NeuroImage 86 (2014) 470–479

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Dynamic gamma frequency feedback coupling between higher and lower order visual cortices underlies perceptual completion in humans ☆

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ARTICLE INFO

Article history:
Accepted 18 October 2013
Available online 1 November 2013

Keywords:
Perceptual completion
Reverse hierarchical visual processing
Feedback
Gamma band activity
Dynamic causal models

ABSTRACT

To perceive a coherent environment, incomplete or overlapping visual forms must be integrated into meaningful coherent percepts, a process referred to as "Gestalt" formation or perceptual completion. Increasing evidence suggests that this process engages oscillatory neuronal activity in a distributed neuronal assembly. A separate line of evidence suggests that Gestalt formation requires top-down feedback from higher order brain regions to early visual cortex. Here we combine magnetoencephalography (MEG) and effective connectivity analysis in the frequency domain to specifically address the effective coupling between sources of oscillatory brain activity during Gestalt formation. We demonstrate that perceptual completion of two-tone "Mooney" faces induces increased gamma frequency band power (55–71 Hz) in human early visual, fusiform and parietal cortices. Within this distributed neuronal assembly fusiform and parietal gamma oscillators are coupled by forward and backward connectivity during Mooney face perception, indicating reciprocal influences of gamma activity between these higher order visual brain regions. Critically, gamma band oscillations in early visual cortex are modulated by top-down feedback connectivity from both fusiform and parietal cortices. Thus, we provide a mechanistic account of Gestalt perception in which gamma oscillations in feature sensitive and spatial attention-relevant brain regions reciprocally drive one another and convey global stimulus aspects to local processing units at low levels of the sensory hierarchy by top-down feedback. Our data therefore support the notion of inverse hierarchical processing within the visual system underlying awareness of coherent percepts.

Introduction

Despite the ease with which we perceive coherent objects in our environment even under poor stimulus conditions, the integration of only partly available visual information into whole percepts is a challenge for the visual system. This integration process has been referred to as perceptual completion or closure. Gestalt psychology considers perceptual completion to arise from processing of a stimulus as a whole, via choosing the simplest interpretation from the interactions of stimulus parts as opposed to the simple summation of single parts themselves (Wertheimer, 1923). Although the Gestalt theoretical framework describes this process at the level of stimulus part interactions, how the brain achieves perceptual completion from a mechanistic point of view is less understood.

Neuroimaging studies highlight a role for ventral visual areas and parietal cortex during perceptual completion of bi-stable (*e.g.* Rubin vases), and degraded figures (Andrews et al., 2002; Dolan et al., 1997; Kleinschmidt et al., 1998; Sehatpour et al., 2006). Perceptual closure of two-tone Mooney faces (Mooney, 1957) elicits increased hemodynamic responses in face sensitive visual ventral brain regions such as the fusiform face area (Andrews and Schluppeck, 2004; Kanwisher et al., 1998; McKeeff and Tong, 2007). Electroencephalogram (EEG) studies have demonstrated a perceptual closure specific event related potential (ERP) occurring in a time window between 230 ms and 400 ms peaking around 320 ms post-stimulus time (Doniger et al., 2000, 2001; Sehatpour et al., 2006). Source localization of this component also revealed that ventral visual cortex (part of the lateral occipital cortex, LOC) and parietal cortex are active at this latency (Sehatpour et al., 2006). Taken together, these findings accord with the suggestion that not only brain regions for cue invariant object/face recognition such as ventral visual cortex (Haxby et al., 1999; Kanwisher and Yovel, 2006; Malach et al., 1995) but also spatial attention relevant parietal brain regions (Corbetta et al., 1998;

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http://dx.doi.org/10.1016/j.neuroimage.2013.10.037

Fernandez-Duque and Posner, 2001) are crucial for perceptual closure and that this process occurs about 230 ms to 400 ms after stimulus onset.

Within the classical view of visual system hierarchy, simple geometric lines and shapes that form complex objects are processed in lower order visual cortex, whereas higher order areas within the ventral visual stream (Mishkin et al., 1983) code invariant object and category information (*e.g.* Vogels and Orban, 1996) based on feedforward communication from early visual cortex (for a review of these models see Hochstein and Ahissar, 2002). However, recent models of conscious visual perception suggest reverse hierarchical processing (for a review see Hochstein and Ahissar, 2002) whereby higher order visual areas in the ventral and dorsal streams provide top-down feedback to early visual cortex (*i.e.*, predictive coding — Friston, 2003; Rao and Ballard, 1999). In the case of perceptual completion, this top-down feedback is suggested to carry global information to local processing units in early visual cortex (Bullier, 2001; Campana and Tallon-Baudry, 2013; Hochstein and Ahissar, 2002; Lamme and Roelfsema, 2000), which accords with Gestalt theory in that global visual information interacts with local stimulus part processing (Wagemans et al., 2012a, 2012b).

The neuroimaging studies of perceptual completion described above do not report engagement of lower order visual cortex. However, one event-related fMRI study (Altmann et al., 2003) reported both primary and higher order visual cortex activity activation during global shape integration of collinear contours. Although these observations were interpreted as potentially reflecting top-down modulation in global shape perception (Altmann et al., 2003), a measure of interaction between these levels of hierarchy was not provided. Transcranial magnetic stimulation (TMS) studies in humans demonstrate that interrupting recurrent interactions between early and higher visual cortices in the ventral visual stream impairs perception of natural scenes (Koivisto et al., 2011) and perceptual completion of illusionary Kanizsa-type figures (Wokke et al., 2013). However, perceptual impairment by TMS-evoked disruption of early visual areas (Wokke et al., 2013) does not directly demonstrate feedback coupling of neuronal activity; an alternative explanation is simply that early visual cortex activates at later latencies independently from any feedback from higher order areas. Thus, although recent evidence suggests that coherent perception relies on feedback from higher to lower order visual cortex, paralleling the global-to-local concept of Gestalt psychology, a characterization of this process in terms of effective connectivity is currently lacking.

To address this, we measured induced neuromagnetic oscillatory brain responses to two-tone Mooney faces that consist of white patches that have to be spatially integrated to perceive a face (Fig. 1; Mooney, 1957). We employ the Mooney face paradigm for two reasons: first, it represents a classical measure of perceptual completion (Mooney, 1957) and brain areas involved in Mooney face perception are well characterized (Andrews and Schluppeck, 2004; Grutzner et al., 2010; Kanwisher et al., 1998; McKeeff and Tong, 2007). Second, Mooney face perception consistently elicits neuronal oscillations in the gamma frequency band (>30 Hz) in the EEG (Rodriguez et al., 1999; Trujillo et al., 2005), intracranial EEG (Lachaux et al., 2005), and MEG (Grutzner et al., 2010). Synchronized oscillatory neuronal gamma band responses

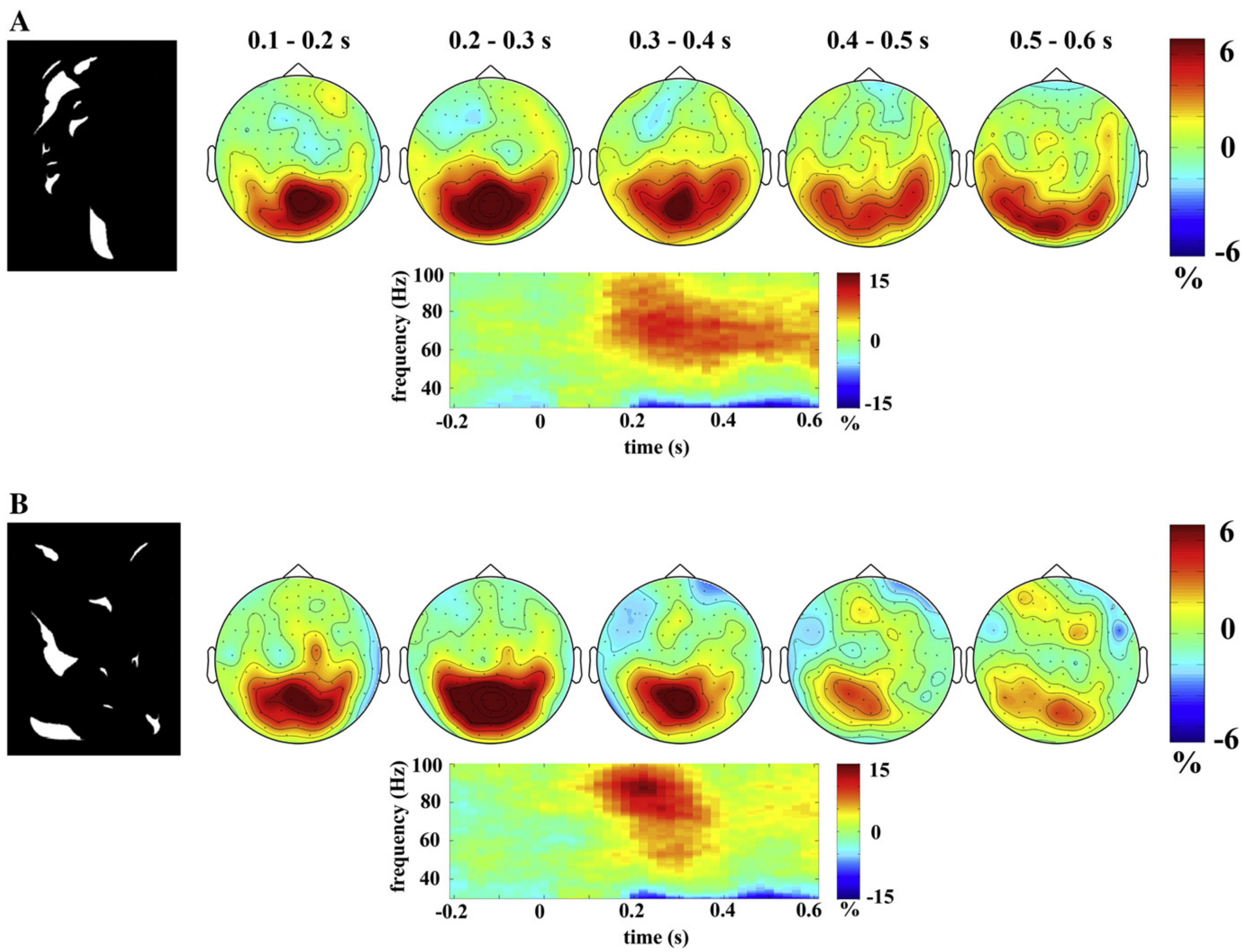

Fig. 1. Gamma power changes by Mooney face perception in sensor space: topographies of gamma power changes (50–100 Hz) with respect to baseline in 100 ms intervals are shown for the Mooney face condition (A) and for the scrambled faces (B). Below each, a time frequency plot of mean relative gamma power changes across posterior MEG sensors is depicted. The colorbars indicate percentage of relative gamma power changes compared to baseline.