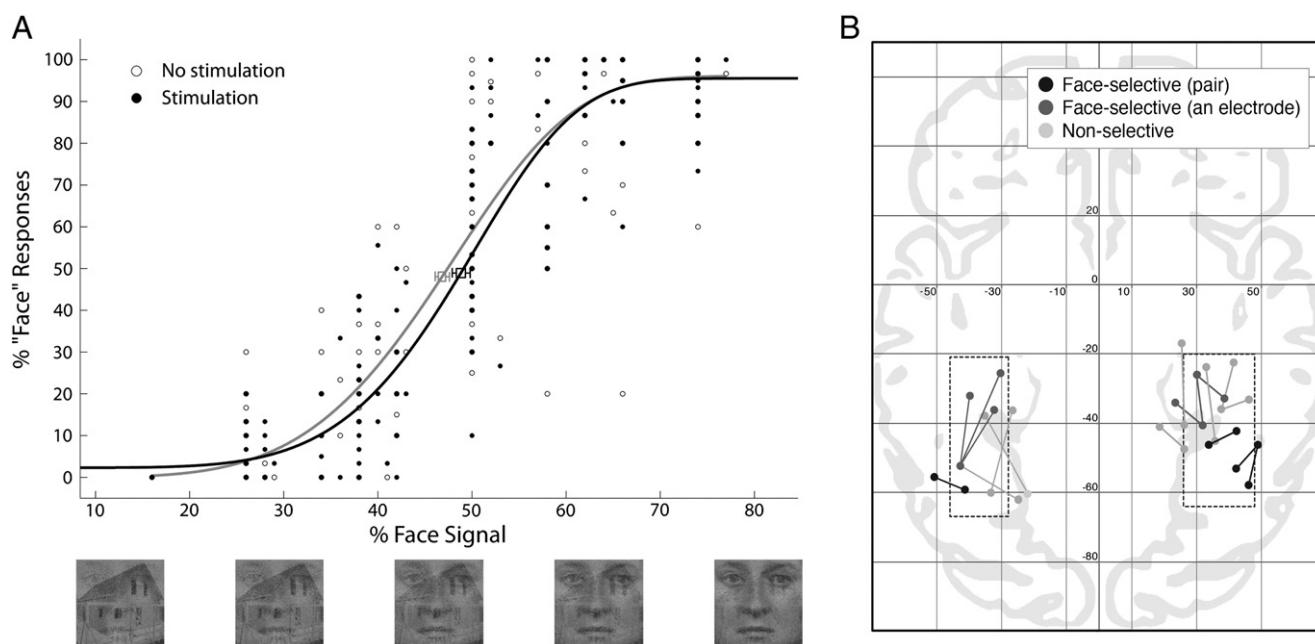
Five Yonsei graduate students (1 female and 4 males; 25–31 years old; all right-handed) participated in the control experiment. They performed a face categorization task either with or without visual noise to estimate the amount of PSE shift depending on the visual noise. A set of compound images for each participant had 5 levels of

face signal percentage, equally spaced around 50% (Fig. 1A). An experimental block consisted of 10 trials (5 face signal levels × 2 levels of visual noise). A session consisted of 30 blocks, and each participant performed 2 sessions.

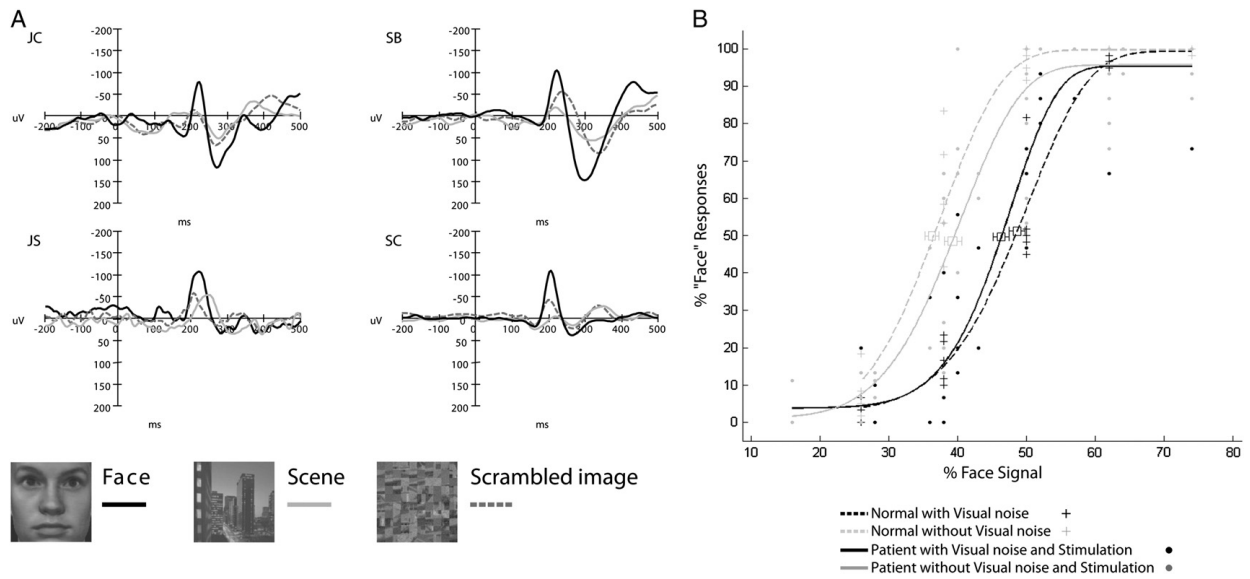
#### Results

We investigated 8 epileptic patients who had subdural electrodes implanted around the fusiform gyrus for clinical purposes. We first determined the exact locations of the implanted electrodes by co-registering CT images on MR images. As shown in Fig. 2B, most of the electrode locations were within the range of the face-selective area as defined by previous studies (Allison et al., 1994; Haxby et al., 1994; see the complete list in Supplemental references). The dotted box in Fig. 2B indicates the face-selective region defined by the maximum and the minimum Talairach coordinates in previous studies. We stimulated 2 electrodes at a time and considered electrodes as face-selective if at least one of the 2 stimulated electrodes was within this region (the diameter of an electrode was 5 mm). The size of the 2 simultaneously stimulated electrodes was similar to the size of the previously described face-selective region (in humans: 155 1 × 1 × 1 mm voxels, Grill-Spector et al., 2006; in monkeys: 16 × 16 mm, Tsao et al., 2008).

We first investigated the effect of electrical stimulation on face categorization using all the electrodes (20 pairs of electrodes) within an anatomically defined face region (the dotted box in Fig. 2B) from all patients. We included all the electrodes in this first analysis because we pre-selected potential face-selective electrodes based on preliminary online analyses of intracranial field potentials and their anatomical locations. This also allowed us to minimize the duration of the experiment to meet the patients' availability. Fig. 2A plots the percentage of face responses against the face signal percentage. The PSE increased significantly under electric stimulation (48.81%) as compared to the no-stimulation condition (46.83%). Although the difference between the stimulation and no-stimulation conditions was small, the PSE between the 2 conditions did not overlap with a 95%



**Fig. 2.** (A) Percentage of “face” responses as a function of the face signal percentage. Patients’ face categorization performance levels significantly decreased with electrical stimulation (black) relative to no stimulation (gray). The error bars indicate a confidence interval of 95% based on 1999 bootstraps. (B) Talairach coordinates of the electrodes. We reviewed 32 papers to define the face-selective region. The dotted box includes all the face-selective areas in previous studies [coordinates: from 26, –20 (X, Y) to 48, –64 (X, Y) in the right hemisphere and from –28, –21 (X, Y) to –46, –67 (X, Y) in the left hemisphere]. We defined a pair of electrodes as face-selective if both neurophysiological and anatomical criteria were satisfied. Black dots indicate when both electrodes within a pair are face-selective. Dark gray dots indicate when one electrode within a pair is face-selective. Light gray dots indicate non-selective electrodes.



**Fig. 3.** (A) N200 responses from 4 representative patients. Intracranial field potentials were plotted against time. Negativity around 200 ms to faces was significantly higher than that to scenes (all  $p$ 's < .05). (B) The black solid line indicates patients' performance of face categorization with both visual noise and stimulation. When visual noise was removed from the stimuli, performance increased even with electrical stimulation (solid gray). The amount of improvement was similar to that of normal controls (dotted light gray: without visual noise, dotted black: with visual noise). The error bars indicate the confidence interval of 95% based on 1999 bootstraps.

confidence interval. Because we stimulated targeted electrodes only for 550 ms, we expected a smaller effect of electrical stimulation than in previous studies (Allison et al., 1994; Jonas et al., 2012; Lee et al., 2000; Mundel et al., 2003). The duration of stimulation in previous work was substantially longer compared to our study (Allison et al., 1994; Jonas et al., 2012; Lee et al., 2000: 5 s, Mundel et al.: 10 s). The duration of stimulation in our study was short because we wanted to present the stimulation condition randomly intermixed with the no-stimulation condition. These results suggest that electrical stimulation of the FFA interferes with face perception, consistent with previous studies (Allison et al., 1994; Jonas et al., 2012; Mundel et al., 2003; Pitcher et al., 2007).

To further specify the selectivity of the electrodes, the response of the N200 component to face stimuli (Allison et al., 1994) was measured before stimulation (Fig. 3A). Fig. 4A plots the amount of PSE shift as a function of the face selectivity of the electrodes. The amount of shift represents the PSE difference between the no-stimulation and stimulation conditions. Therefore, a positive PSE difference indicates the magnitude of the interference of face categorization due to stimulation in terms of the face signal, whereas a negative difference indicates the facilitation of face categorization. We defined electrodes as face-selective when one of the 2 locations of an electrode pair was within the face-selective area (Fig. 2B) and when the N200 was significantly larger for faces than for scenes (all  $p$ 's < 0.05). We further divided face-selective electrodes into 2 categories: in the first

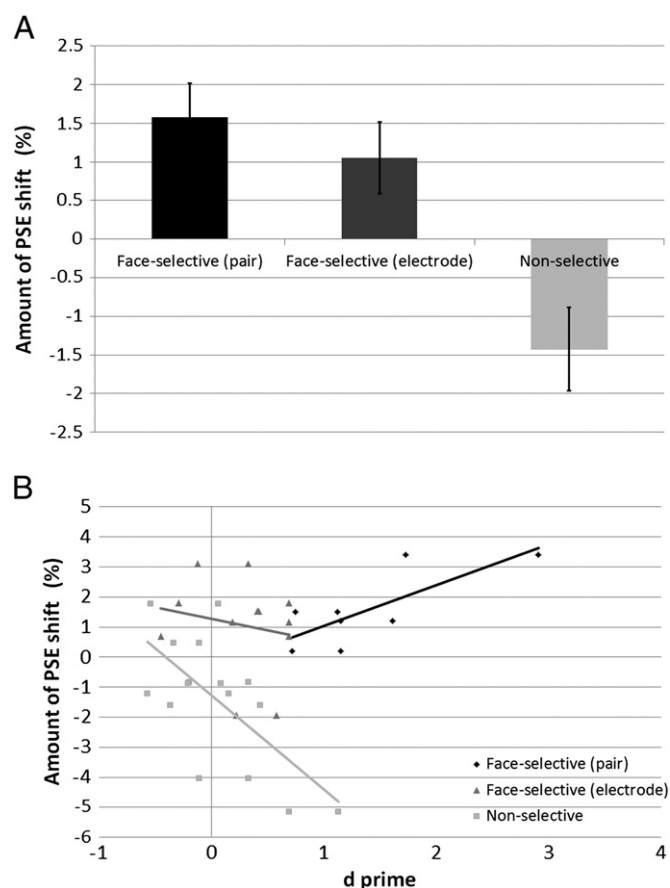
category, both electrodes within a pair were face-selective, whereas only one electrode was face-selective in the other category. When either of the 2 criteria was not met, we categorized these electrodes as non-selective. Out of 20 pairs of electrodes, there were 4 pairs of face-selective electrodes (pair), 6 pairs of partially face-selective electrodes (an electrode), and 8 pairs of non-selective electrodes. Two remaining pairs of electrodes could not be classified because the intracranial field potentials for one electrode of each pair were not recorded due to technical problems.

When both of the electrodes were face-selective, the amount of PSE shift (1.58%) due to electrical stimulation was significantly higher than 0 ( $t(7) = 3.58, p = .009$ ), suggesting that electrical stimulation within the face-selective region interfered with face categorization. Even when only one electrode within a pair was face-selective, the amount of PSE shift (1.05%) was significantly higher than 0 ( $t(11) = 2.28, p = .044$ ).<sup>1</sup> However, the amount of PSE shift (−1.42%) was significantly lower than 0 for the non-selective electrodes ( $t(15) = -2.63, p = .019$ ). Therefore, electrical stimulation of the face-selective electrodes interfered with face perception, whereas electrical stimulation of the non-selective electrodes facilitated face perception. Furthermore, the amount of shift was positively correlated with the  $d'$  value of the face-selective electrodes (Fig. 4B black line,  $r = 0.77, p = .026$ ), whereas negative correlation was found for the non-selective electrodes (light gray line,  $r = -0.66, p = .005$ ). These correlation results rule out the possibility that electrical stimulation disrupted visual perception in general. When the non-selective electrodes were stimulated, the effect of electrical stimulation was manifested in the opposite way as compared to when the face-selective electrodes were stimulated. Therefore, stimulation per se does not cause the interference of face categorization.

Electrical stimulation interfered with face perception when stimulated electrodes were face-selective. If electrical stimulation either generated random neural noise or weakened the face signal (Harris et al., 2008), strengthening the signal of a face stimulus would counteract the effect of stimulation. We increased the face signal by relocating randomly positioned pixels to their original locations and repeated the same stimulation experiment. When we increased the visibility of the stimuli by removing stimulus noise, the effect of electrical stimulation was reduced (Fig. 3B). Due to the limited time, we could not investigate the condition in which electrical stimulation was not given when patients did a face-categorization task without visual noise. However, we instead measured normal controls' PSE shifts depending on the presence of visual noise. We found that the amount of PSE shift in normal controls (from 48.65% to 36.53%) was similar to that in the patients (from 46.40% to 39.22%) despite the fact that only the patients underwent electrical stimulation. To the best of our knowledge, these results are the first demonstration of the interaction between the strength of the visual signal and the strength of the neural signal in humans. These findings suggest that increased strength of physical stimuli can counteract the interference of face categorization by electrical stimulation. These results are consistent with a monkey microstimulation study in which mostly additive effects were noted between electrical and visual stimulation (Moeller et al., 2008).

## Discussion

We investigated how the electrical stimulation of a face-selective region influenced face categorization. Electrical stimulation interfered with face categorization, and this trend was pronounced only in the face-selective electrodes. Moreover, the more face-selective the electrodes were, the stronger the effect of stimulation on face categorization



**Fig. 4.** (A) Amount of PSE shift depending on the face-selectivity of electrodes. The black bar indicates face-selective electrodes (both electrodes), the dark gray bar indicates partially selective electrodes (an electrode), and the light gray bar indicates non-selective electrodes. The effect of electrical stimulation was varied depending on the face-selectivity of the electrodes. (B) In the face-selective electrodes (both electrodes), the face selectivity of electrodes ( $d'$ ) was positively correlated with the effects of electrical stimulation on face categorization (black), whereas the selectivity of the non-selective electrodes was negatively correlated with these effects (light gray).

<sup>1</sup> We also analyzed the amount of PSE shift based on electrode pairs and found essentially the same results. As long as one of two electrodes was face-selective, the amount of PSE shift was significantly larger than 0,  $t(9) = 2.66, p = .026$ .

was. The impairment of face perception due to electrical stimulation could be offset by increasing the strength of the face signal.

The organization principles of higher visual areas are very important when seeking to understand the neural mechanism of object recognition. There are several principles of organization in higher areas. The first is retinotopic organization (Malach et al., 2002). This retinotopic organization has functional significance depending on the resolution required for object recognition. For example, faces are processed in the foveal region of higher areas because fine resolution is needed for recognizing faces (Levy et al., 2001). The second is columnar organization. For example, the inferotemporal cortex in monkeys is organized by columns for visual features (Fujita et al., 1992), and higher areas in humans have category-specific modules (Grill-Spector et al., 2001, but see also Gauthier et al., 1999). The third principle is distributed representation, as higher object areas show mild activation bias towards different object categories (Haxby et al., 2001; Ishai et al., 1999).

The electrodes used in the current study covered a fairly large area (right hemisphere: about 877 mm<sup>2</sup>, left hemisphere: about 701 mm<sup>2</sup> based on surface area in Talairach coordinates) and the face-selectivity of the electrodes varied across this area, consistent with previous research (Engell and McCarthy, 2011). The modulation of face-selectivity was positively correlated with face categorization performance. Although we cannot rule out the retinotopic organization or columnar representation hypotheses, our results support the distributed representation hypothesis because the effect of stimulation varies depending on the category-selectivity of the electrodes and because the degree of selectivity is diverse across the area.

Electrical stimulation of a face-selective region can disrupt face naming (Allison et al., 1994; Jonas et al., 2012), face discrimination (Mundel et al., 2003), and face categorization (our results). Stimulation can disrupt the ongoing processing of faces by either suppressing the face signal or increasing the amount of neural noise. Because neural noise from the stimulation was canceled out by strengthening the face stimuli, electrical stimulation in our study may have generated neural noise in the face-selective region. This conclusion is consistent with the previous finding that electrical stimulation by TMS generated neural noise (Harris et al., 2008). However, in monkey studies, microstimulation either facilitated performance (Afray et al., 2006) or increased the neural signals (Moeller et al., 2008). These differences between monkey and human studies are likely due to the location and size difference of the electrodes and the stimulation parameters. The size of the electrodes was much smaller in the monkey studies, and the amplitude of the stimulation was also very low in those studies.

In summary, we found that the electrical stimulation of the human face-selective area, but not other sites, interfered with face perception. Furthermore, the amount of interference could be offset by increasing the visual signal. Our results demonstrate a direct causal link between the activity in the FFA and face perception.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2013.01.074>.

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## Conflict of interest statement

The authors declare that there is no conflict of interest.

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