# MEG evidence for surround suppression effect in human early visual cortex during illusory contour processing

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## Introduction

Illusory contours (IC) comprise a convenient model for studying neurophysiological properties of the visual system allowing it to support realistic visual perception. This basic feature of visual system functioning seems to be essential for vision, since it allows perception of complete Gestalt objects derived from fragmented physical images. A large body of evidence hints to higher visual areas as critical nodes responsible for the illusory contour detection, with lateral occipital complex (LOC) most often cited (Murray & Herrmann, 2013; Shpaner et al., 2013).

Effects in the V1/V2 related to IC perception mostly remained evasive for EEG and MEG recording, with few exceptions, hinting at rather late activations (Ohtani et al., 2002; Proverbio & Zani, 2002; Halgren et al., 2003; Khoe et al., 2004; Knebel & Murray, 2012; Mijović et al., 2014).

Yet animal studies reported both excitation and inhibition of V1 cells in response to illusory contours (Peterhans & Von der Heydt, 1989; Von der Heydt & Peterhans, 1989; Grosof et al., 1993; Ramsden et al., 2001; Lee & Nguyen, 2001), some of these responses occurring within the first 100 ms after stimulus onset – i.e. earlier than the LOC activation.

Currently there is a growing evidence that surround suppression induced by iso-oriented collinear stimuli is a salient feature of V1 that occurs at rather short latencies (Sillito & Jones, 1996; Jones et al., 2001; Ishikawa et al., 2010; Hashemi-Nezhad & Lyon, 2012; Henry et al., 2013; Vanni & Casanova, 2013). This effect may lead to suppression of early responses to ICs in V1.

Relying on the EEG findings of short-latency suppression of early visual cortices in response to Kanizsa figure compared to control stimuli – an inverted IC effect (Stroganova et al., 2012), we attempted to find direct MEG evidence, as well as localization and timing of this effect.

## Materials and methods

Subjects: 20 healthy participants.

Paradigm: Participants were passively viewing the stimuli (Kanizsa squares and controls) of two sizes (4.5° and 9.0°) - referred to as *small* and *big* correspondingly.



Kanizsa   control   Kanizsa   control
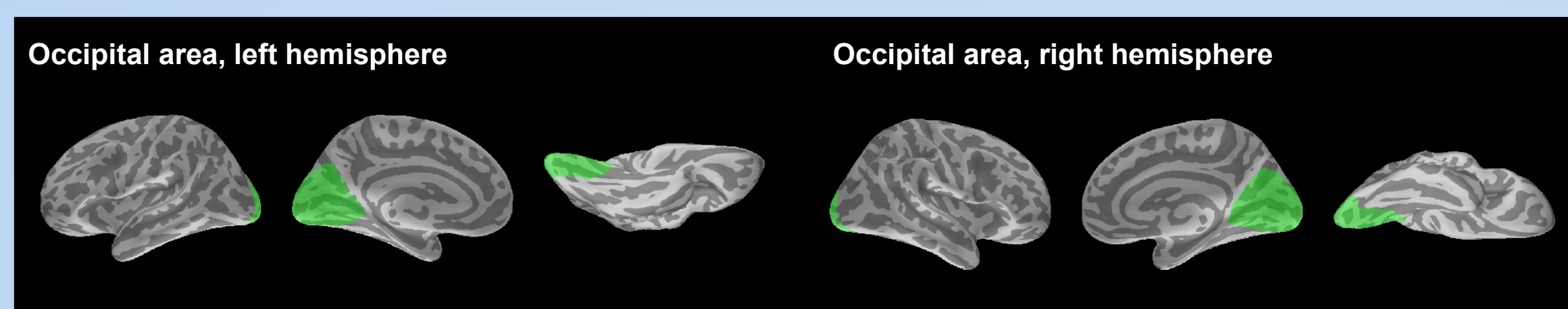**Small stimuli**   **Big stimuli**
**The stimuli**

MEG recording: 306-channel MEG (VectorView, Elekta-Neuromag).

Structural MRI images (1.5T Toshiba, T1-weighted) were obtained for all subjects in order to construct realistic brain model using FreeSurfer software.

Source estimation was performed using unsigned cortical-surface-constrained L2-norm-based minimum norm estimation using the MNE software suite

Data Analysis: All analyses were restricted spatially to medial occipital area and occipital pole representing early stages of visual processing, and temporally to 40-120 ms time window (Stroganova et al., 2012).



Occipital area, left hemisphere    Occipital area, right hemisphere

**The occipital area used to assess the inverted IC effect in the source space.**
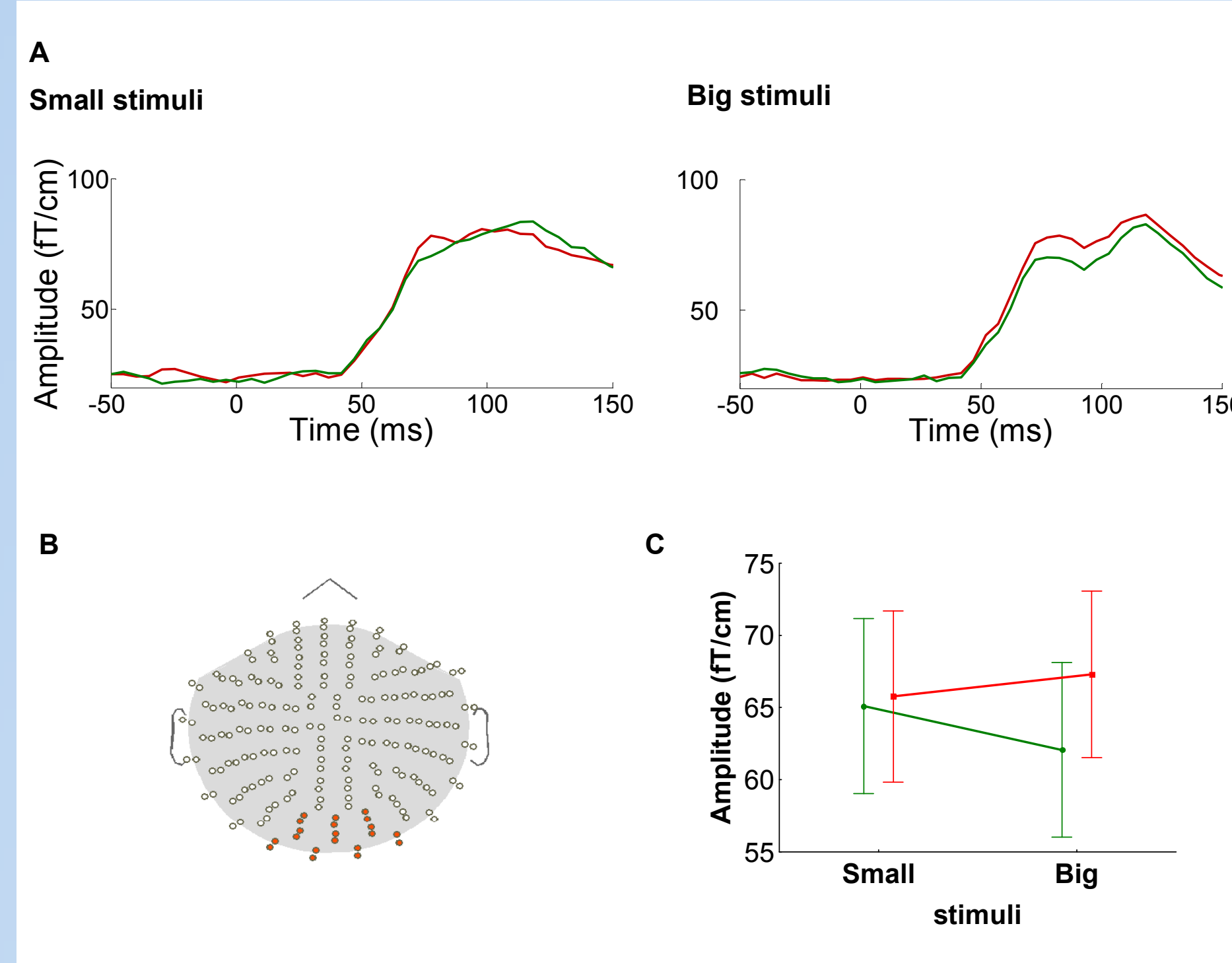
Spatial loci of effect (SLEs) were defined using permutational statistics on data processed with threshold-free cluster enhancement (TFCE) technique (Mensen & Khatami, 2013). One-sided statistics was used in the search of the inverted IC effect. Time spans of statistically significant IC effect within SLEs were assessed with the help of permutational statistics based on the approach devised by Nichols & Holmes (2002).

## Results: sensor level
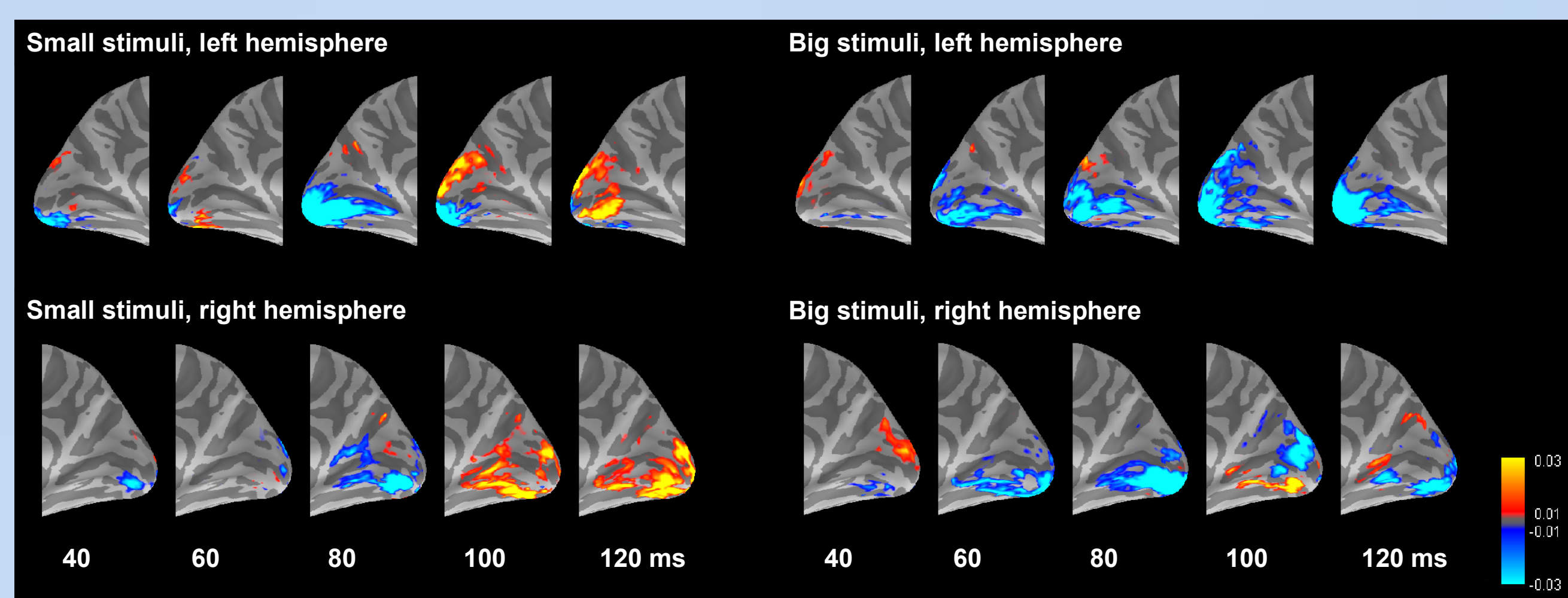


A   Small stimuli   Big stimuli

B

C

Two-way ANOVA with repeated measures performed on RMS amplitude values averaged within 40 – 120 ms time window demonstrated a significant inverted IC effect ($F(1,19) = 4.90$, $p = .039$, $\eta_p^2 = .205$), while the effect of the stimulus size was not evident ($F(1,19) = 0.10$, $p = .75$, $\eta_p^2 = .005$), and the interaction between stimulus type and size was also non-significant ($F(1,19) = 1.71$, $p = .20$, $\eta_p^2 = .083$). Post-hoc comparison revealed that the amplitude of the response was significantly lower to big Kanizsa stimuli compared with big control stimuli ($p<.05$).

**Gradiometer RMS values averaged over occipital sensors (averaged across all participants).**
**(A) Timecourses for small and big stimuli.**
**(B) Occipital gradiometers used for averaging (filled circles).**
**(C) Amplitude averaged over 40-120 time window (M ± SEM).**

— Kanizsa stimulus
— control stimulus

## Results: source level



Small stimuli, left hemisphere    Big stimuli, left hemisphere
Small stimuli, right hemisphere   Big stimuli, right hemisphere
40   60   80   100   120 ms

An inverted IC effect was evident for both stimulus sizes both in the left and right hemispheres.

**Difference in the absolute source strength between Kanizsa and control stimuli plotted on the medial occipital aspects of the inflated brain surface (averaged across all participants). Negative values depicted in blue represent the inverted IC effect. Scale: nA.**

For small stimuli the TFCE procedure yielded a narrowly focused cluster of significantly activated vertices at the occipital pole of the left hemisphere below the end of the calcarine sulcus. A similar cluster in the right hemisphere was located symmetrically, but it did not reach the significance level and thus it was not used in the further analysis.

For big stimuli the TFCE procedure yielded statically significant loci both in the left and in the right hemispheres, which occupied most of the lingual gyrus along the ventral bank of the calcarine sulcus.



Small stimuli, left hemisphere
Big stimuli, left hemisphere
Big stimuli, right hemisphere
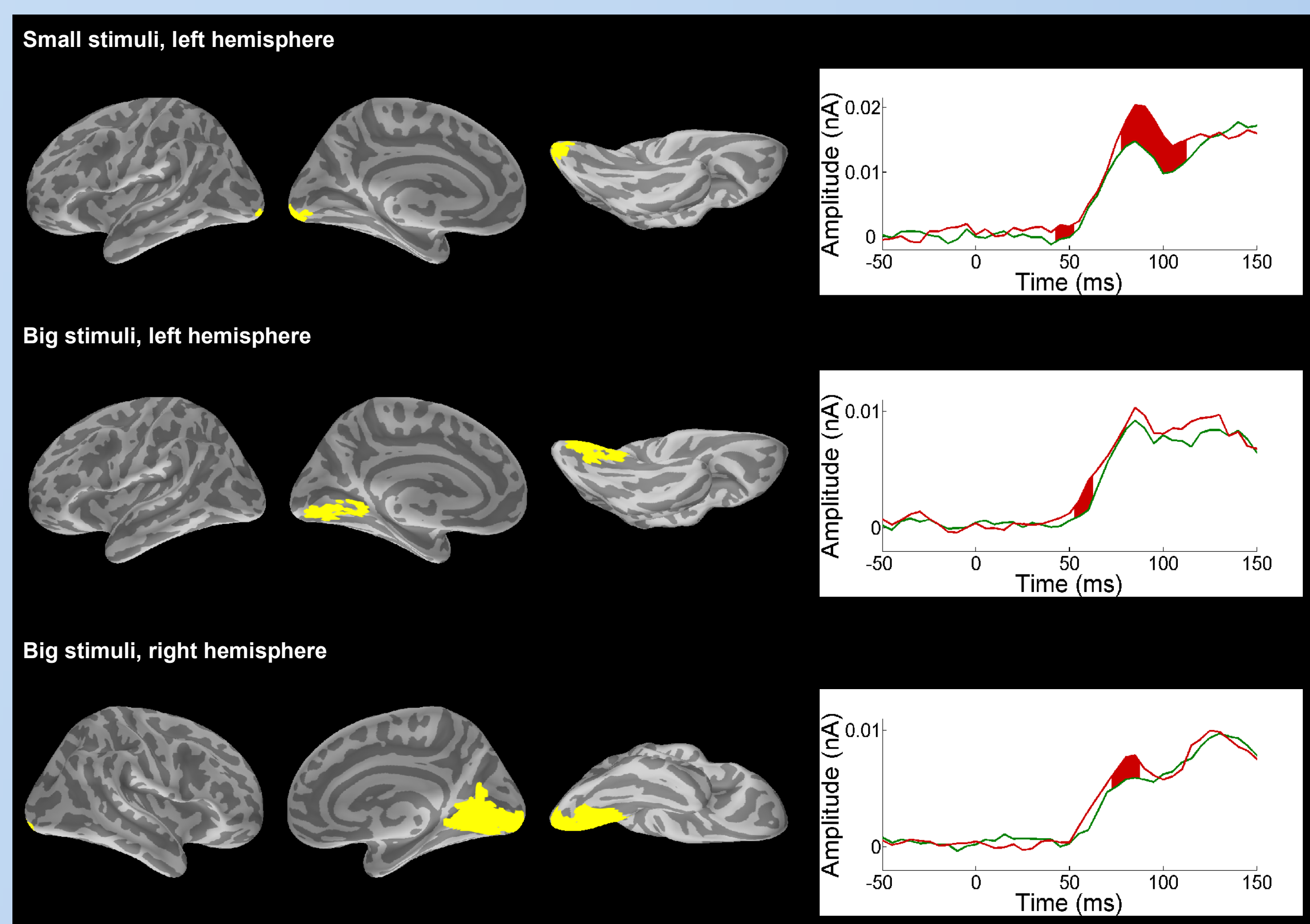
**Source localization of the illusory contour (IC) effect. The spatial loci of the effect (SLEs) defined on the basis of permutation of TFCE-corrected statistics (left) and timecourses of brain activity within corresponding SLEs (right).**

— Kanizsa stimulus
— control stimulus

**Color filling between the timecourses shows statistically significant differences.**

## Discussion

Using a specifically aimed approach we found the early inverted IC effect, which to our knowledge has never been reported in neuroimaging literature. Validity of the early inverted IC effect found is supported by the facts that the effect was reproduced for stimuli of the two sizes, and that cortical localization of the inverted IC effect seems to be adequately related to the stimulus features, with bigger stimuli differentially activating peripheral parts of the primary visual cortex, and smaller stimuli – its central parts.

In view of current literature data this effect is most likely explained by iso-orientation surround suppression, which is known to inhibit responses to collinear stimuli in primary visual cortices (Sillito & Jones, 1996; Jones et al., 2001; Ishikawa et al., 2010; Hashemi-Nezhad & Lyon, 2012; Henry et al., 2013; Vanni & Casanova, 2013). As such it may be related to "sparse" coding, or information maximization principle (Series et al., 2003; Tanaka & Nakamura, 2013; Zhu & Rozell, 2013). In application to illusory borders formed by collinear lines (as in Kanizsa figures) this principle means that at the level of V1 the representations of middle parts of borders are suppressed and eliminated from coding as being informationally redundant.

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