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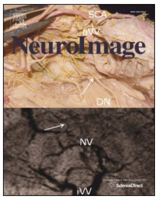

Upright face-preferential high-gamma responses in lower-order visual areas: Evidence from intracranial recordings in children

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ABSTRACT

Behavioral studies demonstrate that a face presented in the upright orientation attracts attention more rapidly than an inverted face. Saccades toward an upright face take place in 100–140 ms following presentation. The present study using electrocorticography determined whether upright face-preferential neural activation, as reflected by augmentation of high-gamma activity at 80–150 Hz, involved the lower-order visual cortex within the first 100 ms post-stimulus presentation. Sampled lower-order visual areas were verified by the induction of phosphenes upon electrical stimulation. These areas resided in the lateral-occipital, lingual, and cuneus gyri along the calcarine sulcus, roughly corresponding to V1 and V2. Measurement of high-gamma augmentation during central (circular) and peripheral (annular) checkerboard reversal pattern stimulation indicated that central-field stimuli were processed by the more polar surface whereas peripheral-field stimuli by the more anterior medial surface. Upright face stimuli, compared to inverted ones, elicited up to 23% larger augmentation of high-gamma activity in the lower-order visual regions at 40–90 ms. Upright face-preferential high-gamma augmentation was more highly correlated with high-gamma augmentation for central than peripheral stimuli. Our observations are consistent with the hypothesis that lower-order visual regions, especially those for the central field, are involved in visual cues for rapid detection of upright face stimuli.

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Introduction

The human brain has a remarkable ability to efficiently recognize faces. Behavioral studies have shown that picture stimuli containing the faces of living things, compared to those with other non-face objects, more rapidly attract gazes from healthy participants, including infants (Quinn and Eimas, 1998) and adults (Kirchner and Thorpe, 2006; Fletcher-Watson et al., 2008). Among the most investigated features of human face recognition is its selectivity to upright orientation (Farah et al., 1998; Haxby et al., 1999; Yovel and Kanwisher, 2004). A face presented in the upright orientation, compared to one flipped upside down, is more easily recognized and automatically draws earlier and more sustained attention from healthy infants (Valenza et al., 1996; Quinn et al., 2009) and adults (Hochberg and Galper, 1967; Yin, 1969). Furthermore, preferential saccades toward an upright face take place within 100–140 ms following presentation (Kirchner and Thorpe, 2006; Crouzet et al., 2010), demonstrating that detection of an upright face occurs quite early in visual processing.

Neural correlates of face recognition have been extensively examined using functional MRI (fMRI) (Puce et al., 1995; Kanwisher et al., 1997; Summerfield et al., 2006; Mendola and Buckthought, 2013) and electrocorticography (ECoG) (Miller et al., 2009; Engell and McCarthy, 2010; Vidal et al., 2010). These studies have consistently localized regions of face-selectivity around the fusiform and inferior occipital gyri. Disruption of the region around the inferior occipital gyrus using repetitive transcranial magnetic stimulation (rTMS) at 60 and 100 ms after presentation of face stimuli impairs performance on a discrimination task with face parts, demonstrating the early involvement of face-selective areas in face processing (Pitcher et al., 2007). Combined with the observed preferential saccades to upright faces within 100 and 140 ms of stimulus presentation (Kirchner and Thorpe, 2006; Crouzet et al., 2010), these short timescales highlight the rapid nature of face detection and processing. Our knowledge of the time course of face processing is further informed by the findings from ECoG studies that activity for face stimuli, compared to non-face stimuli, elicit greater high-gamma augmentation in the ventral occipital–temporal junction at 200–300 ms after the onset of stimulus presentation (Engell and McCarthy, 2010; Vidal et al., 2010).

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The roles of lower-order visual cortex in face recognition have been relatively under-reported. Taking into account that speeded saccadic responses toward an upright face take place as early as 100 ms, it is feasible to hypothesize that the lower-order visual cortex is involved in low-level visual cues for saccades toward upright face stimuli at <100 ms (Crouzet et al., 2010; Rossion and Caharel, 2011). In the present study of patients with focal epilepsy who underwent chronic ECoG recording, we investigated this idea using event-related augmentation of high-gamma activity at >80 Hz as a surrogate marker of *in-situ* cortical activation. The strengths of measurement of ECoG high-gamma augmentation include: (i) 20 to >100 times better signal-to-noise ratio compared to noninvasive neurophysiology modality (Ball et al., 2009), (ii) a temporal resolution of <20 ms (Fukuda et al., 2008), and (iii) direct signal sampling from deep structures such as medial and inferior surfaces of the occipital lobes (Uematsu et al., 2013).

In this study, we specifically determined if upright compared to inverted face stimuli would elicit larger high-gamma augmentation in lower-order visual sites at <100 ms following stimuli presentation. We hypothesized that upright face-preferential high-gamma augmentation would involve the lower-order visual regions, especially the portions of these regions dedicated to the central rather than the peripheral field, as humans tend to fixate face parts (such as eyes, nose, and mouth) rather than the facial contour or peripheral background during natural viewing (Birmingham et al., 2013; Vaidya et al., 2014).

Methods

Patients

The inclusion criteria of the present study included: (i) extraoperative ECoG recording as a part of clinical management of medically-uncontrolled seizures at Children's Hospital of Michigan in Detroit, (ii) ECoG sampling from the occipital and occipital–temporal regions, (iii) completion of a visual task described below, and (iv) age of 5 years and above. The exclusion criteria included: (i) brain malformations or seizure onset zone involving the occipital lobe, (ii) oculomotor dysfunction or visual field deficits detected by confrontation, and (iii) severe cognitive dysfunction reflected by verbal comprehension index of <70. The study was approved by the Institutional Review Board at Wayne State University, and written informed consent was obtained from the guardians of all participants.

Subdural electrode placement

Platinum grid and strip electrodes (10 mm intercontact distance, 4 mm diameter) were surgically implanted for extraoperative ECoG recording (Fig. 1; Asano et al., 2009a). All electrode plates were stitched to adjacent plates and/or the edge of dura mater, to avoid movement of subdural electrodes after placement. Intraoperative pictures were taken with a digital camera before dural closure. Planar x-ray images (lateral and anteroposterior) were subsequently acquired with the subdural electrodes in place for electrode localization on the brain surface (Miller et al., 2007; Muzik et al., 2007; Dalal et al., 2008); three metallic fiducial markers were placed at anatomically well-defined locations on the patient's head for co-registration of the x-ray image with the T1-weighted spoiled gradient echo MR image. A three-dimensional surface image was finally created with the location of electrodes directly defined on the brain surface (Muzik et al., 2007; Alkonyi et al., 2009). We confirmed the spatial accuracy of electrode display on the three-dimensional brain surface image using intraoperative pictures (Wellmer et al., 2002; Dalal et al., 2008; Pieters et al., 2013). By the age of 5 years, brain size becomes comparable to that of an adult (Dekaban and Sadowsky, 1978), while the youngest patient in the present study was 9 year old. Automatic parcellation of cortical gyri was performed using FreeSurfer software (Desikan et al., 2006), and subdural electrodes were assigned anatomical labels (Pieters et al., 2013; Fig. 1). The regions of interest in the present study included: (i) lingual gyrus, (ii) cuneus gyrus, (iii) lateral occipital region, and (iv) fusiform gyrus posterior to the midbrain (Desikan et al., 2006).

Localization of lower-order visual function by electrical stimulation

We localized lower-order visual areas with electrical stimulation mapping performed as a part of presurgical evaluation of medically uncontrolled focal seizures (Asano et al., 2009b; Zijlmans et al., 2009; Kumar et al., 2012). In short, we defined the lower-order visual areas as the sites at which stimulation constantly resulted in phosphene, or percepts of simple shape, color, or flush light (Murphey et al., 2009; Kim et al., 2013). Areas were not treated as lower-order visual areas if their stimulation elicited other types of visual symptoms, such as distortion (Parvizi et al., 2012). We expected that lower-order visual function would involve the lingual, cuneus, and lateral occipital regions close to the calcarine sulcus.

A train of repetitive electrical stimuli was delivered to a pair of subdural electrodes using the Grass stimulator (Astro-Med, Inc, West Warwick, RI), and clinical symptoms elicited by stimulation were observed by at least two investigators including a neuropsychologist. The stimulus frequency was 50 Hz, the pulse duration was 300 μs, and the train duration ranged up to 2 s. To determine the presence of after-discharges, video-ECoG was recorded continuously during the entire mapping session. When a clinical symptom was elicited, the train of stimuli was immediately terminated. Stimulus intensity was initially set to 3 mA and was increased to 6 and 9 mA in a stepwise manner until a clinical symptom or after-discharge was observed. Once the after-discharge threshold was determined, stimulus intensity above that threshold was no longer utilized. Sites at which stimulation consistently (at least twice) elicited a clinical symptom were classified as eloquent areas specific to a given symptom. Sites were declared 'not proven to be eloquent' if after-discharges were elicited without a symptom, or a symptom failed to be elicited by maximal stimuli. To minimize worry or fear on the part of the patient, each individual was informed prior to the stimulation study that she/he might have a transient sensorimotor, auditory, visual, olfactory, gustatory, or language symptom. Each patient was aware of the timing of each stimulation trial but unaware of the location of stimulated sites.

Extraoperative ECoG recording

Extraoperative video-ECoG recordings were obtained using a 192-channel Nihon Kohden Neurofax 1100A Digital System (Nihon Kohden America Inc, Foothill Ranch, CA, USA). The sampling frequency was set at 1000 Hz with the amplifier band pass at 0.08–300 Hz (Kojima et al., 2013a). The averaged voltage of ECoG signals derived from the fifth and sixth intracranial electrodes of the ECoG amplifier was used as the original reference. ECoG signals were then re-montaged to a common average reference (Korzeniewska et al., 2011; Wu et al., 2011). Channels contaminated with large interictal epileptiform discharges or artifacts were excluded from the common average reference. No notch filter was used. All antiepileptic medications were discontinued on the day of subdural electrode placement. Electrodes overlying seizure onset zones or structural lesions were excluded from further analysis (Jacobs et al., 2009). Surface EMG electrodes were placed on the left and right deltoid muscles, and electrooculography (EOG) electrodes were placed 2.5 cm below and 2.5 cm lateral to the left and right outer canthi.

Task

During video-ECoG recording, a series of visual stimuli were presented to each patient using a 22-inch Dell P2213 LCD monitor (a refresh rate of 60 Hz; a pixel resolution of 1600 × 1050; Dell Inc, Round Rock, TX, USA) placed 60 cm away from the patient. The task lasted approximately four minutes. Each patient completed the task while awake, unsedated, and comfortably seated on the bed in a

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