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Frequency tagging yields an objective neural signature of Gestalt formation

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ABSTRACT

The human visual system integrates separate visual inputs into coherently organized percepts, going beyond the information given. A striking example is the perception of an illusory square when physically separated inducers are positioned and oriented in a square-like configuration (illusory condition). This illusory square disappears when the specific configuration is broken, for instance, by rotating each inducer (non-illusory condition). Here we used frequency tagging and electroencephalography (EEG) to identify an objective neural signature of the global integration required for illusory surface perception. Two diagonal inducers were contrast-modulated at different frequency rates f_1 and f_2, leading to EEG responses exactly at these frequencies over the occipital cortex. Most importantly, nonlinear intermodulation (IM) components (e.g., $f_1 + f_2$) appeared in the frequency spectrum, and were much larger in response to the illusory square figure than the non-illusory control condition. Since the IMs reflect long-range interactions between the signals from the inducers, these data provide an objective (i.e., at a precise and predicted EEG frequency) signature of neural processes involved in the emergence of illusory surface perception. More generally, these findings help to establish EEG frequency-tagging as a highly valuable approach to investigate the underlying neural mechanisms of subjective Gestalt phenomena in an objective and quantitative manner, at the system level in humans.

1. Introduction

The human visual system does not only extract information about the local properties of an image, but is also capable of combining all the information to construct a coherently integrated whole. In some cases, the integrated wholes are different than the sum of the parts (Wertheimer, 1923; for recent reviews, see Wagemans, Elder, et al., 2012; Wagemans, Feldman, et al., 2012). One of the well-known examples representing this holistic property of vision is the Kanizsa figure (Kanizsa, 1955). By placing inducers so that neighboring straight edges are aligned collinearly, a central illusory surface is perceived (Fig. 1A). This percept is accompanied by (1) an illusory lightness perception—the illusory surface appearing brighter than the background, (2) the perception of illusory contours in the gaps between the collinear inducer edges, together outlining the shape of the illusory surface, and (3) an illusory depth stratification—the illusory surface appearing to occlude the surrounding objects (and the inducers appearing as complete disks). By comparing it with a non-illusory variation of the figure, Kanizsa showed that the perception of an illusory surface reflects the global configuration of the image. Hence, it is a context-sensitive phenomenon. It is this property that makes the perception of this figure a true Gestalt phenomenon (Kogo & Wagemans, 2013).

The underlying neural mechanisms of the illusory surface perception have been first investigated in the non-human primate brain. von der Heydt, Peterhans, and Baumgartner (1984) showed that neurons in the secondary visual area (V2) of the monkey brain that are sensitive to luminance-defined boundaries also respond when illusory contours with the same orientation fall in their receptive field. Subsequent studies also showed neural responses corresponding to illusory contours in the Kanizsa figure in low level visual cortex (V1 and V2; Lee & Nguyen, 2001). This observation is important since it identifies neural activities corresponding to the subjective properties of perception, instead of merely reflecting the physical inputs. As a matter of fact, these neurons were activated by illusory figures but their responses were reduced significantly in non-illusory variations (Lee & Nguyen, 2001; Peterhans & von der Heydt, 1989; von der Heydt et al., 1984),

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indicating that they are activated as a result of the global coherence of the local signals responding to the individual inducers.

Further single cell recording studies in monkeys, as well as scalp electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) in humans have shown neural activities corresponding to the perception of an illusory surface at higher levels in the visual hierarchy (e.g., V4: Cox et al., 2013; V3, V4, V7, V8: Mendola, Dale, Fischl, Liu, & Tootell, 1999; lateral occipital complex (LOC): Murray et al., 2002; Stanley & Rubin, 2003). Populations of neurons in these areas are tuned to higher-order configurations and shapes, while the neurons active at illusory contours in V1 and V2 are tuned to the orientation of boundaries. Accordingly, it has been suggested that feedback projections from higher-level visual areas to lower-level areas are involved in illusory surface perception—the higher-level signaling the overall configuration of the image while the lower-level articulates the position and orientation of the illusory contours (Lee & Mumford, 2003; Stanley & Rubin, 2003). In this framework, the illusory surface emerges through inter-areal dynamic interactions in the hierarchy of visual cortex, responding to edges, computing border-ownership (figural side) and depth-order, constructing surfaces, and detecting shapes (Grossberg, 1994; Kogo, Strecha, Van Gool, & Wagemans, 2010; Kogo & Wagemans, 2013; Lee & Mumford, 2003; Stanley & Rubin, 2003). The neural activities that constitute illusory surface perception suggest that large-scale integration of neural signals is a key mechanism underlying the emergence of global, Gestalt-like properties (for reviews, see Lesher, 1995; Murray & Herrmann, 2013).

An important next step is to investigate how such global level integration is achieved. To do so, it is essential to go beyond increased signals in response to the Kanizsa figure, and identify an objective signature of neural activities underlying global integration, as indexed by the illusory surface perception. Importantly, this signature should be objectively dissociated from the neural response to the local elements forming the illusory percept. This issue can be tackled by the "frequency-tagging" approach obtained from EEG recorded on the human scalp. The frequency-tagging approach (Regan & Cartwright, 1970; Regan & Heron, 1969) takes advantage of the fact that presenting a periodic visual stimulus to the human brain leads to periodic responses directly related to the frequency of stimulation (the "steady state visual evoked potential", SSVEP, Regan, 1966; for a review, see Norcia, Appelbaum, Ales, Cottereau, & Rossion, 2015). This property allows the use of highly selective frequency markers that can define the signal objectively and precisely (i.e., the response to the stimulus at the experimentally-defined stimulation frequency). Moreover, the approach can be used to record responses from multiple, simultaneously presented stimuli "tagged" at different frequencies (i.e., "fundamental frequencies", which are the physically given frequencies to an image), and disentangle objectively their contribution to the brain's overall response (e.g., Andersen, Müller, & Hillyard, 2009; Appelbaum, Wade, Vildavski, Pettet, & Norcia, 2006; Boremanse, Norcia, & Rossion, 2013; Morgan, Hansen, & Hillyard, 1996; Regan & Cartwright, 1970; Regan & Heron, 1969; Regan & Regan, 1988).

Of particular interest for the present purpose are frequency components that are not present in the input but correspond to nonlinear combinations of these frequency inputs (Regan & Regan, 1988; Zemon & Ratliff, 1984). For example, if two fundamental frequencies f_1 and f_2 are applied to two separate elements in an image, responses at frequencies such as $f_1 + f_2$, or $f_1 - f_2$ ($nf_1 \pm mf_2$, in general, with n and m being any positive integers) may be observed. These responses are referred to as "intermodulation components" (IMs, Zemon & Ratliff, 1984). The emergence of these frequencies cannot be explained by an independent modulation by the individual frequencies given in the input, but only as the result of non-linear responses of the system to the interactions of fundamental frequencies (Regan & Regan, 1988; Zemon & Ratliff, 1984). These properties of IMs suggest that this approach is ideal to objectively record neural activities that correspond to the *emergence* of a holistic representation, i.e. a representation that goes beyond the physically given stimulus by causing new frequency components in the frequency spectrum, and that can be objectively separated from the responses to the stimulus elements.

Although the EEG frequency-tagging combined with the analysis of IMs is not a new technique, its significance in investigating the neural basis of Gestalt-like visual integration has been realized relatively recently and only in a handful of studies. For instance, this approach has been used to investigate the neural basis of spatial integration in Vernier stimuli (Victor & Conte, 2000), to detect contextual effects in orientation-sensitive neural responses (Hou, Pettet, Sampath, Candy, & Norcia, 2003), and of interactions between a figure and its background (Appelbaum, Wade, Pettet, Vildavski, & Norcia, 2008). Recent studies have also shown that the IMs generated by two halves of a face directly correlate with the integration of the two halves into a coherent percept of the face (Boremanse, Norcia, & Rossion, 2014; Boremanse et al., 2013). Hence, these studies indicate that populations of neurons whose receptive fields cover the nearby elements with the two different frequencies, such as the two neighboring line segments in the Vernier stimuli, or figure and ground regions that abut at a boundary or two face halves, can create IMs. Importantly, a study on motion binding (Aissani, Cottereau, Dumas, Paradis, & Lorenceau, 2011) also reported IMs when the two frequency tags were assigned to elements that are physically distant in the image (see also Fuchs, Andersen, Gruber, & Müller, 2008; Gundlach & Müller, 2013). Therefore, IMs can also arise from long-range interactions between populations of neurons that represent retinotopically distal elements.

These recent developments suggest that applying EEG frequency-tagging with the IM signal analysis can provide an objective signature of the emergence of Gestalt-like properties as the result of global integration. Here, as a representative example of a holistic, Gestalt-like phenomenon, we investigate the IM signals corresponding the illusory surface perception in the Kanizsa figure. Since the illusory surface is assumed to result from the coherent integration of the locally triggered neural signals, long-range neural interactions should generate IM components. In fact, a recent study used two lateralized flickering stimuli (inducers) giving rise to an illusory surface perception, and reported IM components (Gundlach & Müller, 2013). The experimental stimulus in that study consists of three "incomplete" circles that give rise to a long horizontal illusory rectangle perceived to be in front of the three circles, a percept that is changed by completing the contour drawing of the central circle in the control stimulus (see Fig. 1a in that study). However, the control condition used in that study is somewhat ambiguous. In addition to giving rise to the (intended) percept of three separate shapes without any perceptual completion, it can also be perceived as perceptually completed, with a combination of modal and amodal completion. Specifically, the horizontal illusory rectangle is sometimes perceived (modal completion induced by the two peripheral circles) while being occluded by the central circle (amodal completion). To circumvent this problem, we rely here on Kanizsa's original square configuration and the standard non-illusory control (with rotated inducers) in the present study (Fig. 1), in which the perception of an illusory surface and its disappearance are well-established. Moreover, this previous study used relatively high frequency rates of stimulation (i.e., 8.5 Hz and 14.17 Hz). While such frequency rates generally provide robust SSVEPs, these responses are generally restricted to low-level visual areas such as the primary visual cortex, projecting to medial occipital sites (i.e. around electrode Oz), even when high-level visual stimuli are used (Alonso-Prieto et al., 2013; Bekthereva