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EXPLORATORY MEG STUDY OF THE ILLUSORY CONTOUR PERCEPTION: POSITIVE AND INVERTED EFFECTS

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EXPLORATORY MEG STUDY OF THE ILLUSORY CONTOUR PERCEPTION: POSITIVE AND INVERTED EFFECTS⁵

The illusory contour is one of the most often used models in studies of Gestalt perception. In our MEG study we observed the so-called illusory contour effect (IC-effect): the activity of non-primary visual and associative cortical areas was increased during the 150-250 ms time window after a stimulus onset in response to illusory stimulus, compared with the control stimulus. In addition to the positive IC-effect, the inverted IC-effect was revealed for the first time in adults. In our study it was manifested during the 60-120 ms window after the onset of stimulus. The inverted IC-effect is an early decrease in the activity of the visual cortex in response to the illusory contour compared with the control stimulus. The mechanism of the inverted IC-effect is yet unclear. The “bottom-up” and “top-down” hypotheses of the origin of the inverted IC-effect are discussed.

JEL Classification: Z

Keywords: Gestalt perception, vision, illusory contour, MEG, Kanizsa figure.

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Introduction

The picture of the surrounding world is very complex but still very efficient because our perception tends to operate predominantly through Gestalts. Therefore, the majority of issues, such as whether our perception bears an objective character and whether it is influenced by our experience, lead to questions about the mechanisms of the inner Gestalt representation. It was shown that perception of a Gestalt object could occur even in the absence of a real contour [Ginsburg, 1975; Petry et al., 1987]. A striking example of Gestalt phenomenon is the illusion of a “subjective contour” [Kanizsa, 1976]. The phenomenon of a subjective contour is an automatic process of grouping several elements in a visual field. As a result of this grouping, an illusory figure contour appears: one sees a physically non-existent figure overlaid over these elements – a white square over four black discs in a given example (Fig. 1).

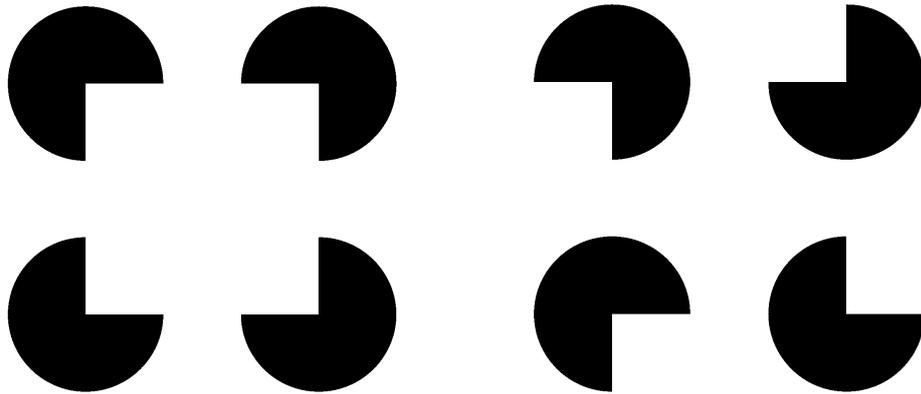
At present, the subjective illusory contour is one of the most frequently used models of Gestalt visual perception research. Concerning the mechanisms of illusory contours formation, it is supposed that both “ascending” and “descending” ways of visual information processing operate within this process. In order to study the mechanisms of illusory contour perception, different psychophysiological methods were used: functional magneto-resonance imaging (fMRI), positron-emission tomography (PET), magnetoencephalography (MEG), and electroencephalography (EEG). These methods help to answer questions such as where, when, and how the illusory contour formation takes place in the brain.

With the help of the fMRI method, the illusory contour effect (IC-effect) was found in extrastriate and visual associative areas of the cerebral cortex (V3A, V7, V4v, V8); it was manifested as an increase in activity in response to illusory contour compared to the control stimulus (Fig. 1), which does create an illusion [Mendola et al., 1999; Murray et al., 2002].

The majority of authors revealed a significant increase of activity in response to the illusory contour occurring in the lateral occipital complex (LOC) [Mendola et al., 1999; Seghier et al., 2000; Ritzl et al., 2003; Murray et al., 2002]. At the same time, the role of the primary visual areas V1 and V2 in processing of the visual illusion remains unclear.

fMRI and PET methods have low temporal resolution. Therefore, with the help of these methods it is impossible to study the exact time of activity onset in the cerebral cortex, and also to find the order of activation of different cortical areas. Lately, the methods of EEG and MEG have been used more often. The study of brain activity with EEG and especially MEG

Fig. 1. The square of Kanizsa (left) and a typical control stimulus (right), formed by the same inducer discs as the square of Kanizsa, but without an illusion of a subjective contour.



methods allow us to study the onset time and the following dynamics of the processes in the brain with millisecond precision.

In a number of studies done with EEG and MEG, event-related potentials or fields were used. As a rule, event-related components with a latency of more than 150 ms were studied, because around this time the IC-effect was revealed in a majority of the studies. Still, the question about the contribution of these components to the formation of illusion remains open. However, on the basis of the data available, several models of illusory contours perception were proposed.

According to Murray's model [Murray et al., 2006], processing visual information and forming Gestalt images have the following structure. At the first stage, the ensembles of neurons in the primary visual cortex process data about the physical characteristics of separate elements based on their brightness and color contrasts. This process (or processes) takes place within the first 50 ms after the stimulus onset.

The second stage of processing takes place in extrastriate and associative areas of the visual cortex and begins about 100 ms after the stimulus onset. This stage approximately corresponds to the component N1 of the evoked potential. The changes in the brain activity at the time of Gestalt image formation can reflect modulations of involuntary spatial and visual attention. This stage is most interesting in relation to the cooperation of ascending and descending processes, because in these conditions their influence is shown to be most pronounced. It is important that during the period of 230-290 ms, which also belongs to the second stage, according to Murray's model, the component Nc1 is revealed in the lateral occipital complex (LOC), which is linked to the completion of the Gestalt image – which, according to the authors' opinion, precedes the recognition of the image [Doniger et al., 2000].

Finally, the third stage of Gestalt image processing begins approximately 300 ms after the stimulus onset and involves both the caudal (parietal and occipital) and frontal areas of the cerebral cortex. During this period the final recognition of an object takes place and – if the object is of special importance – a perceptive decision is made as to whether the object is the target or not. In a few studies dedicated to the component P300, it was supposed that this component reflects the complex cognitive identification of the Gestalt figure itself. Proverbio and Zani [2002] demonstrated increases in P3 amplitudes in the right occipital pole in response to the illusory square of Kanizsa in comparison to the control stimulus.

In addition to event-related potentials and fields, there were several studies dedicated to the gamma-activity associated with the illusory contour perception. For example, according to Tallon-Baudry et al. [1996], late induced (non-phase-locked) gamma activity (at 200-400 ms after stimulus onset) could reflect binding processes. However, the IC-effect was found earlier (within 100-200 ms after stimulus onset, corresponding to the second stage of Murray's model). Thus, one should expect that the binding might occur much earlier than it was initially believed. This hypothesis can be tested by additional studies of the early IC-effects (at 100-200 ms and earlier). Moreover, the results obtained by Tallon-Baudry were subsequently criticized in a methodological respect. Yuval-Greenberg and colleagues, using a single-trial analysis of concomitant EEG and eye tracking, argued that late induced gamma-activity was a reflection of a saccadic spike potential [Yuval-Greenberg et al., 2008].

The other model [Heider et al., 2002; Dresch, Bonnet, 1993; Lee, Nguyen, 2001; Li, Guo, 1995; Kruggel et al, 2001; Pillow, Rubin, 2003; Seghier et al., 2000a, 2000b] implies the presence of two parallel mechanisms of illusory contour perception. The first mechanism – fast and local – predominantly involves the right hemisphere and is carried out by the magnocellular way of the visual system. The second mechanism – slow and global – is carried out basically in the left hemisphere by the parvocellular pathway of the visual system. The majority of researchers suppose that the integration of these two mechanisms takes place in the frontal areas of the cerebral cortex; however, the nature of this integration is still unclear at present. It would be very interesting to compare this model with the existing ideas of the dorsal and ventral pathways of visual processing – the “where” and “what” ways, respectively. According to the literature, the dorsal pathway is based on the information supplied by the magnocellular way, and the ventral one is based predominantly on the parvocellular way output. It should be noted that several studies demonstrated that activation of the dorsal pathway occurs earlier than activation of the ventral pathway. At the beginning, an approximate assessment of the object shape and position is performed, and only after this is the object analyzed in detail, and then the object is recognized [Seghier, Vuilleumier, 2006].

Therefore, the data obtained up to the given moment do not allow one to speak confidently about the mechanisms of illusory contour perception. The aim of the current exploratory research is to observe the IC-effect in detail with the help of MEG recording, which offers an unprecedented combination of excellent temporal and good spatial resolution. Regions of interest were chosen on the basis of standard anatomical definitions. Brain activity was analyzed within the latencies of 60-250 ms, corresponding to early stages of Gestalt visual processing.

Methods

Participants

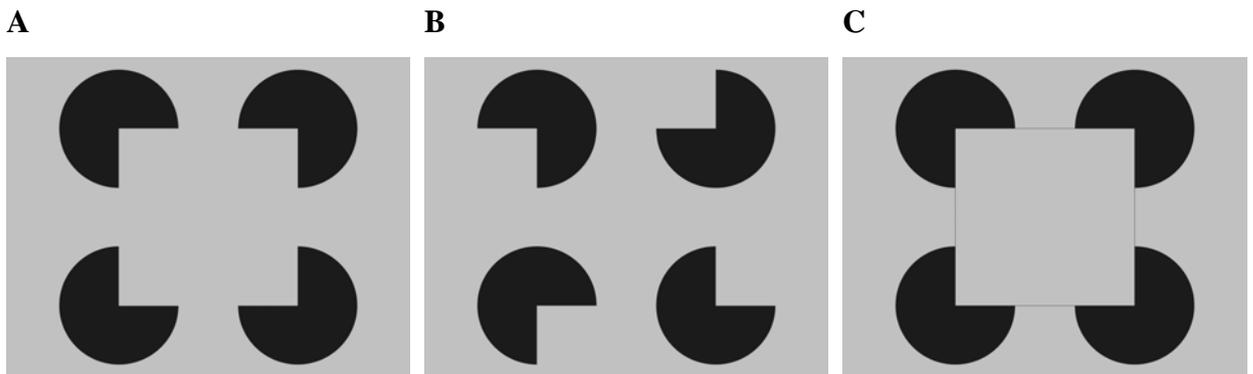
Sixteen subjects (6 males, 10 females, all 18-30 years old) participated in this study. All subjects had normal or corrected to normal vision, and did not have any neurological or psychiatric disorders.

Materials and experimental procedure

Stimuli. Three types of stimuli were used in this study: a stimulus with an illusory contour (Kanizsa square), a control stimulus, and a stimulus with the real contour (Fig. 2). All stimuli were formed by four black inducer discs and presented on a neutral gray background. A grey background, rather than a bright white background, was used in order to avoid visual fatigue in the subjects. Each inducer disc had one 90°-segment missing with the length of inducing edges equal to its radius. These disks were arranged in two ways: either to produce the illusory percept, (Kanizsa square) or to not produce it (the control stimulus). The real contour stimulus was otherwise identical to the Kanizsa square, but the illusory square was explicitly outlined with a drawn border. Two sizes of each stimulus were used: 4.5° and 9.0°.

Experimental task. All stimuli were presented using “Presentation” software (Neurobehavioral Systems Inc., USA) on a 17-inch projection monitor with a refresh rate of 75 Hz. The monitor was located 1.7 m in front of the subject.

Fig. 2. Stimuli used in the study: (A) illusory stimulus (Kanizsa square); (B) control stimulus; (C) real contour stimulus.



The subjects were instructed to maintain their gaze fixed on a small cross in the center of the monitor. Stimuli were presented randomly in the center of the monitor. In half of the subjects the experimental series with 4.5° stimuli was carried out before the experimental series with 9.0° stimuli (150 trials for each stimulus); in the other half of the subjects the order was reversed. The stimulus duration was 500 ms, while the interstimulus interval varied randomly between 500 and 1000 ms.

After the experiment all subjects were asked to report on their subjective perception of the stimuli they saw. The illusory contour was described by all of them as a gray square superimposed on the four black circles. Thus all subjects perceived the illusion.

MEG recording. Before the experiment, we determined the coordinates of anatomical reference points with a three-dimensional digitizing device “FASTRAK” (Polhemus, USA). These points were the left and right preauricular points and the nasion. Four indicator coils attached to the surface of the scalp (in the upper part of the forehead and behind the ears) were also marked and digitized.

MEG was recorded using a 306-channel hardware-software complex “VectorView” (Elekta Neuromag Oy, Finland). The MEG sensor array covered the entire surface of the head and consisted of 102 triplets (each triplet consisting of two planar gradiometers and one magnetometer, measuring mutually orthogonal components of the magnetic field).

Bipolar electromyogram (EMG) and electrooculogram (EOG) were recorded in all subjects with the purpose of artifact monitoring. MEG, EMG, and EOG were recorded using a sampling rate of 1000 Hz, a high-pass filter of 0.1 Hz, and low-pass filter of 330 Hz. The head position during the experiment was monitored in real time by the indicator coils.

The eye tracking was conducted using an infrared camera “IView X MEG”. This system is based on eye-movement detection using the pupil and the light glare on the cornea as referent

points. A sampling frequency was set to 60 Hz, the ranges of measurements in the vertical and horizontal axes were $\pm 25^\circ$ and $\pm 15^\circ$ respectively, with a resolution of 0.1° and an accuracy of 0.5° to 1.0° .

MEG-MRI co-registration (the combining of MEG brain imaging data with a structural MRI using anatomical points) was carried out for individual sequences of the 176 structural T1-weighted MRI slices in the sagittal plane made with a 1.5 T scanner Siemens (a slice thickness of 1 mm).

Data analysis

MEG preprocessing. All raw MEG data were first processed using the signal-space separation (SSS) method to remove biological artifacts and other environmental magnetic sources originating outside the head. Trials were also rejected if they were contaminated with eye movements or blinks (if the bipolar EOG electrode pairs showed a voltage difference greater than $200 \mu\text{V}$), or if the peak-to-peak MEG amplitude exceeded 12000 fT/cm for magnetometers or 3000 fT/cm for gradiometers in either direction. The individualized three-layer boundary element models (BEMs) were constructed for each subject using T1-weighted MRI scans. The cortical, inner, and outer skull surfaces were reconstructed using FreeSurfer software. Individual brains were spatially co-registered by morphing them into the FreeSurfer average brain via a spherical surface. The surface was also “inflated” to unfold the cortical sulci, providing a convenient view of cortical activation patterns. The source estimation was performed using cortical-surface-constrained – both signed and unsigned – L2-norm-based minimum norm estimation by using the MNE software suite. A grid spacing of 5 mm was used for dipole placement, yielding roughly 10000 sources per hemisphere. Dipole orientations were constrained normal to the cortical surface.

Statistical analysis. The brain surface was segmented into separate anatomical regions. In those regions, the average activation level for each time point was calculated. For several time spans (60-120 ms, 120-150 ms, 150-190 ms, 190-220 ms, and 220-250 ms after stimulus onset), the average activity level across the whole time span was obtained in order to account for differences in the timing of activation peaks between subjects.

For assessing the statistical significance in all comparisons, Student's paired t-test was used. Results with $p < 0.05$ were taken to be statistically significant. Since this study was designed as an exploratory one, no corrections for multiple comparisons were used.

Results

In this study, we analyzed the components of the total brain activity with latencies from 60 to 250 ms, which were divided into six 30-ms windows. Illustrations of the data obtained are presented as time courses of the total brain activity, plots of localization for the sources of brain activity on an averaged brain surface, and diagrams of activity values averaged throughout the selected time windows.

60-90 ms time window

As can be seen in Table 1, a significant inverted IC-effect was observed in a number of occipital areas in both hemispheres.

The time courses of responses to 4.5° illusory and control stimuli in the left occipital pole are shown in Fig. 3. There were significant differences between amplitudes of the total brain activity to these stimuli in the 60-90 ms time window, with the amplitude of the total brain activity in the response to the control stimulus being higher compared to the response to the illusory stimulus (the inverted IC-effect).

A comparison of average amplitudes of the total brain activity in responses to 4.5° illusory and control stimuli within the 60-90 ms time window confirmed the inverted IC-effect in the left occipital pole (Fig. 4) ($t(15) = -3.51$, $p = 0.003$). During this period there were no significant differences between average amplitudes in response to the 4.5° illusory stimulus and to the real contour ($t(15) = -1.34$, ns).

The results from the source mapping of brain activity in response to illusory and control stimuli are shown in Fig. 5.

The inverted IC-effect to 9.0° illusory and control stimuli in the right occipital pole is shown in Fig. 6 and Fig. 7. A comparison of average values of brain activity in the right occipital pole in a given time period for 9.0° illusory and control stimuli confirmed the inverted IC-effect ($t(15) = -2.14$, $p = 0.04$) (Fig. 7).

Table 1. IC-effect in the total brain activity in the 60-90 ms time window.
 * - $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Gyrus/sulcus	Stimulus size	
	4.5°	9.0°
Pole occipital (left)	** (inverted)	ns
Gyrus occipital-temporal medial (Lingual) (left)	ns	** (inverted)
Sulcus calcarine (left)	ns	** (inverted)
Gyrus occipital middle (right)	ns	* (inverted)
Pole occipital (right)	ns	* (inverted)
Sulcus occipital middle and Lunatus (right)	ns	* (inverted)

Fig. 3. The time course of total brain activity in response to 4.5° illusory and control stimuli in the left occipital pole (Polus occipitalis). Green represents total activity in response to the illusory stimulus, red is total activity in response to the control. “0” on the time scale is the stimulus onset. Statistically significant differences ($p < 0.05$, paired t-test) are marked by vertical painted zones; the color depends on the predominance of the total activity to one stimulus or the other.

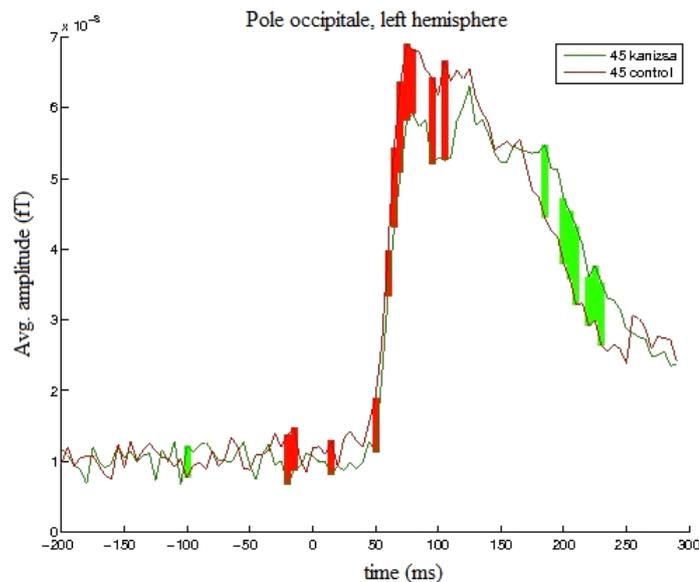


Fig. 4. The average values (\pm SEM) of total brain activity amplitudes in response to all types of stimuli: 4.5° and 9.0° illusory stimuli (“45, Kanizsa”; “90, Kanizsa”), 4.5° and 9.0° control stimuli (“45, control”; “90, control”), 4.5° and 9.0° real contour stimuli (“45, real”; “90, real”) in the 60-90 ms time window in the left occipital pole (Polus occipitalis).

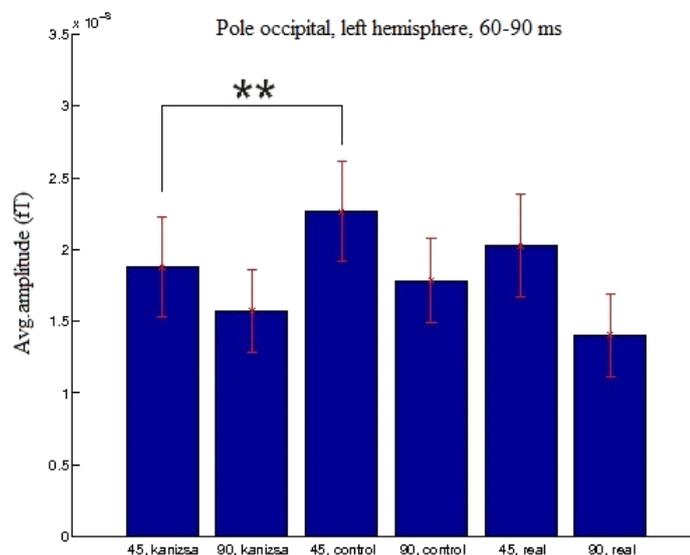


Fig. 5. Localization of the sources of brain activity on an averaged brain surface, left hemisphere, 65 ms after the stimulus onset. The data here are averaged across all trials. Inverted IC-effect for 4.5° stimuli in the area of the occipital pole is represented by the blue area.

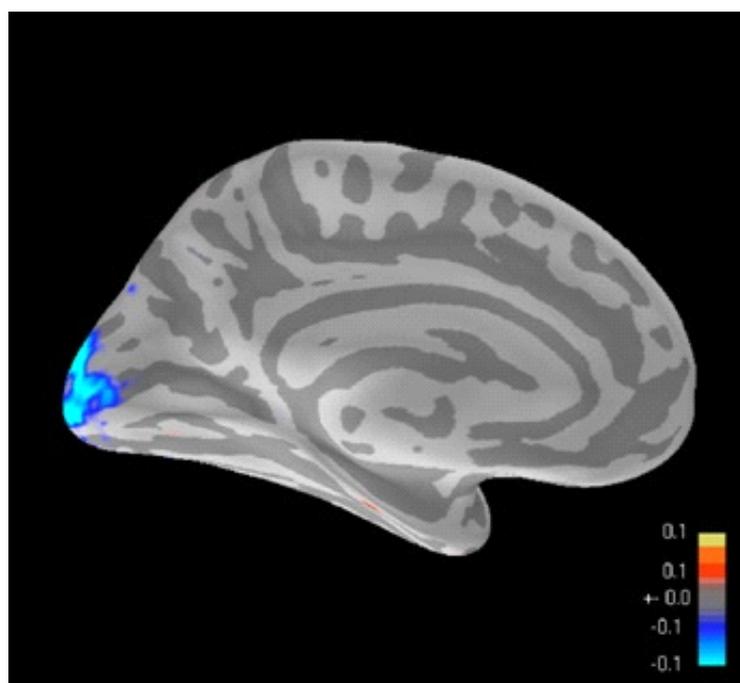


Fig. 6. The time course of total brain activity in response to 9.0° illusory and control stimuli in the right occipital pole (Polus occipitalis). Green represents total activity in response to the illusory stimulus, red is total activity in response to the control. Conventions as in Fig. 3.

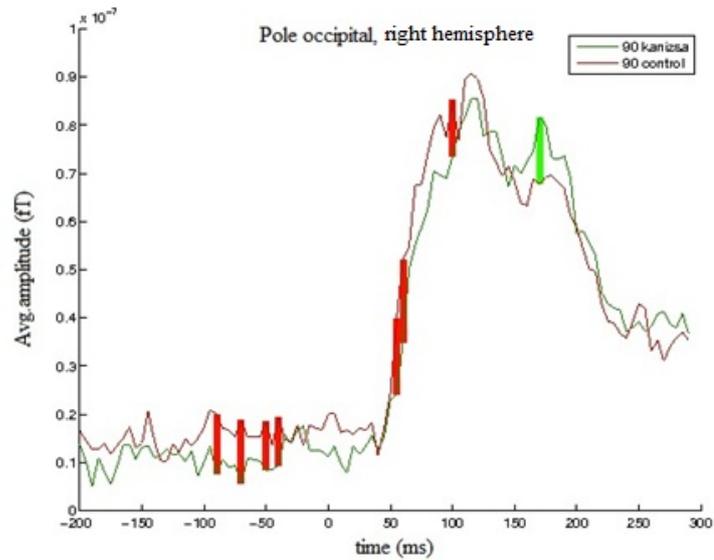
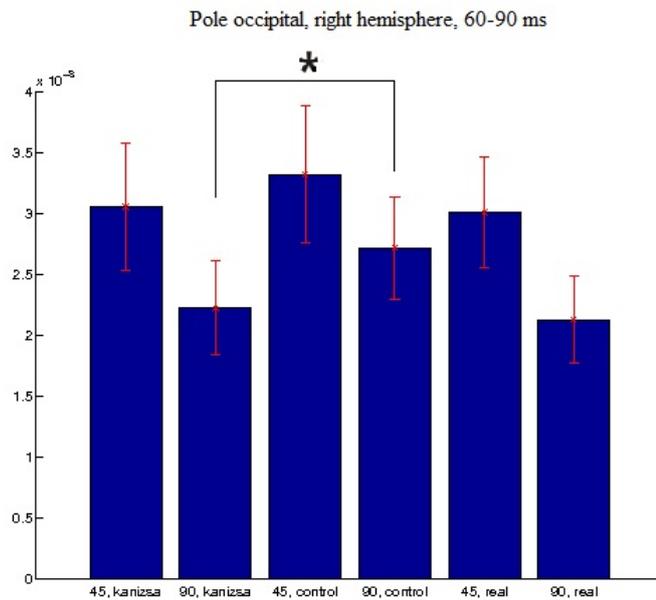


Fig. 7. The average values of total brain activity in response to all types of stimuli for the 60-90 ms time window in the left occipital pole (Polus occipitalis). Conventions as in Fig. 4.



90-120 ms time window

During this period, both positive (for 4.5° figures) and inverted (for 9.0° figures) IC-effects were found.

Table 2 lists the brain areas in which a significant IC-effect was observed in the 90-120 ms time window. A significant positive IC-effect for 4.5° figures was most often recorded in the temporal areas of the cortex.

An analysis of the average dynamics of the total brain activity in the left inferior temporal sulcus revealed a positive IC-effect. As shown in Fig. 8, the total brain activity in response to the 4.5° illusory stimulus in the 90-120 ms time window was higher than in response to the control stimulus. An analysis of the average amplitude values confirmed a positive IC-effect for 4.5° stimuli in the left inferior temporal sulcus ($t(15) = 2.43$, $p = 0.03$) (Fig. 9).

Unlike smaller 4.5° figures, bigger 9.0° figures tended to evoke the inverted IC-effect (Table 2). Fig. 10 shows the dynamics of the total brain activity in the left occipital pole (Polus occipitalis) for 9.0° illusory and control stimuli. The analysis of the averaged total activity confirmed the negative IC-effect in the left occipital pole ($t(15) = -2.89$, $p = 0.01$) (Fig. 11).

Fig. 12 shows the results of source mapping for brain activity in response to illusory and control stimuli in the 90-120 ms time window to the 4.5° stimuli.

Table 2. IC-effect in the total brain activity during the 90-120 ms time window. * - $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Gyrus/sulcus	Stimulus size	
	4.5°	9.0°
Gyrus temporal inferior (left)	**	ns
Sulcus temporal inferior (left)	*	ns
Pole occipital (left)	ns	* (inverted)
Sulcus collateral transverses posterior (left)	ns	** (inverted)
Gyrus cuneus (right)	ns	* (inverted)

Fig. 8. The time course of total brain activity in response to 4.5° illusory and control stimuli in the left inferior temporal sulcus (Sulcus temporalis inferior). Green represents total activity in response to the illusory stimulus, red is total activity in response to the control. Conventions as in Fig. 3.

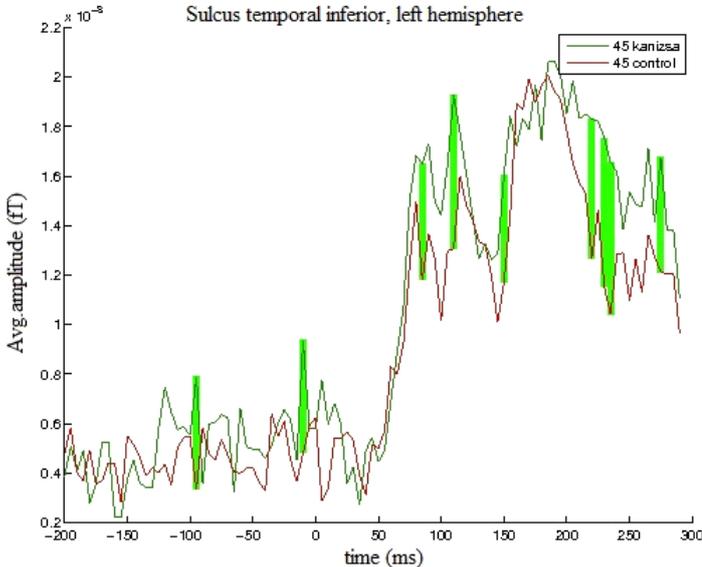


Fig. 9. Average total brain activity values in response to all types of stimuli in the 120-150 ms time window in the left inferior temporal sulcus (Sulcus temporalis inferior). Conventions as in Fig. 4.

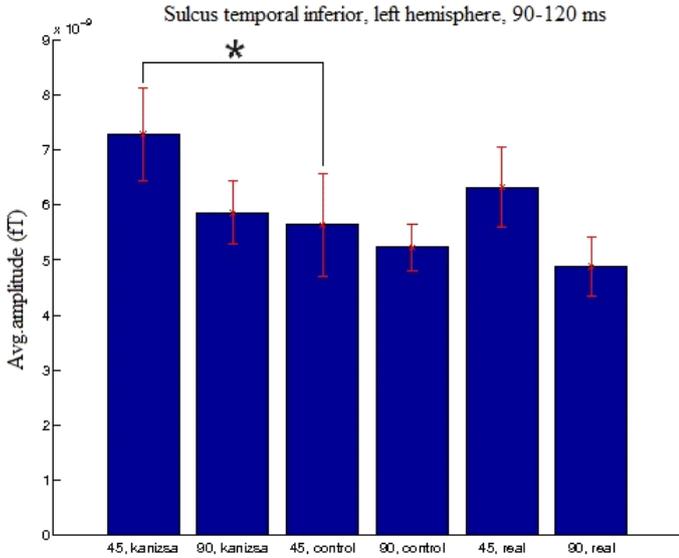


Fig. 10. The time course of total brain activity in response to 9.0° illusory and control stimuli in the left occipital pole (Polus occipitalis). Green represents total activity in response to the illusory stimulus, red is the response to the control one. Conventions as in Fig. 3.

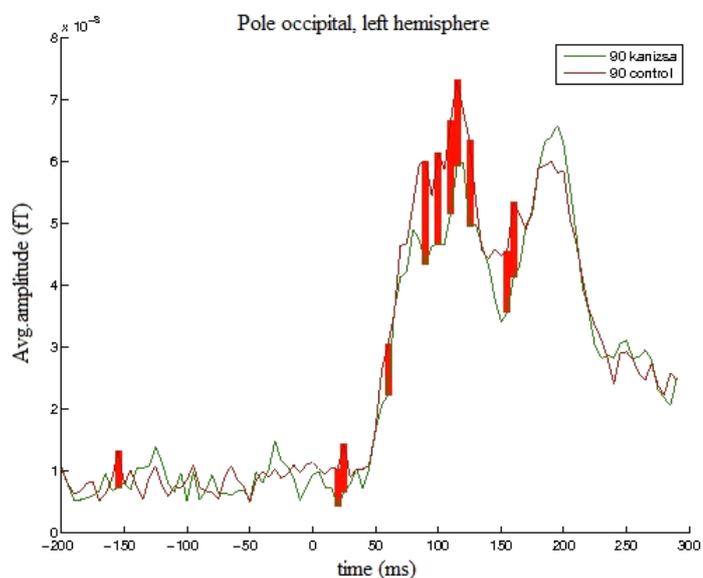


Fig. 11. Average total brain activity in response to all types of stimuli for the 90-120 ms time window in the left occipital pole (Polus occipitalis). Conventions as in Fig. 4.

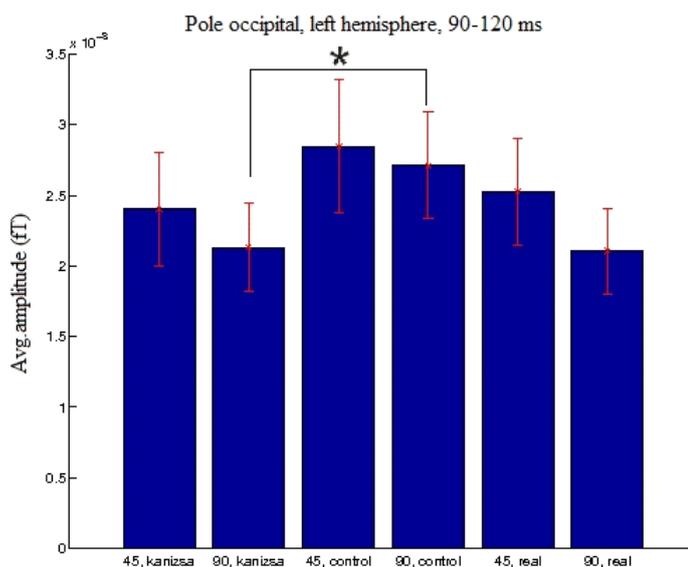
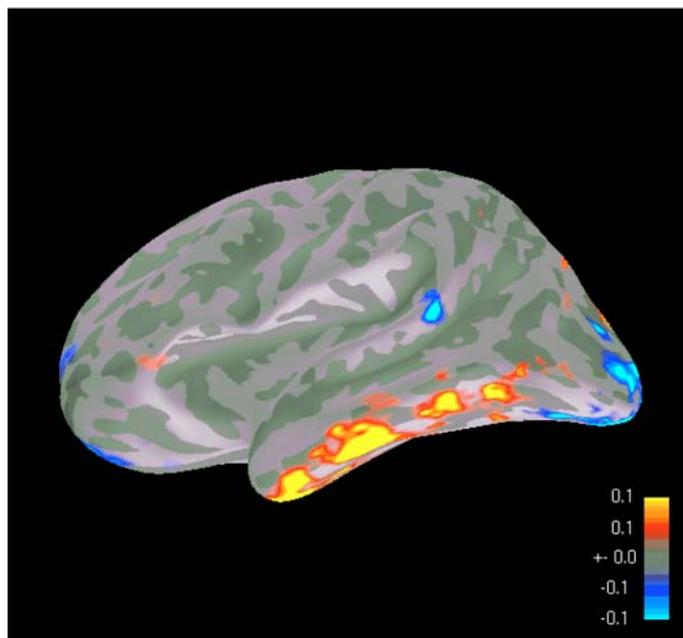


Fig. 12. Localization of the sources of brain activity on an averaged surface of the brain, left hemisphere, 110 ms after the stimulus onset. The data were averaged across all trials. Positive IC-effect for 4.5° stimuli in the inferior temporal sulcus are represented by the yellow and red areas.



120-150 ms time window

A positive IC-effect was found in the 120-150 ms time window for the 9.0° stimuli. Fig. 13 shows the dynamics of the total activity in the right angular gyrus of the inferior parietal lobule. Within the 120-150 ms time window, activation in response to 9.0° illusory stimulus was higher than in response to the control stimulus of the same angular size. An analysis of the average amplitude values confirmed this observation in the right angular gyrus ($t(15) = 3.42$, $p = 0.004$).

Fig. 13. The time course of the total brain activity in response to 9.0° illusory and control stimuli in the right angular gyrus (Gyrus parietalis inferior angular). Green represents total activity in response to the illusory stimulus, red represents the response to the control one. Conventions as in Fig. 3.

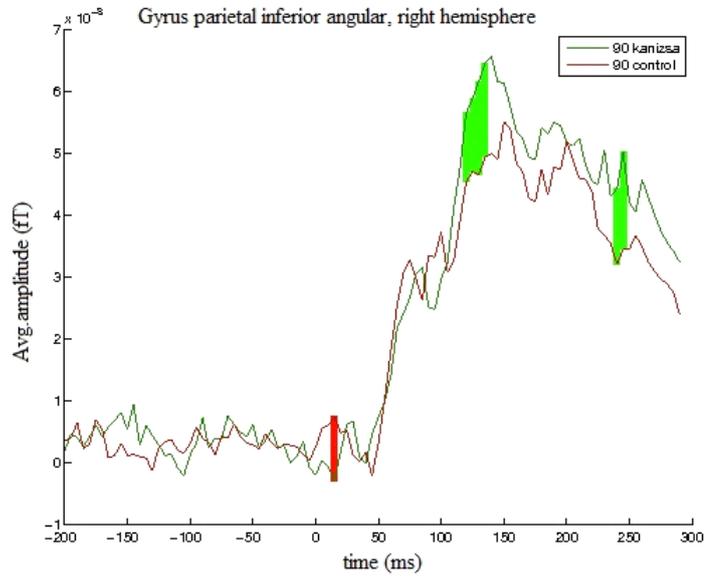
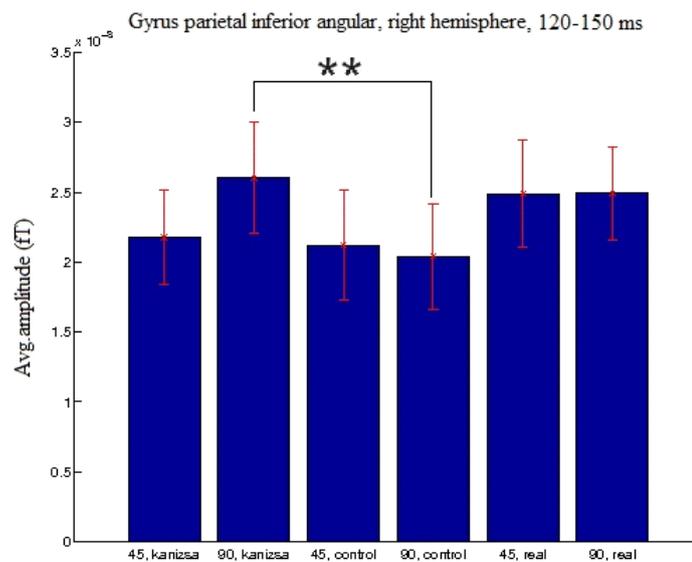


Fig. 14. Average values of the total brain activity in response to all types of stimuli in the 120-150 ms time window in the right angular gyrus (Gyrus parietalis inferior angular). Conventions as in Fig. 4.



150-190 ms time window

In this time window, an inverted IC-effect was prominent. An analysis of the total activity dynamics showed an inverted IC-effect in the subparietal sulcus of the right hemisphere. Fig. 15 shows that the activity to the 4.5° control stimulus was higher than for to the illusory stimulus of the same size. An analysis of average values of the total brain activity in 150-190 ms window confirmed the significance of this effect ($t(15) = -2.18$, $p = 0.04$) (Fig. 16).

An analysis of the total activity dynamics for 9.0° stimuli did not show any significant differences ($t(15) = 1.14$, ns).

Fig. 15. The time course of total brain activity in response to 9.0° illusory and control stimuli in subparietal sulci. Green represents total activity in response to the illusory stimulus, while red is total activity in response to the control one. Conventions as in Fig. 3.

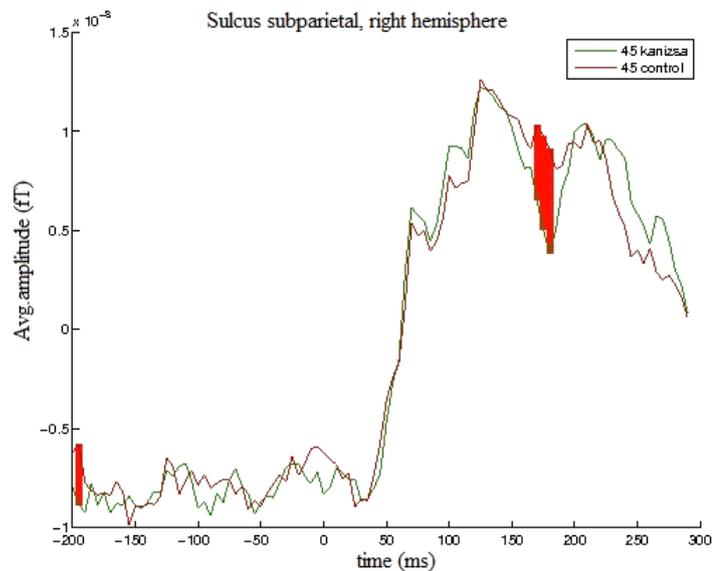
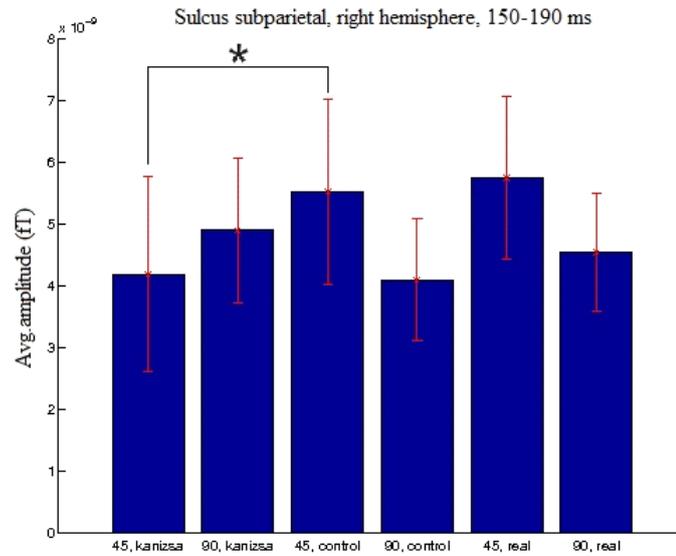


Fig. 16. Average total brain activity in response to all types of stimuli in the 150-190 ms time window in the right subparietal sulcus. Conventions as in Fig. 4.



190-220 ms time window

A significant positive IC-effect in the 190-220 ms time window was found in the left occipital and occipital-parietal regions (for 4.5° stimuli it was found exclusively in the left hemisphere) (Table 3).

The IC-effect was particularly found for 9.0° stimuli in the left lateral occipital-temporal sulcus (Fig. 17). The figure shows that, in the 190-220 ms time window, the amplitude of the total brain activity for 9.0° illusory stimulus was significantly higher than for the control stimulus. This effect was also significant for the averaged values of the total brain activity across this time window ($t(15) = 2.35$, $p = 0.03$) (Fig. 18).

An analysis of the total brain activity in response to the 9.0° illusory stimulus and real contour stimulus revealed some differences in the left lateral occipital-temporal sulcus activation. The amplitude of the response to the illusory stimulus was higher than to the real contour stimulus (Fig. 19).

An analysis of the average amplitude values demonstrated that the activity in response to the real contour was lower than to the illusory stimulus ($t(15) = 2.56$, $p = 0.02$) (Fig. 20).

Table 3. IC-effect in the total brain activity during the 190-220 ms time window.
 * - $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Gyrus/sulcus	Stimulus size	
	4.5°	9.0°
Gyrus cuneus (left)	*	ns
Gyrus occipital middle (left)	**	**
Pole occipital (left)	*	ns
Sulcus occipital middle and Lunatus (left)	*	*
Sulcus occipital-temporal lateral (left)	ns	*
Sulcus calcarine (left)	*	*
Sulcus parietal-occipital (left)	**	ns
Gyrus occipital superior (right)	*	ns

Fig. 17. The time course of total brain activity in response to 9.0° illusory and control stimuli in the left lateral occipital-temporal sulcus. Green represents total activity in response to the illusory stimulus, red is total activity in response to the control. Conventions as in Fig. 3.

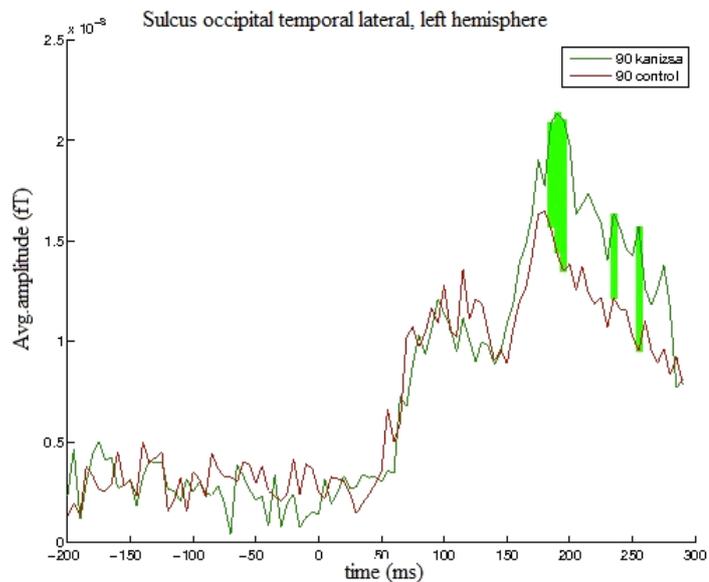


Fig. 18. Average values of the total brain activity in response to all types of stimuli in the 190-220 ms time window in the left lateral occipital-temporal sulcus. Conventions as in Fig. 4.

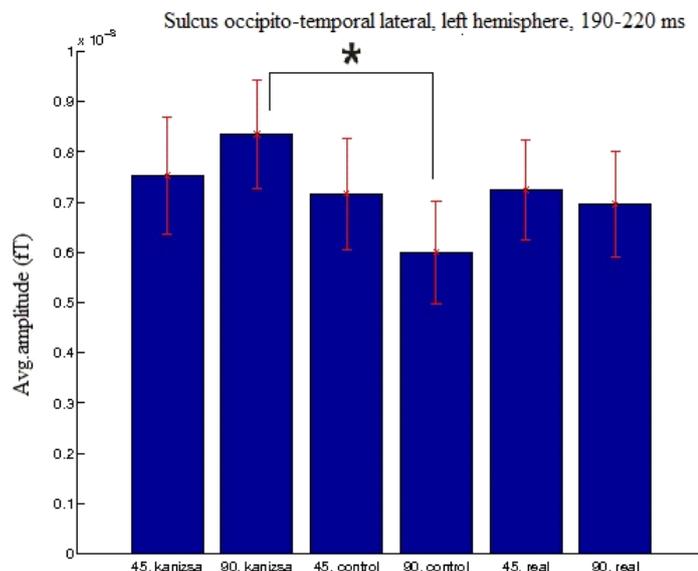


Fig. 19. The time course of total brain activity in response to 9.0° illusory and real stimuli in the left lateral occipital-temporal sulci. Green represents total activity in response to the illusory stimulus, red represents the response to the real one. Conventions as in Fig. 3.

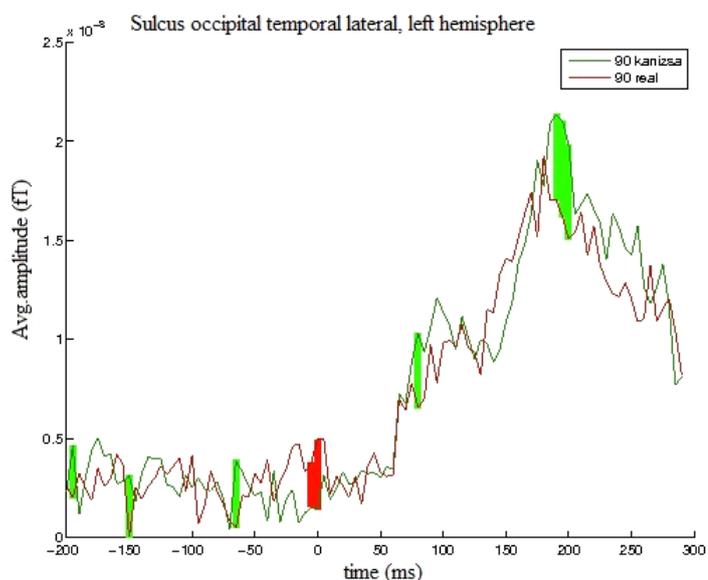
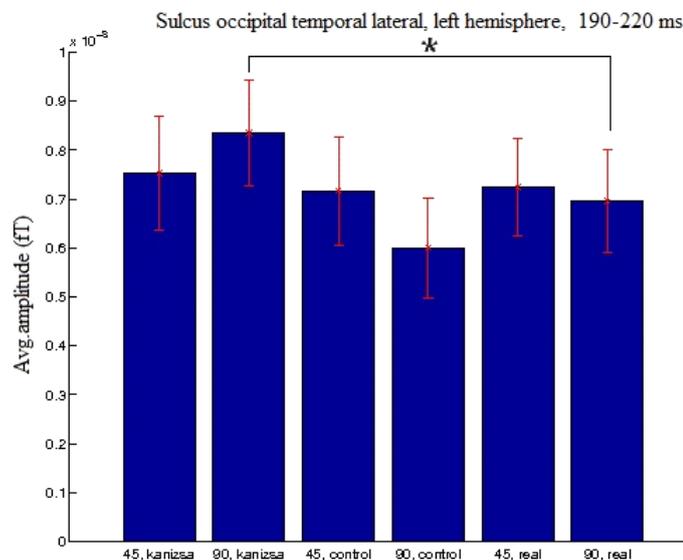


Fig. 20. Average values of the total brain activity in response to all types of stimuli in the 190-220 ms time window in the left lateral occipital-temporal sulcus. Conventions as in Fig. 4.



220-250 ms time window

The brain areas revealing a significant IC-effect in the total brain activity within in the 220-250 ms time window are listed in Table 4. These brain areas are located in the occipital, parietal and temporal brain regions, where primary and secondary association areas of the visual cortex are located. Particularly, the total brain activity in response to 4.5° real contour stimulus was higher than to illusory stimulus in the left cuneus (Fig. 21). An analysis of the averaged total brain activity confirmed this result ($t(15) = -2,22$, $p = 0.04$) (Fig. 22).

Table 4. IC-effect on the total brain activity in the 220-250 ms time window. * - $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Gyrus/sulcus	Stimulus size	
	4.5°	9.0°
Gyrus cuneus (left)	**	ns
Gyrus occipital middle (left)	**	***
Pole occipital (left)	***	ns
Sulcus occipital middle and Lunatus (left)	*	*
Sulcus occipital middle and Lunatus (right)	*	ns
Gyrus parietal inferior Angular (left)	*	**

Fig. 21. The time course of the total brain activity in response to 9.0° illusory and control stimuli in the left cuneus. Green represents total activity in response to the illusory stimulus, red is total activity in response to the control. Conventions as in Fig. 3.

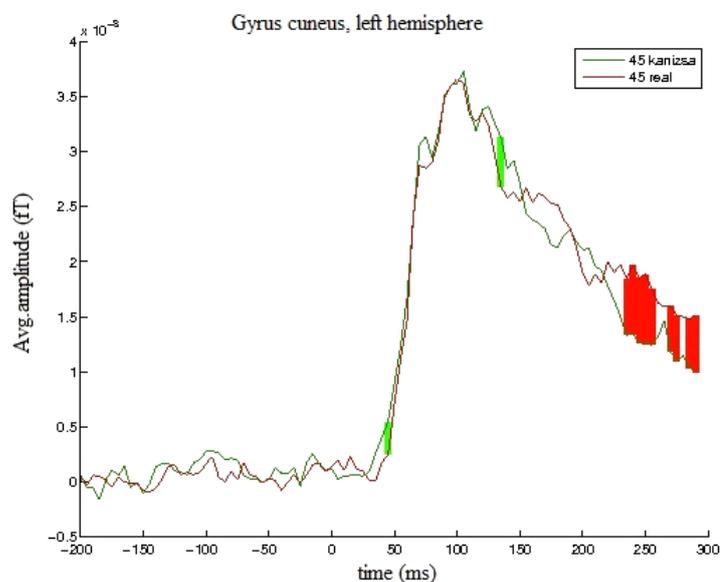
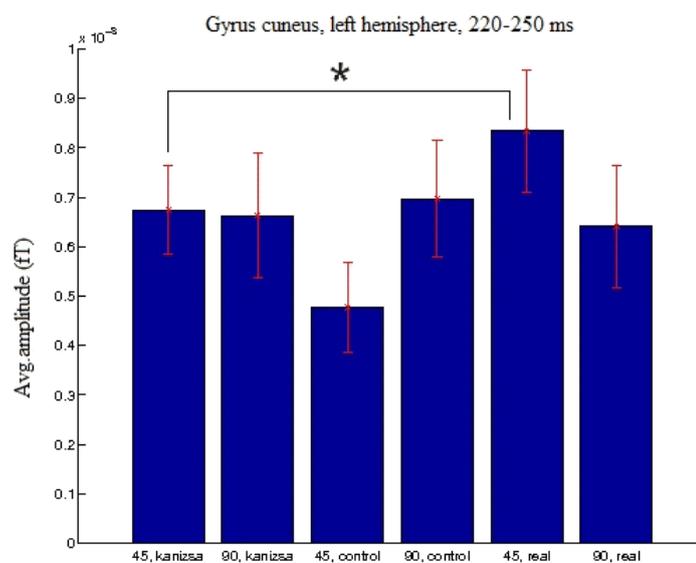


Fig. 22. Average values of the total brain activity in response to all types of stimuli in the 220-250 ms time window in the left cuneus. Conventions as in Fig. 4.



Results summary

In the 60-90 ms time window the inverted IC-effect was found in the left occipital pole for 4.5° figures. The total brain activity analysis for 9.0° stimulus showed the inverted IC-effect in the occipital and occipital-temporal areas. Thus, both sizes produced an inverted IC-effect in occipital areas within the earliest time window of 60-90 ms.

In the 90-120 ms time window a positive IC-effect was found in the right temporal and occipital-temporal areas for the 4.5° stimuli. Within the same time window the inverted IC-effect was revealed in the left occipital pole to 9.0° stimuli.

The positive IC-effect was detected in the 120-150 ms time window in the parietal-occipital regions to 9.0° stimuli.

Within the 150-190 ms time window an inverted IC-effect was revealed in the subparietal sulcus.

Various effects were observed in the 190-220 ms time window. The IC-effect was revealed in the total brain activity dynamics in the left occipital and occipital-parietal regions for 4.5° stimuli. The brain activity dynamics analysis for 9.0° stimuli showed the IC-effect in the left occipital-temporal cortex.

It was also found that the activity amplitude to the 9.0° real contour stimulus is lower than to the illusory stimulus of the same angular size in the left occipital-temporal brain areas.

An IC-effect was also detected in the later time period of 220 to 250 ms. An analysis of the total brain activity dynamics for small figures showed an IC-effect in the left parietal-occipital areas.

In the time window of 220-250 ms it was also found that the amplitude of the total brain activity for the 4.5° real contour stimulus was higher than for the illusory stimulus.

Discussion

In the current study, an inverted IC-effect – lower response to the illusory stimulus compared to the control one – was discovered for the first time in the total brain activity using MEG recording. This effect was manifested in early components. An analysis of the 60-90 ms time window of the total brain activity showed a great inverted IC-effect in the occipital areas, in the area of the calcarine sulcus, and in the occipital pole (i.e., mostly in the primary visual cortex).

Stroganova et al. [2007] found a similar effect in preschoolers using a different method. It was manifested as higher amplitude of a phase-locked gamma band EEG response to the control

compared to the illusory contour stimulus. A decrease in activity in the primary visual cortex V1 in response to the illusory contour compared with control stimulus was also demonstrated by Ramsden et al. [2001] on macaque monkeys with the use of optical imaging; it is likely that the mechanism of inverted IC-effect must be the same in all cases.

Two hypotheses can be put forward to explain the phenomenon with the inverted IC-effect:

1. A “bottom-up” effect, determined by the physical characteristics of the stimulus.
2. A “top-down” effect, determined by the feedback from higher associative cortical areas (frontal, temporal, parietal).

The first hypothesis is based on the fact that neurons in the primary visual cortex have receptive fields that are too small to be able to successfully distinguish an integral figure [Hubel, 1990]. Therefore, the early brain evoked responses are related to visual boundary detection and contour segregation [Vandenbroucke et al., 2008]. According to this statement, the inverted IC-effect can be explained by local differences in the contours of illusory and control stimulus, orientation of inducer disks, brightness of stimuli, etc. The lateral interactions among neurons in the primary visual cortex were considered as physiological mechanism of such early modulation.

However, there are some contradictions to this hypothesis. According to Ramsden et al. [2001], who obtained data in monkeys from the presentation of horizontal and vertical illusory contours formed by “abutting grating”, the observed effect can not be explained by the inner properties of the primary cortex itself. One can presume that the inhibition of activity in response to an illusory contour occurs due to the integration of end-cells responses by horizontal connections. However, the authors did not find such integrative responses in V1. Thereby the authors supposed that the inverted effect could be the result of inhibitory feedback from V2 [Ramsden et al., 2001].

The second hypothesis was confirmed by several studies [Rossi, Pourtois, 2012; Rauss et al., 2011; Zani, Proverbio, 2012; Kelly et al., 2008], which indicated the sensitivity of early components to the “cognitive task” executed by the subject (for example, in a competitive presentation of stimuli), as well as to the emotional state of the subject.

Interesting data were also obtained in a study conducted by Foxe and Simpson [2001]. The authors carried out a visual experiment in 12 healthy subjects. The visual stimuli did not contain an illusory contour. One of the most important findings of this research was that the propagation of the evoked activity from the primary visual cortex area to the associative areas was faster than it was supposed to be: An evoked response within the non-primary occipital areas was observed at 56 ms, and in frontoparietal areas it was observed at 80 ms [Foxe, Simpson, 2001]. It is well known that the primary visual cortex receives descending feedback from secon-

dary and associative areas [Lamme, 1995; Zipser et al., 1996; Lamme et al., 1998a; Angelucci and Bullier, 2003; Lee, 2002; Buffalo et al., 2010; Xing et al., 2012]. Based on the results of Foxe and Simpson, we can speculatively suppose that such feedback comes fast enough to affect the primary visual cortex activity within the 60-90 ms time window.

The second hypothesis is substantiated by the absence of any differences between the real and illusory contours within the 60-90 ms time window. If the activity of the calcarine sulcus area and the occipital pole were determined by physical characteristics of stimuli only (the number of borders between dark and light), then the response to the real contour stimulus would be higher, because the presence of a real contour increases the number of boundaries. On the other hand, it is probable that the real contour was not contrasted and visible enough to provoke a significant activity increase compared with the contour's absence. Thus, it would be interesting to conduct a study in which the brightness of the contour, disposition of inducer discs, as well as the gradation of stimuli sizes would be varied.

In contrast to our research, in which the subjects were not given any instructions except to maintain their gaze fixation in the center of screen, in a majority of other studies of illusory contour perception the subjects were asked to respond in some or other way to target stimuli appearing in the screen in order to capture the subject's attention and focus its gaze on the screen [Tallon-Baudry, 1996; Murray et al., 2002; Proverbio, Zani, 2002; Murray et al., 2006]. However, we suppose that such a "cognitive task" might distract a subject's attention from the actual stimuli under study (including the illusory contour), thereby affecting the illusory contour perception and intensity of the IC-effect. It would be interesting to carry out a supplementary series of experiments in which subjects will be instructed to count the target stimuli. Thus we will be able to find out if the capture of attention to the target stimuli influences the early inverted IC-effect. Modulation of the inverted effect in such conditions would be an indicator of a top-down influence on early components and would confirm the second hypothesis, because the physical characteristics of stimuli under study will stay invariable.

We also observed a positive IC-effect, which was manifested in a higher-amplitude response to the illusory stimulus compared with the control stimulus. The positive IC-effect was revealed in later time windows: 120-150 ms, 190-220 ms, and 220-250 ms. This effect was found to have a high statistical significance in extrastriate areas (parietal, parietal-occipital, and occipital-temporal). It is of interest that for the 9.0° figures, the earliest robust IC-effect was observed in the angular gyrus within the 120-150 ms time window. A later effect (190-220 and 220-250 ms) was associated with the occipital and parietal-occipital areas, as well as the occipital-temporal area: the middle occipital gyrus and the lateral occipital-temporal sulcus. Such data are in accordance with the idea that the Gestalt perception of visual information starts in the

magnocellular pathway, gives rise to the dorsal stream, and only thereafter does it enter into the ventral stream through the parvocellular pathway [Seghier, Vuilleumier, 2006]. Besides this, a significant positive IC-effect was found at 220-250 ms in the occipital pole and calcarine sulcus, where the inverted IC-effect was evident at earlier latencies. Using MEG recording, Halgren et al. [2003] showed that evoked activity in the cortex can sometimes be found returning two or more times into one and the same area at different latencies [Halgren et al., 2003]. This phenomenon is supposed to be the result of a feedback between different cortex areas.

It is also important that for 9.0° figures the early IC-effect (120-150 ms) in the angular gyrus took place in the right hemisphere. These data stay in agreement with the hypothesis of a local and fast mechanism of illusory contour perception associated with the activity of the dorsal stream and predominantly in the right hemisphere [Seghier, Vuilleumier, 2006]. This observation generally corresponds to the results of Halgren et al., in which the early stages of IC-effect are apparently more widely expressed in the right hemisphere [Halgren et al., 2003].

Later, in the 190-220 ms time window, the significant IC-effect changes its location and becomes most prominent in the left hemisphere. Within the next time window of 220-250 ms, the intensity of the IC-effect is almost equal in the left and right hemispheres. We can suppose that in the time window of 190-220 ms the late global processing of Gestalt perception starts in the left hemisphere. Appealing to the results of Foxe and Simpson, we can propose that the right hemisphere gets the first feedback during the time window of 220-250 ms – which takes about 30 ms – and the process of initial image recognition begins.

According to Murray's model [Murray et al., 2006] a primary binding of the picture elements in a Gestalt image takes place in the time period of 100 to 300 ms. In particular, recognized fragments of the object can move the focus of involuntary spatial visual attention, binding these fragments in a preliminary rough image of the object and collating this image with patterns in our memory. However, it is important to note that Murray's model does not take into account and explain the inverted IC-effect that we observed in the early time window of 60-90 ms. Therefore, this model can not be adequately used to explain our results.

It is important to note that for the 4.5° figures the dynamics of spatial propagation of activity through the cortical areas was quite different. For these stimuli the early positive IC-effect was revealed with reduced latencies in the time window of 90-120 ms. It was observed in the occipital-temporal areas, which approximately correspond to the lateral occipital complex (LOC). In order to understand the observed differences in the dynamics of propagating activity in response to the stimuli of the two sizes, further research is needed.

Significant differences in activation to the 4.5° real and illusory contour were also revealed in the time window of 220-250 ms: The response to the real contour was higher than the

response to the stimulus with illusory contour. In the study of Tallon-Baudry et al. [1996], in which, like in the present study, a control, illusory, and real contour stimuli were used, the real contour was found to produce a negative shift of the evoked potential within 200-300 ms latencies in response to the illusory stimulus compared to the two control and real contour stimuli. This effect was observed in all electrode locations with the shortest latencies at occipital leads. However, differences in experimental design and methods make our data not fully comparable with those of Tallon-Baudry. In the study of Kinsey et al. [2009] that used frequency analysis, a decrease in activity in the extrastriate areas in the 10-30 Hz band as a response to both the real and illusory figures compared to the control stimulus was found. Still the authors did not find any significant differences between the responses to the real and illusory figures. They supposed that this effect is based on some general, basic mechanism of Gestalt-figure perception (for example, increasing attention in the period of stimulus presentation) and does not depend on the type of the contour (real or illusory). It is important to note that low-contrast figures (dark-grey figures on a bright-grey background) were used in the study of Kinsey et al. Perhaps the real contour was not bright and visible enough to evoke any activation that would significantly differ from the activation in response to the illusory contour.

Stroganova et al. [2009] supposed that increasing the angular sizes of stimuli should evoke a more expressed alpha-response and, perhaps, a more significant IC-effect, since alpha-activity should bind remote neuron ensembles. Our results did not show any greater intensity of the IC-effect for large stimulus. We can suppose that, in order to reveal the effect of large stimuli, phase-locked rhythmic activity should be analyzed instead of the evoked total brain activity. We cannot exclude the possibility that stimuli that are greater in size than the limits of the central visual field are more difficult to perceive as Gestalt figures, because the subjects in our experiment fixed their gaze strictly in the center of the screen under the control video-oculographic recording, and the figures were much bigger than the central visual field. And, lastly, it is possible that the effect proposed by Stroganova et al. may be observed in cortical areas other than those used in the present study.

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