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Rapid, high-frequency, and theta-coupled gamma oscillations in the inferior occipital gyrus during face processing

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ABSTRACT

Neuroimaging studies have found greater activation in the inferior occipital gyrus (IOG), or occipital face area, in response to faces relative to non-facial stimuli. However, the temporal, frequency, and functional profiles of IOG activity during face processing remain unclear. Here, this issue was investigated by recording intracranial field potentials in the IOG during the presentation of faces, mosaics, and houses in upright and inverted orientations. Time–frequency statistical parametric mapping analyses revealed greater gamma-band activation in the IOG beginning at 110 msec and covering 40–300 Hz in response to upright faces relative to upright houses and mosaics. Phase–amplitude cross-frequency coupling analyses revealed more evident theta–gamma couplings at 115–256 msec during the processing of upright faces as compared with that of upright houses and mosaics. Comparable gamma-band activity was observed during the processing of inverted and upright faces at about 100–200 msec, but weaker activity and different coupling with theta-band activity after 200 msec. These patterns of activity were more evident in the right than in the left IOG. These results, together with other evidence on neural communication, suggest that broadband gamma oscillations in the right IOG conduct rapid and multistage (i.e., both featural and configural) face processing in collaboration with theta oscillations transmitted from other brain regions.

1. Introduction

Faces play an important role in human social interactions owing to the rapid and momentary transmission of various communicative signals from their features/parts (e.g., gaze directions; Kingstone, Friesen, & Gazzaniga, 2000) and configurations/wholes (e.g., emotional facial expressions; McKelvie, 1995). Throughout evolution, the efficient detection

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and recognition of conspecific faces would have helped humans take collective action in response to biologically important events. Consistent with this notion, behavioral studies have shown that the detection of faces is more rapid compared with that of control stimuli such as houses (e.g., Purcell & Stewart, 1986; Tottenham, Leon, & Casey, 2006).

Lesion, stimulation, and neuroimaging studies have found that, in collaboration with other brain regions such as the fusiform gyrus and the superior temporal sulcus, the inferior occipital gyrus (IOG), also known as the occipital face area, plays a crucial role as the neural substrate underlying face processing. Several lesion studies have demonstrated that damage to the IOG induced impaired identity recognition of faces (e.g., Rossion et al., 2003; for a review see Bouvier & Engel, 2006). Likewise, stimulation studies have revealed that electrical activation of the IOG led to various types of impaired face processing including impairments in facial feature perception (e.g., Pitcher, Walsh, Yovel, & Duchaine, 2007), facial configuration perception (Jonas et al., 2012), and the identity recognition of faces (e.g., Allison et al., 1994). Moreover, several neuroimaging studies have reported that the IOG was more active when participants observed faces compared with observing control stimuli such as mosaics and houses (e.g., Liu, Harris, & Kanwisher, 2010; Sergent, Ohta, & MacDonald, 1992; Strother et al., 2011; for a review, see Pitcher, Walsh, & Duchaine, 2011). Because some of these data implicate the IOG in the computationally early stages of face processing, such as the visual analysis of facial features, and because the IOG is the most posterior of the face-related brain regions, some researchers have speculated that the IOG represents the initial stages of a computational hierarchical brain network specific to face processing (e.g., Haxby, Hoffman, & Gobbini, 2000; Pitcher et al., 2011). However, debate remains regarding this issue because other studies indicate that the IOG is important in the late-stage face processing, such as the visual analysis of facial configuration and facial identity recognition (e.g., Rossion, Dricot, Goebel, & Busigny, 2011).

Electrophysiological studies can provide valuable information about the neural activity underlying the stages of information processing. Specifically, intracranial electroencephalography (EEG) can directly record electrical neural activity (field potentials) with high spatial and temporal resolution without the interfering influence of the cranium or scalp in electrical conductance (Mukamel & Fried, 2012). Some previous intracranial EEG studies have recorded the electrical activity of neurons in the IOG or in the adjacent lateral occipital cortex during the processing of faces and other stimuli and have conducted event-related potential (ERP) analyses (Allison, Puce, Spencer, & McCarthy, 1999; Jonas et al., 2012; Rosburg et al., 2010). These studies have consistently shown that the IOG exhibited stronger activity in response to faces than to other stimuli during the 150–200-msec ERP component, which typically peaked at about 170 msec. Several scalp-recorded EEG studies have shown that this component was the first robust face-specific ERP component identified (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; for a review, see Rossion & Jacques, 2008). Taken together, these data suggest that the IOG manages initial face-specific neural processing at this stage.

However, an analysis of temporal information in the IOG across broad frequency ranges during face processing is lacking. A previous methodological study showed that the ERP analysis of intracranial EEG recordings detects primarily low-frequency components of the electrical neuronal activity (Edwards et al., 2009). To fully elucidate the high- and low-frequency neuronal activity at high temporal resolution, researchers need to conduct time–frequency analyses (Makeig, Debener, Onton, & Delorme, 2004). A previous intracranial EEG study conducting time–frequency analyses for such activity in the occipital cortex in response to non-facial stimuli identified high-frequency activity related to visual processing at 100–150 msec (Tallon-Baudry, Bertrand, Hénaff, Isnard, & Fischer, 2005). These data suggest that analogous high-frequency activity might be rapidly elicited in the IOG in response to faces.

Among high-frequency neuronal activity, activation in the gamma-band (higher than 30 Hz; e.g., Adrian, 1942) would be of particular interest to the investigation of face-related processing in the IOG. Previous scalp-recorded EEG and magnetoencephalography (MEG) studies have shown that gamma-band neural activity was related to several types of information processing (e.g., Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996; for a review, see Herrmann, Fründ, & Lenz, 2010), including face processing (e.g., Gao et al., 2013). Previous intracranial EEG studies have also identified gamma-band activity during face processing in brain regions other than the IOG (e.g., Engell & McCarthy, 2010; Klopp, Halgren, Marinkovic, & Nenov, 1999; Lachaux et al., 2005). Furthermore, because several studies have reported that hemodynamic responses reflected electrical activity in the gamma band (e.g., Foucher, Otzenberger, & Gounot, 2003), the face-related activity in the IOG that has been reported in previous neuroimaging studies (e.g., Liu et al., 2010) would be evident in this frequency range. Based on these data, we hypothesized that the IOG would show rapid gamma-band activity during face processing.

Regarding gamma-band neuronal activity, several previous studies have shown that different gamma subbands reflected different functional correlates and microscopic mechanisms (e.g., Edwards, Soltani, Deouell, Berger, & Knight, 2005; Scheffer-Teixeira et al., 2012; for a review, see Tort, Scheffer-Teixeira, Souza, Draguhn, & Brankačk, 2013). It has been proposed that gamma-band components within the traditionally defined frequency range of 30–100 Hz (Herrmann et al., 2010), as well as a higher range (up to 250 Hz; Edwards et al., 2005), reflect different neural computations (Crone, Sinai, & Korzeniewska, 2006). These data suggest that the IOG might exhibit different patterns of activity across the gamma subbands during face processing.

When considering gamma-band activity in the IOG, its coupling patterns with activity at lower frequency ranges could also be of interest. Several previous studies in humans and animals have shown that gamma-band activity in which the amplitudes were associated with phases of theta-band activity were critically involved in several information processes such as learning and decision making (e.g., Canolty et al., 2006; for a review, see Lisman & Jensen, 2013). Ample evidence suggests that such phase–amplitude cross-frequency coupling between theta and gamma oscillations reflects neural network interactions between long-range inter-regional communications (reflected in theta oscillations) and local intra-regional computations (reflected in