



Perception of illusory contours forms intermodulation responses of steady state visual evoked potentials as a neural signature of spatial integration



Christopher Gundlach, Matthias M. Müller*

Institute of Psychology, University of Leipzig, 04103 Leipzig, Germany

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ABSTRACT

Perception of illusory contours was shown to be a consequence of neural activity related to spatial integration in early visual areas. Candidates for such filling-in phenomena are long-range horizontal connections of neurons in V1/V2, and feedback from higher order visual areas. To get a direct measure of spatial integration in early visual cortex, we presented two differently flickering inducers, which evoked steady-state visual evoked potentials (SSVEPs) while manipulating the formation of an illusory rectangle. As a neural marker of integration we tested differences in amplitudes of intermodulation frequencies i.e. linear combinations of the driving frequencies. These were significantly increased when an illusory rectangle was perceived. Increases were neither due to changes of any of the two driving frequencies nor in the frequency that tagged the processing of the compound object, indicating that results are not a consequence of paying more attention to inducers when the illusory rectangle was visible.

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1. Introduction

Perception of illusory contours is a fundamental capability of the visual system. Typical illusory contours are based on Kanizsa figures (Kanizsa, 1979) in which the formation of illusory percepts relies on the presence of inducers that form real physical contours and edges. More and more evidence was provided that this is achieved in early visual cortex, as early as in V1 and V2 (Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Hou, Pettet, Sampath, Candy, & Norcia, 2003; Larsson et al., 1999; Seghier et al., 2000; von der Heydt, Peterhans, & Baumgartner, 1984). Furthermore, higher visual areas such as V3, V4, V7, V8 (Mendola, Dale, Fischl, Liu, & Tootell, 1999) and lateral occipital cortex (LOC) seem to play an important role (de-Wit, Kentridge, & Milner, 2009; Murray, Foxe, Javitt, & Foxe, 2004; Seghier et al., 2000). While in animal studies activations of illusory contours were frequently detected in early visual areas such as V1 and V2 (Ramsden, Hung, & Roe, 2001; Sheth, Sharma, Rao, & Sur, 1996) such activations were detected far less reliably in humans (Seghier & Vuilleumier, 2006). Although some recent studies favor the involvement of late visual processing stages in the perception of illusory contours (de-Wit et al., 2009; Knebel & Murray, 2012);

as of today the cortical dynamics are not fully understood (Seghier & Vuilleumier, 2006).

While some studies considered perception of illusory contours as a higher cognitive achievement (cf. Pessoa et al., 1998), it seems also plausible that early visual areas drive the perception of illusory contours via feed-forward and horizontal axonal connections (Bakar, Liu, Conci, Elliott, & Ioannides, 2008). Besides feedback mechanisms from higher visual areas, these horizontal axonal connections are seen to provide an additional anatomical basis for spatial integration in particular in V1 (Gilbert et al., 1996; Hou et al., 2003). All these neural mechanisms have in common that information from different stimuli has to be integrated. As a product of this integration illusory contours obviously emerge from complex interactions between numerous visual areas, and are not the result of one single processing stage. However, what is still an open question is to what extent perception of illusory contours requires full integration of visual information provided by the inducers. In other words, is the perception of illusory contours linked to neural grouping of inducers to one coherent object that includes all features of the spatially separated inducers.

An elegant tool to investigate that question is to present inducers or “pacmen” frequency-tagged at different frequencies to evoke distinguishable steady state visual evoked potentials (SSVEPs). The SSVEP is a continuous oscillatory electrophysiological signal that has the same frequency as the driving stimulus including higher harmonics (Regan, 1989). Its amplitude can easily be analyzed in the frequency domain and is modulated by attention (cf.

* Corresponding author at: Institute of Psychology, University of Leipzig, Seeburgstrasse 14-20, 04103 Leipzig, Germany. Tel.: +49 0341 973 9543; fax: +49 0341 973 5969.

E-mail address: m.mueller@rz.uni-leipzig.de (M.M. Müller).

Andersen, Hillyard, & Müller, 2008; Morgan, Hansen, & Hillyard, 1996; Müller, Malinowski, Gruber, & Hillyard, 2003; Müller, Teder-Sälejärvi, & Hillyard, 1998; Müller et al., 2006). Furthermore SSVEPs were shown to index early visual processes as their sources were found in low tier visual areas (Di Russo et al., 2007; Hillyard et al., 1997; Müller et al., 2006). A spectral decomposition of the measured electrophysiological signal (EEG) can show additional peaks at frequencies that are linear combinations of the driving frequencies. These so-called intermodulation frequencies are found when neuronal populations process and integrate input non-linearly from more than one frequency-tagged stimulus (Zemon & Ratliff, 1982, 1984). If inputs are processed by a single nonlinear site, such as a neuron which processes and transmits signals non-linearly (Tiesinga, Fellous, & Sejnowski, 2008), neuronal responses contain combinations of input frequencies (Hou et al., 2003). For large neuronal populations their specific responses are measurable as intermodulation frequencies in the EEG. Consequently, intermodulation frequencies have been reported as a robust signal in experimental designs where frequency-tagged stimuli needed or were very likely to be integrated (cf. Appelbaum, Wade, Pettet, Vildavski, & Norcia, 2008; Fuchs, Andersen, Gruber, & Müller, 2008; Hou et al., 2003; Regan & Regan, 1987). Here, we tested intermodulation frequencies as a neural signature of information integration provided by the flickering inducers. We therefore presented inducers that flickered at two different frequencies. We manipulated perception of an illusory rectangle, i.e. either facilitated or inhibited that perception. If perception of an illusory contour required grouping of spatially separated inducers, intermodulation frequencies should be found in the EEG as a marker of this integration when the rectangle was perceived.

2. Methods

2.1. Subjects and EEG recording

Electrical brain activity was recorded from 18 participants with normal or corrected-to-normal visual acuity (10 female, age range 22–27) with 64 Ag/AgCl electrodes mounted in an elastic cap at a sampling rate of 256 Hz using an ActiveTwo amplifier system (BioSemi, Amsterdam). Horizontal eye movements were monitored with two electrodes placed on the canthi of both eyes (horizontal electrooculogram), while blinks and vertical eye movements were monitored with two electrodes positioned below and above the right eye (vertical electrooculogram). All subjects were informed on the purpose of the experiment and the experimental procedures and gave written consent. The study was consistent with guidelines from the Code of Ethics from the World Medical Association. Five participants were excluded from the final analysis: four showed excessive eye movements resulting in more than 50% of trials contaminated with artifacts and one participant did not exhibit an SSVEP signal above noise level.

2.2. Stimuli and task

All stimuli were presented on a 19-inch monitor set at a resolution of 1024×768 pixels and a color depth of 32 bits per pixel with a refresh rate of 85 Hz. During the experiment two flickering inducers were presented on a gray background. From a viewing distance of 80 cm, both circular inducers had a size of 4° of visual angle. They were placed 3.75° left and right to the center of the screen (center of screen to center of inducers) and were facing inwards (see Fig. 1). To form a pacman, a rectangle of $3^\circ \times 1.1^\circ$ of visual angle was cut out from each of the disks. To elicit distinguishable SSVEPs by the two pacmen the left one changed its luminance at a rate of 8.5 Hz (f_1) and the right one at a rate of 14.17 Hz (f_2), alternating between 10 and 70 cd, respectively. The luminance of the background was kept constant at 40 cd. A black fixation cross of $0.3^\circ \times 0.3^\circ$ was presented centrally. Similar to Halko and colleagues (Halko, Mingolla, & Somers, 2008), to inhibit the perception of the illusory rectangle, a gray ring with a luminance of 10 cd, an outer diameter of 2.4° and a width of 0.2° surrounded the fixation cross. In trials in which the perception of the illusory rectangle was facilitated the ring was incomplete and formed an upper and lower bow (Fig. 1A).

Each trial started with the synchronous onset of all stimuli. In order to assure that participants were attending to the stimuli, we instructed them to fixate the central fixation cross and to discriminate between changes in the height of each pacman's rectangular mouth. Changes in height varied randomly between 0.2° and 0.7° of visual angle with a duration of 200 ms. While subjects had to ignore increases in height (distracter) they had to press a button upon the detection of a decrease in height as accurately and fast as possible (target). A change in height occurred either

at the left or right pacman and these changes were equally distributed across all trials. The earliest onset of an event was 400 ms after the onset of stimulation and two events were separated by at least 705 ms. Each trial lasted for 3170 ms with an inter-trial interval of 1000–1250 ms with only the central fixation cross presented on the screen. Facilitation or inhibition of the illusory rectangle was randomized on a trial-by-trial basis with 168 trials for each condition, respectively. The whole experiment consisted of six blocks with 56 trials per block. In 50% of all trials no events were presented while 1–3 events could occur in the rest of the trials. Only trials without any event were considered for the analysis of the SSVEP, resulting in a maximum of 84 trials for each condition.

2.3. Data analysis

2.3.1. Behavioral data

Only responses from 250 ms to 900 ms after onset of a target were considered as a hit. Responses in the same time window to a distracter were counted as false alarms. Hit and false alarm rates were used to calculate d' -values as a sensitivity measure. Reaction times (RT) and d' -values of the two conditions were statistically tested with a paired t -test, respectively.

2.3.2. EEG data

As mentioned above, only trials without any targets or distracters were considered for EEG analysis to introduce no additional noise due to motor responses and their EEG correlates. Epochs starting at stimulation onset and lasting 3170 ms were extracted and any linear trend was subtracted. Epochs containing blinks or eye movements were rejected from further analysis. Additionally the "statistical control of artifacts in dense array EEG/MEG studies (SCADS)" was performed (Junghofer, Elbert, Tucker, & Rockstroh, 2000). SCADS uses channel approximations and trial exclusions based on different statistical parameters of the data to reduce noise in the data. Epochs with more than 12 noise-contaminated channels were discarded. Altogether these preprocessing steps resulted in an average rejection rate of 22% of all epochs. The remaining data was re-referenced to average reference and averaged for each perceptual condition. SSVEP amplitudes were extracted by fast-Fourier Transformations (FFTs) from the averaged epochs from a time window from 500 to 3100 ms after stimulus onset. The first 500 ms were discarded to not include the visual evoked potential (VEP) to flicker onset in the estimation of SSVEP amplitudes

To determine appropriate electrodes for statistical analysis we calculated SSVEP amplitudes averaged across both experimental conditions and both driving frequencies of the pacmen (i.e. 8.5 Hz and 14.17 Hz). For the averaged frequencies we drew an iso-contour voltage map and identified the electrodes with greatest amplitudes. This resulted in an electrode cluster of eight electrodes at occipito-temporal sites that are depicted by the blue circles in Fig. 1B. For statistical analysis we calculated the average SSVEP amplitude across these eight electrodes for each experimental condition, respectively. The major aim of the present study was to identify and to statistically test intermodulation frequencies. Such intermodulation terms are represented by linear combinations of the driving frequencies of 8.5 Hz (f_1) and 14.17 Hz (f_2). In our analysis we focused on ($f_2 - f_1$) = 5.6 Hz, ($2f_1 - 2f_2$) = 11.33 Hz, ($f_1 + f_2$) = 22.67 Hz, and ($2f_1 + 2f_2$) = 45.33 Hz.

We tested SSVEP amplitude differences for the driving frequencies and these intermodulation terms with paired t -tests (*illusory rectangle vs. no illusory rectangle*), adjusting the significance level by means of Bonferroni correction controlling for multiple comparisons of our six analyzed frequencies. All analysis was made by using EEGLab (Delorme & Makeig, 2004) together with custom routines written in MATLAB (The Mathworks, Natick, MA).

3. Results

3.1. Behavioral data

Participants were able to discriminate targets from distractors as indicated by an average observer sensitivity d' of 1.96 ± 0.42 . Sensitivity measure d' did not differ between perceptual conditions (*illusory rectangle*: $M = 1.97$, $SD = 0.52$; *no illusory rectangle*: $M = 1.96$, $SD = 0.40$; $t(12) = 0.17$, $p = 0.87$) while reaction times differed ($M = 504.32$ ms, $SD = 46.62$ ms vs. $M = 514.33$ ms, $SD = 45.90$ ms; $t(12) = -2.44$, $p < 0.05$). In general participants were faster in discriminating brief changes in height of pacmen when they formed an illusory figure while their overall performance accuracy did not differ.

3.2. SSVEP amplitudes

As depicted in Fig. 1B, both pacmen elicited SSVEPs that clearly peaked in the spectrum at 8.5 Hz and 14.17 Hz. Additional peaks are

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