ACTA NEUROBIOLOGIAE EXPERIMENTALIS

Research paper Acta Neurobiol Exp 2014, 74: 443–455

Temporal dynamics of the Oppel-Kundt Illusion compared to the Müller-Lyer Illusion

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In psychophysical experiments, subjects reported whether the filled part of the Oppel-Kundt stimulus was longer than the empty one at different durations of the stimuli presentations. The experimental data yielded a smooth function indicating a gradual augmentation of the illusion strength within a relatively wide 100–1000 ms interval of the exposure durations. On the contrary, the experiments with the Müller-Lyer stimuli showed a gradual decrease of the illusion magnitude within the same interval of expositions. In the supplementary experiments, the stimuli with uniformly filled or outlined rectangles of fixed duration were used; various combinations of the rectangles with the regular sequences of filling stripes were also taken. It was demonstrated that the superposition of the stimuli did not change the illusion strength noticeably. The results obtained in the study support the suggestion that the filled interval overestimation in the Oppel-Kundt stimulus may be related to spatiotemporal integration along a continuous path of neural excitation evoked by the real and illusory contours of the filling.

Key words: illusions of extent, filled-unfilled illusion, exposure duration, illusory contours, contour integration

INTRODUCTION

The phenomenon of the Oppel-Kundt illusion represents an overestimation of the filled (by a regular sequence of uniform elements) spatial interval when compared to the empty one of the same length. After Oppel introduced (1855) the figure with a horizontal line subdivided by a series of equally spaced vertical line segments, a number of stimuli modifications have been studied. The segmented line figure was reshaped into the pattern of vertical stripes of varying height, number, and distribution (Kundt 1863). It was demonstrated that a certain number of stripes might be more effective than many lines fused into a solid object (Ebbinghaus 1902), and the maximum illusion strength was found with 7 to 13 (Obonai 1933) or 9 to 14 (Piaget and Osterrieth 1953) stripes in the filled stimulus part. Uniformity and regular distribution of the stripes was critical for the illusion manifestation (Oyama 1960, Nouguchi et al. 1990, Wackermann and Kastner 2010): if the filling stripes were irregularly spaced or unequal in height, thickness, brightness, or were dotted, then the effect of the illusion was less prominent. However, if the whole figure was formed just of dots, the illusion strength appeared similar to that made up of stripes (Bulatov et al. 1997, Bertulis and Bulatov 2001). The difference in the brightness contrast between two stimulus parts decreased the illusion (Long and Murtagh 1984, Dworkin and Bross 1998); the luminance contrast absence (isoluminant colors of the stimulus and background) may also reduce the illusion magnitude (Surkys 2007). It was found that the O-K effect slightly increased with the absolute luminance contrast and was higher for the negative (white figures against a dark background) than for the positive polarity (Wackermann 2012). The three-part O-K figure (with two filled intervals flanking the empty one) induced the illusion, which was about 25% stronger than that caused by conventional two-part figure with one filled interval (Bertulis et al. 2009).

The spatial parameters of the O-K stimulus make a substantial influence on the illusion strength. However, there are several arguments suggesting that the stimulus presentation duration may also be considered as

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Received 26 May 2014, accepted 19 September 2014

one of the important determinants of the illusion magnitude. Firstly, the filled-unfilled illusion occurs not only in vision, but also in audition: temporal intervals filled with a sound are judged as being longer when compared with the blank ones, and time intervals with evenly distributed ticks are judged as longer than the same intervals comprising these ticks in an asymmetric pattern (Buffardi 1971). Secondly, the psychophysical phenomena *tau* and *kappa* indicate that the encoding of spatial extent is related to temporal factors, and *vice versa* (Russo and Dellantonio 1989). Finally, the visuospatial processing is a dynamic time-evolving phenomenon (VanRullen and Thorpe 2001).

A significant decrement of the O-K illusion magnitude during a prolonged inspection period was registered for subjects making saccadic eye movements over the stimulus (Coren and Hoenig 1972): for subjects, whose gaze direction was changed continuously from one end of the O-K figure to the other, the illusion magnitude decreased by 20%, 25%, and 30% at 2 min, 4 min, and 6 min after the stimulus onset, respectively; for subjects, who maintained a steady gaze fixation no illusion decrement was found. Bailes (1995) performed experiments with varying filling density and exposure time of the O-K stimulus. For prolonged durations (about 3 s), a typical non-linear function was obtained indicating that the illusion strength increased to maximum with an increase of the density of filling up to 12 stripes, and slightly decreased afterwards. At short durations, the illusion was rather weak or absent. At the durations less than 200 ms for the highest density of filling, even the opposite sign of the illusion magnitude was obtained. Somewhat later, Dworkin and Bross (1998) reported the O-K study regarding stimulus presentation time and brightness. Observers judged the parts of the O-K stimuli at the presentation times of 100 ms, 500 ms, and 1000 ms. The results showed that brighter stimuli appeared as more effective at all three exposure times, but at the shortest duration (100 ms) they yielded the strongest illusion, i.e., opposite to the previous findings.

Thus, different studies of the O-K illusion agree that the illusion magnitude varies with the presentation duration; however, it still remains unclear whether the illusion strength increases or decreases at shorter stimulus presentations. These contradictory results might have been obtained due to differences and relative weaknesses of the methods used. Therefore, in the present study, in order to diminish uncertainty concerning the temporal characteristics of the O-K illusion, a rather reliable (Morgan et al. 2013) method of forced-choice discrimination with the backward masking paradigm was applied, which is an important methodological tool (Bachmann 1994, Lamme et al. 2002) useful for investigating the temporal sequences with stimuli ranging from simple geometric forms to faces and complex scenes.

The Müller-Lyer (M-L) illusion is another well-known example of perceptual length distortions, which has been systematically studied since the end of the nineteenth century. The M-L stimulus is significantly different from that of the O-K: the figure elements are not uniform; the contextual distracters formed of intersecting lines are present; the analogous stimulus is not known in the auditory modality. However, as with the O-K illusion, the strength of the M-L illusion changes with the duration of stimulus presentation. It was convincingly demonstrated that the M-L illusion decreases with prolonged visual inspection (Judd 1902, Lewis 1908, Mountjoy 1958, Day 1962, Festinger et al. 1968, Coren and Girgus 1972). At the same time, as in the case of the O-K illusion, there is not much information concerning the M-L illusion behavior at short durations (i.e., less than 1000 ms) of stimulus presentations. Only a tendency of weakening of the M-L illusion (de Brouwer et al. 2014) and its Judd modification (van Zoest and Hunt 2011) for brief display durations was observed in experiments with saccadic eye movements.

The results of fMRI experiments have demonstrated that the temporal dynamics of the M-L illusion may be associated with the time course of subsequent neural activation at different levels of the visual system (Weidner and Fink 2007, Weidner et al. 2010). The early visual areas (cuneus and lingual gyrus in the occipital lobe) become activated between 85 and 130 ms after the M-L stimulus onset. Strong activation within the range of 195–220 ms involves the ventral visual stream including the inferior occipital, inferior temporal, and fusiform gyri. These locations of activation suggest a contribution of higher-level visual processing to the M-L illusion manifestation and show that the underlying neural mechanisms may be associated with the brain areas responsible for objects identification, shape-size representation, and detail image analysis. Mikellidou (2012) carried out an fMRI study to investigate whether activity in the primary visual cortex (V1) could be linked to perceptual experience with the Helmholtz filled-squares illusion (the variant of the filled-space illusion). The results revealed a significant effect in the V1 associated with physical differences between visual stimuli rather than perceived differences; therefore, it was concluded that intrinsic processing in the V1 is not responsible for inducing illusion-related activity and it is likely that feedback from higher areas of the brain dominates in the occurrence of the illusion.

Although both the O-K and M-L illusions are rather well studied experimentally, at present there are no generally accepted theoretical explanations for their occurrence (in particular, regarding the O-K illusion). It is believed that investigations of temporal dynamics of visuospatial processing can shed additional light on issues concerning the features of neural mechanisms underlying these visual phenomena; therefore, it appears quite reasonable to compare time courses of the effects of the O-K and M-L illusions. With this aim, in the present study, the M-L illusion was tested in parallel with the O-K illusion within the same range of the stimuli presentation durations using the same forced-choice method with backward masking.

It was assumed that an overestimation of the filled interval in the O-K stimulus may be related to spatial and temporal integration along a continuous path of neural excitation (Kojo et al. 1993, Field et al. 1993) evoked by the real and illusory contours of the filling. With the aim of checking the validity of this assumption, a supplementary set of experiments was performed: the illusion strength was measured for different modifications the O-K stimuli comprising uniformly filled or outlined rectangles of fixed duration.

METHODS

Apparatus and stimuli

The stimuli, masking patterns, and gaze fixation spots were drawn by the Cambridge Research Systems VSG 2/3 and displayed on the monitor EIZO T562 calibrated and gamma corrected by using a Cambridge Research Systems OptiCAL photometer. The Psychophysical Experiment Toolbox in Mathworks Matlab software platform controlled the presentations of the stimuli. In order to minimize optical aberrations, subjects observed the monitor screen monocularly through an artificial pupil of 3 mm diameter. A chin holder was used to limit the subject's head movements. The distance between the monitor screen and subject's eye was 400 cm; it caused a screen pixel to subtend 0.33×0.33 arc min. The stimuli were presented horizontally against a dark (0.1 cd/m^2 luminance) background. Each stimulus presentation consisted of three parts (Figs 1 and 2): (A) the fixation point (2×3 arc min size and 52 cd/m^2 luminance) exposed for 700 ms; (B) the stimulus itself with varying duration of presentation; and (C) the mask appearing after the figure offset and lasting 2 s. There was a delay of 400 ms in between the fixation point offset and the stimulus onset but not in between the stimulus and masking.

The O-K stimulus was formed of stripes of the 1.3 arc min width, 28 arc min height, and 52 cd/m^2 lumi-

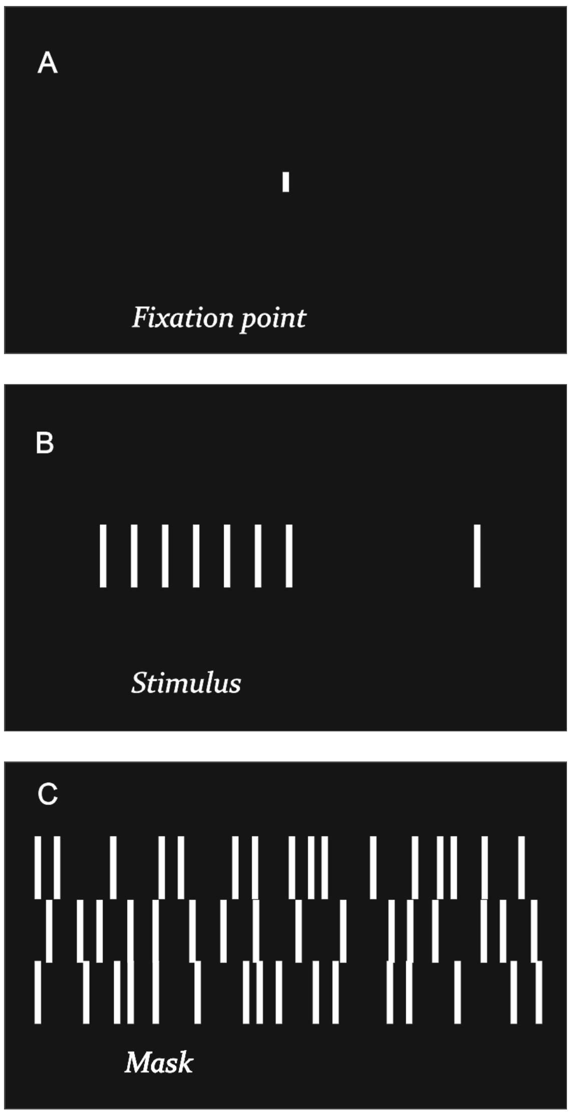

Fig. 1. The Oppel-Kundt stimulus presentation. (A) the gaze fixation point; (B) filled-unfilled figure with reference on the left; (C) the masking pattern.

nance (Fig. 1B). The empty stimulus interval (the test part) was terminated by a single stripe. In the filled stimulus interval (the reference part of 70 arc min length), the number of equally spaced stripes was 4, 7, or 12. The solid filling and the control stimulus without filling (just three terminal stripes) were also employed. The stimulus durations were 60, 80, 120, 200, 400, 700, 1000, and 1300 ms. The mask (Fig. 1C) was designed to resemble the spatial properties of the O-K figure. It was presented as a flickering (with 50 Hz frequency) pattern of the 132×264 arc min size consisting of three rows of vertical stripes equivalent to those of the O-K figure but twice as bright (100 cd/m^2) and distributed at random. The mask for the stimulus with solid filling was formed of flickering blocks similar in size and distributed randomly.

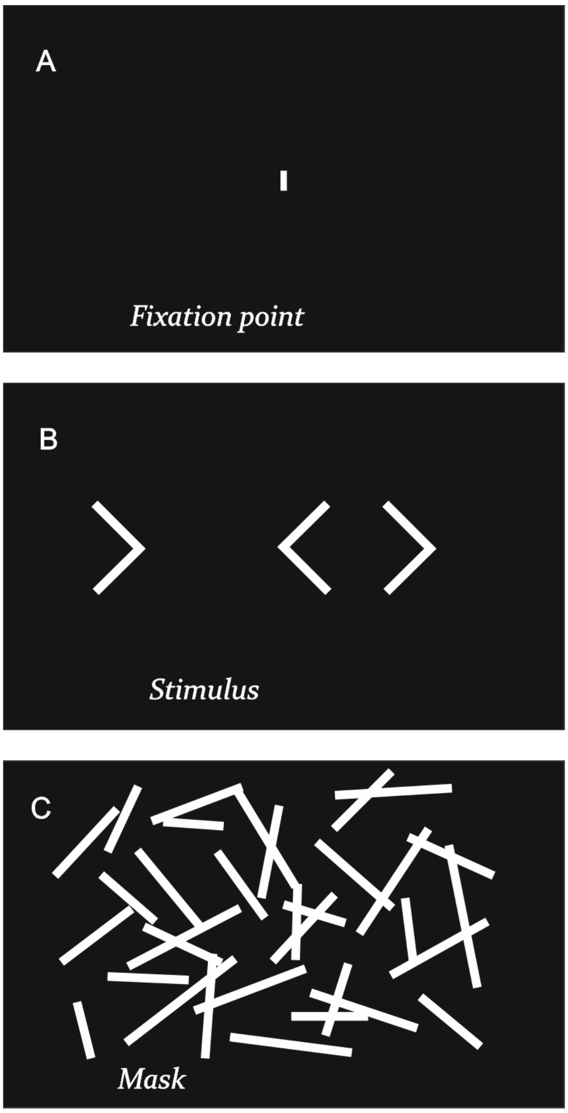

Fig. 2. The Müller-Lyer stimulus presentation. (A) the gaze fixation point; (B) the Müller-Lyer figure with outward-pointing wings on the left (reference); (C) the masking pattern.

The M-L stimulus (Brentano version; Fig. 2B) comprised three pairs of wings (the arrowheads with a 90° internal angle) arranged in a horizontal sequence; the shaft line was absent. The lateral arrowheads pointed in the same direction while the middle one had the opposite turn thus producing two spatial intervals limited by the outward (> <) and inward (< >) wings. During the subsequent presentations, the position of intervals with inward and outward wings within the stimuli varied (left vs. right) at random, but in all presentations, the left part of the stimulus was considered as the referent interval (70 arc min in length) and the right part as the test interval. The vertex of the middle wings of the M-L figure coincided spatially with the gaze fixation point. The width of the wing lines was 1.3 arc min, length 28 arc min, and luminance 52 cd/m^2. The stimulus display durations varied from 60 to 1300 ms. The mask was made up of randomly distributed line segments (luminance 100 cd/m^2); their length, position, and orientation varied each 20 ms.

In the supplementary experiments, the stimuli of fixed duration (1300 ms) with uniformly filled or outlined rectangles were used (Fig. 8, bottom). Also, combinations of the filled and outlined rectangles with a regular sequence of uniform stripes were taken.

Procedure

In the experiments, the two-alternative forced-choice method (2AFC) was used to measure the illusions magnitude. In a darkened room, subjects watched the monitor screen during the period of stimulus presentation and judged the stimulus extent after the masking pattern offset. Subjects reported (by pressing the corresponding keyboard buttons) whether the referent part appeared longer than the test part or not. In subsequent presentations, the length of the referent stimulus part remained constant and fixed at 70 arc min, while the length of the test part varied within an interval comprising 17–27 values selected from the 70–110 arc min range. During a single experiment, the stimulus exposure time was constant. The computer program presented the stimuli with varying test length in a random order, and subjects did not know in advance the stimuli presentation sequence. For each stimulus parameter, subjects carried out at least five experimental runs on different days.

Psychometric logistic functions were fitted using the Psignifit toolbox version 2.5.6 for Matlab Mathworks (see http://bootstrap-software.org) which implements the maximum-likelihood method described by Wichmann and Hill (2001a). Confidence intervals were found by the bootstrap method implemented by the Psignifit, based on 2000 simulations (Wichmann and Hill 2001b). To compare statistically the thresholds obtained in the experimental data fittings (psychometric functions), a thousand of the Monte-Carlo simulations were taken in order to estimate each *P*-value by assessment of likelihood ratio, *LR* (Kingdom and Prins 2009). The Palamedes toolbox for Matlab (Prins and Kingdom: Matlab routines 2014) computation code was used.

Subjects

Fifteen observers, University students and teachers, 19–70-year-old males and females, took part in the study. Six of them attended only the O-K experiments, and seven subjects participated in the M-L studies, exclusively. The remaining two subjects were present in both sessions. Three subjects performed the supplementary experiments. All subjects were normally sighted or were wearing their usual optical corrections. Eleven of the subjects (AR, NT, OR, NR, OU, AI, UR, IC, IA, EL, and KA) were *naïve* with respect to the goals of the study, and all gave their informed consent before taking part in the experiments performed in accordance with the ethical standards of the 1964 Helsinki Declaration. Permission for the experiments was received from the Ethics Committee of Kaunas Biomedical Research (protocol No. BC-MF-17).

RESULTS

The Oppel-Kundt illusion

Psychometric functions (Fig. 3) were obtained for various display durations used in the experiments. The "longer-than" response frequency was plotted against the difference of the physical lengths of the test and reference intervals. The points of subjective equality (50% "longer-than" judgments) on the psychometric functions were considered as indicating the illusion magnitude.

For all observers, the curves of the O-K illusion magnitude as functions of the stimulus display duration were established (Fig. 4). As can be seen from the graphs in Figure 4, there are individual variations of the illusion magnitude among the observers, e.g., about 42 arc min for IC, 26 arc min for EN, and 9 arc min for AD; the maxima correspond to different stimulus display durations (700 ms for ER, EN, and EL; 200 ms for IA and IC; 1000 ms for IN). In some cases (subjects EN and KA), the illusion shows a clear tendency to decrease rather than increase at the shortest stimulus durations. Nevertheless, the curves in Figure 4 can be considered as similar regarding their shape which illustrates a common regularity (Fig. 5): the illusion

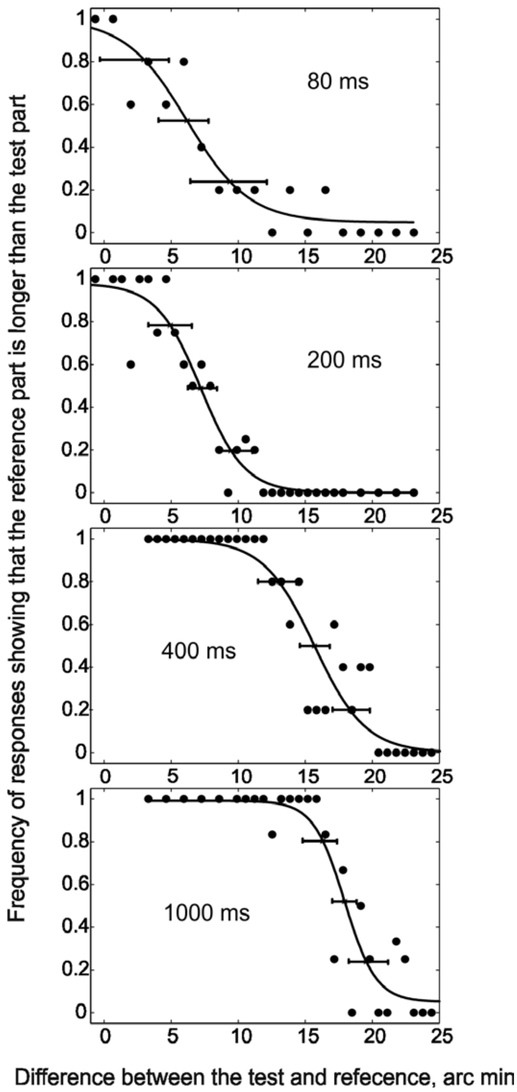

Fig. 3. Examples of individual psychometric functions (subject EN) for different durations of the Oppel-Kundt stimulus: 80, 200, 400, and 1000 ms. Dots, the experimental data. The horizontal line segments indicate 95% confidence intervals at the levels of the "longer-than" judgments with the 0.25, 0.50, and 0.75 frequencies. There were 7 stripes forming the filled stimulus part.

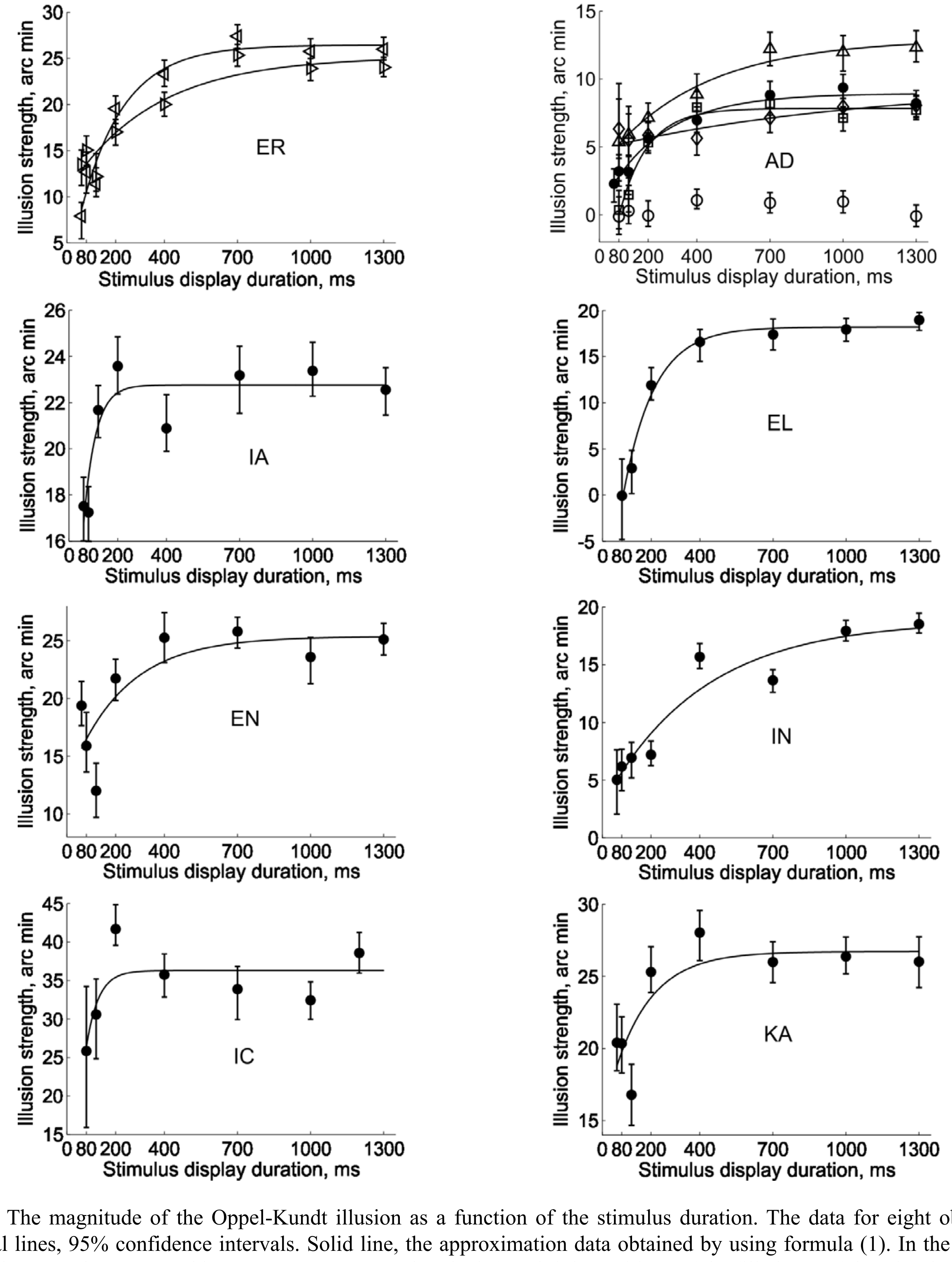

Fig. 4. The magnitude of the Oppel-Kundt illusion as a function of the stimulus duration. The data for eight observers. Vertical lines, 95% confidence intervals. Solid line, the approximation data obtained by using formula (1). In the diagram for subject ER, the upper and lower curves correspond to the left and right positions of the filled part of the stimulus, respectively. For the other seven subjects, the filled stimulus interval was always situated on the left. For subject AD, the top curve (triangles) shows the results obtained with 12 stripes in the filled stimulus part; the middle three coinciding curves (squares, dots, and diamonds) indicate the results obtained with 4 and 7 stripes and a solid filling, respectively; the bottom curve (circles) refers to the control stimulus without filling. For the remaining seven observers, including ER, the data obtained with 7 filling stripes are shown.

magnitude increases for stimulus display durations in the range from 100 to 700 ms, and remains almost constant afterwards. Linear regression analysis (Matlab statistics toolbox, regression diagnostics: F_{22}=0.067, P=0.80) indicates the absence of significant changes in the illusion magnitude within the range of the 700–1300 ms stimulus exposure durations.

The curves were fitted by the exponential function often used to describe temporal dynamics in physical and biological systems:

$$I_{O-K}(t) = b(1 - e^{-rt}) + c \qquad (1)$$

where I_{O-K} represents the illusion strength; t is the exposure time; b, r, and c are coefficients. The obtained values of coefficient of determination R^2 ranged from 0.5 (for subject IC) to 0.96 (for subject EL).

The averaged data of the eight observers emphasize the main regularity: the smooth curve in Fig. 5 indicates a gradual augmentation of the illusion within a relatively wide interval of the exposure time. The illusion strength develops from 13 arc min at 80 ms to 22 arc min (paired t-test: t_7=6.3, P<0.01) at 700 ms. At longer exposures, such as, 1000 ms and 1300 ms, the illusion remains at the saturation level of about 22 arc min. According to the data in Figure 5, the 700–1000 ms display durations can be considered as the minimum exposure time adequate for the complete performance of the O-K illusion under our experimental conditions. The illusion "starts" at the early stages of visual processing, which is accessed at 80–120 ms; at these stimulus durations, the illusion is present, relatively weak, and not reversed.

The experiments with various filling density (4, 7 and 12 stripes, or a solid filling) show similar results (Fig. 4, observer AD). In the control experiments with the stimulus having no filling within the referent part, the illusory effect is not present at any stimulus exposure duration used (the bottom curve with circles in Fig. 4, observer AD). The right and left localizations of the referent part of the stimulus yielded results with non-significant differences (paired t-test: t_7=0.34, P>0.05; Fig. 4, observer ER); this difference may be caused by the left-right meridian anisotropy of the visual field (Bulatov and Bertulis 1999).

The Müller-Lyer illusion

In the experiments with the M-L illusion, the psychometric functions were generated as well (Fig. 6). Routinely, on the curves of Figure 6, the 0.5 frequency indicates the perceived equality of the reference and test. The graphs of Figure 6A refer to the inward wings, and those of Figure 6B correspond to the outward wings when they are considered as the stimulus references.

Both for inward and outward wings, the 80 ms, 120 ms, and 200 ms exposure durations provide the psychometric functions extending over the complete frequency scale (from 0 to 1.0) and increasing in slope (0.074; 0.085; 0.11 for the inward wings and 0.072; 0.094; 0.14 for the outward ones). But at the 60 ms exposure, the frequencies of the "longer-than" response are restricted within the 0.2–0.8 range with the curves sloping 0.023 and 0.034. This refers to the difficulties of the subject to perform the length comparison task at very short stimuli expositions. Nevertheless, the stimulus expositions slightly longer than 60 ms, e.g., 80–100 ms may be considered as the minimum (temporal threshold), which is sufficient for the M-L illusion to arise, and this threshold is similar to that of the O-K illusion.

At the supra-threshold durations, both individual (Fig. 7A, B, and C) and averaged data on the M-L illusion (Fig. 7D) for nine observers show a clear opposite changing, if compared to the O-K illusion (Fig. 5): there is a general decrease of the M-L illusion magnitude with prolongation of the exposure duration. According to the averaged data of Figure 7D, the M-L illusion magnitude is 28 arc min at the 80 ms duration and about 22 arc min at the stimulus expositions lasting 700 ms (paired t-test: t_7=3.5, P=0.01). Such a result is consistent with the findings on the M-L illusion decrement for brief visual inspection (van Zoest and Hunt 2011, de Brouwer et al. 2014) and its Judd modification.

The magnitude of the M-L illusion (Fig. 7D) remains almost constant approximately after 700 ms. Linear regression analysis (Matlab statistics toolbox, regres-

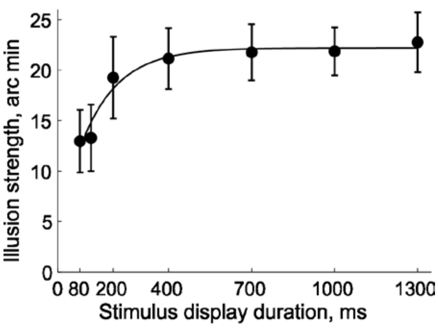

Fig. 5. The averaged data (for eight subjects) on the Oppel-Kundt illusion as a function of the stimulus duration. Solid line, the fitting results (Eq. 1).

sion diagnostics: F_{22}=0.057, P=0.81) indicates the absence of significant changes in the illusion magnitude within the range of the 700–1300 ms stimulus exposure durations.

The experimental data on the M-L illusion were fitted with the exponential function:

$$I_{M-L}(t) = be^{-rt} + c \quad (2)$$

where I_{M-L} represents illusion strength, t is duration, and r, b, and c are coefficients.

For the averaged data in Figure 7D the coefficient of determination R^2 is 0.86. The values of coefficient r (time constant reciprocal) in formulas (1) and (2) obtained from fitting the O-K illusion increase and the M-L illusion decrease during stimulus display prolongation are 0.0075±0.0064 s^{-1} (133±155 ms) and 0.0045±0.0062 s^{-1} (222±160 ms), respectively. It should be noted that these values obtained from the averaged data are only illustrative because of the great inter-individual differences among single subjects' fits (Figs 4 and 7). Therefore, no definite conclusions can be drawn from their difference.

Supplementary experiments

In these experiments, various modes of filling in the O-K stimulus were tested (Fig. 8). Stimulus 1 having no filling in the referent part was used for assessment of the subject-specific biases (e.g., influenced by the visual field anisotropy, gaze fixation peculiarities, or some other factors) in the length judgment task. It was assumed that the obtained individual values: −2.0, 1.0,

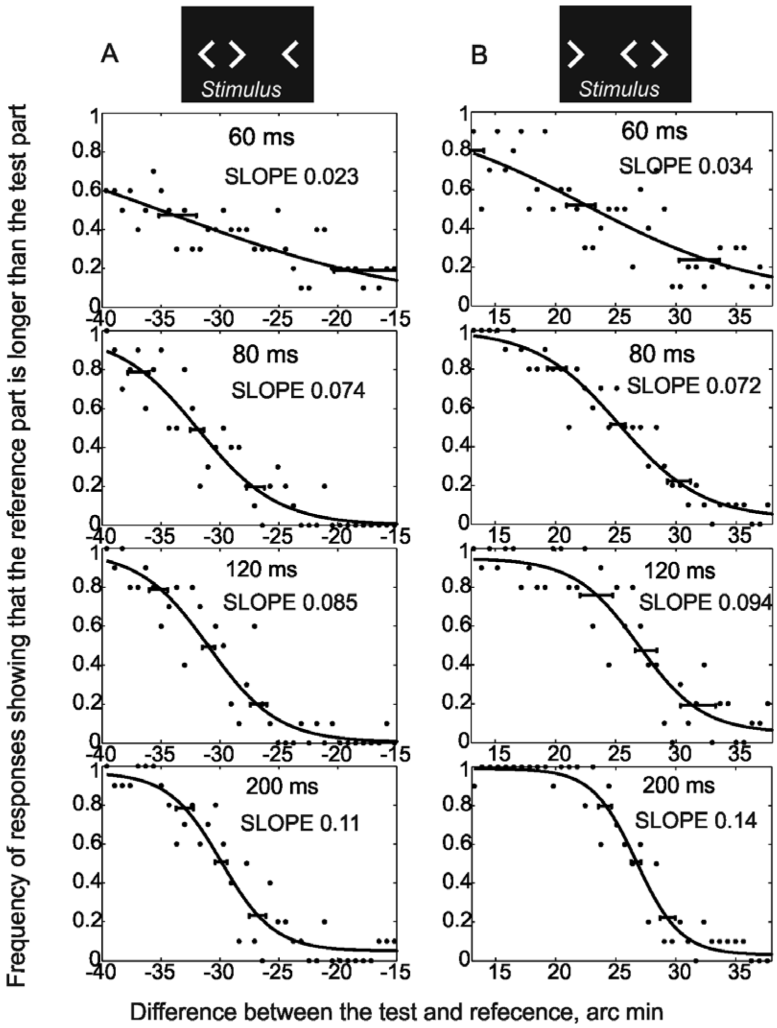

Fig. 6. Examples of individual psychometric functions (subject ER) for different durations of the Müller-Lyer stimulus: 60, 80, 120, and 200 ms. Dots, the experimental data. The horizontal line segments indicate 95% confidence intervals at the levels of the "longer-than" judgments with the 0.25, 0.50, and 0.75 frequencies.

and 0 arc min (for subjects LE, ER, and AD, respectively) should be recognized as additional systematic biases when estimating the strength of the illusion caused by the stimuli comprising filling elements.

Stimulus 2 (the base type) with seven stripes in the referent part induced distortions of about 11.5, 8.5, and 6.5 arc min for subjects LE, ER, and AD, respectively. Stimulus 3 with the filling bar caused an illusion less than stimulus 2 for subjects LE and ER (likelihood ratios, *LR* for model pairs are 1 000:4, $P<0.01$, and 1 000:7, $P<0.01$, respectively) but not for AD (*LR* is 1 000:94, $P>0.05$). Stimulus 4, which is a composition of stimuli 2 and 3, caused illusion approximately as strong as stimulus 2 alone (*LR* is 1 000:314, $P>0.05$ for LE, 1 000:382, $P>0.05$ for ER, and 1 000:65, $P>0.05$ for AD) indicating the absence of summation of stimulations. Stimulus 5 with an outlined rectangle in the referent part evoked an effect similar to the previous ones, and the illusion strength did not differ significantly (*LR* is 1 000:116, $P>0.05$ for LE, and 1 000:394, $P>0.05$ for AD) except for ER (*LR* is 1 000:35, $P<0.05$) in comparison with that caused by stimulus 2. Stimulus 6 is a combination of stimuli 2 and 5, but again the illusions were not added, and the resulting value of illusion magnitude remained at the same level for LE and AD (*LR* is 1 000:451, $P>0.05$ for LE, and 1 000:649, $P>0.05$ for AD) but not for ER (*LR* is 1 000:46, $P<0.05$).

The results of the supplementary experiments support the suggestion (Bulatov et al. 2001, Bulatov and Bertulis 2005) that the visual system processes the combined stimulus as a single pattern without fragmenting it into its components when performing the size judgment task. In general, five different stimuli used in the present experiments determine practically the same strength of perceptual distortions, and only individual differences of the illusion magnitude between subjects are present.

DISCUSSION

The findings of this study represent the stimulus-processing time as a weighting factor that makes an evident influence on the magnitude of both the O-K and M-L illusions. Under the same experimental conditions, the illusions "start" at similar (80–100 ms) exposure durations, however, at longer presentations, they demonstrate the opposite effects: the O-K illusion increases while the M-L illusion decreases in strength (Figs 5 and 7D). Such opposite dependences of the illu-

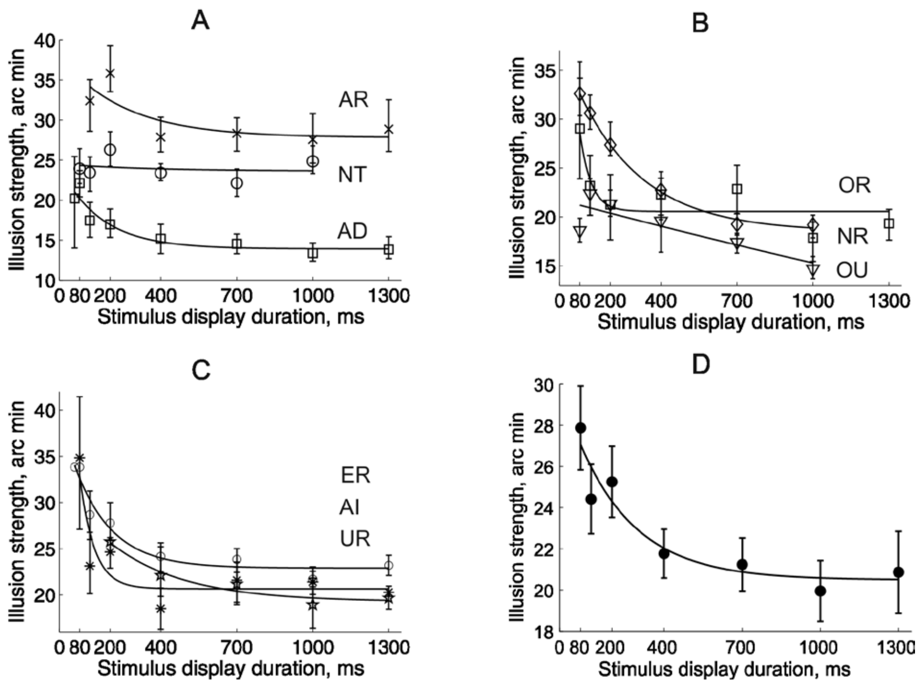

Fig. 7. The magnitude of the Müller-Lyer illusion as a function of the stimulus exposure duration. (A), (B), (C) individual results for the inward wings as the reference. (D) the averaged data for nine subjects. Solid line, the fitting results (Eq. 2). Vertical lines, 95% confidence intervals for observed data mean.

sions on the exposure time are consistent with previous findings for the O-K (Bailes 1995) and for the M-L (van Zoest and Hunt 2011, de Brouwer et al. 2014) illusions and extend the list of known determinants, thus, confirming the suggestion that the effects of the illusions are characterized by multivariate functions in the multidimensional space of stimulus parameters (Wackermann and Kastner 2009, 2010). Despite rather large inter-subject variability, it can be seen (Fig. 4) that the full-scaled O-K illusion is achieved only for prolonged (about 700–1000 ms) stimuli observations. The magnitude of the M-L illusion (Fig. 7D) also "saturates" approximately after 700 ms, however, the strongest illusion appears at the shortest stimulus durations.

The temporal dynamics of the O-K and M-L phenomena suggest a sort of accumulation or integration over the stimuli observation time, however, the opposite time courses within the 100–1000 ms interval of

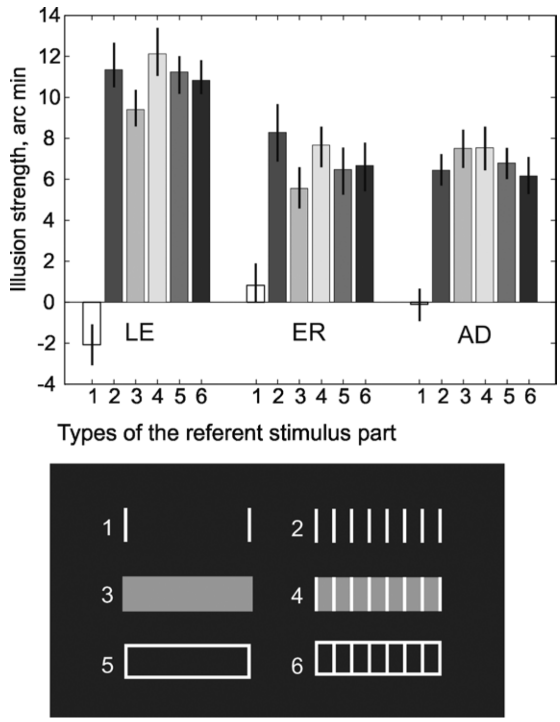

Fig. 8. The filled-unfilled illusions caused by different stimuli modifications. The data for three subjects: LE, ER, and AD. Vertical lines, 95% confidence intervals. The control stimulus, (1) has empty reference. The mode of reference filling in the other five stimuli varied: a regular sequence of 7 stripes, (2); solid block, (3); stripes on the block, (4); contour rectangle, (5); and stripes within the rectangle, (6). The referent part length, 70 arc min; luminance of the line segments, 52 cd/m^2; luminance of the solid pattern, 20 cd/m^2. Stimulus duration, 1300 ms.

the stimuli presentations indicate different neural mechanisms involved in the occurrence of these two illusions at least below the decision-making stages.

The fact that the strongest M-L effect corresponds to the shortest stimulus display durations is consistent with the predictions of the theories of low- or band-pass spatial frequency filtering (Ginsburg 1984, Morgan and Casco 1990, Bulatov et al. 1997, Di Maio and Lansky 1998, Sierra-Vázquez and Serrano-Pedraza 2010), including the centroid concept (Morgan et al. 1990, Bulatov et al. 2009). According to the filtering approach, the illusions arise due to neural processing at relatively low levels of the visual system (cortical areas V1–V4 or even some sub-cortical structures, e.g., superficial layers of the superior colliculus) that affects perceptual localization of the terminal elements of the stimulus. Thus, a relatively quick decrease in the M-L illusion magnitude at short (less than 150 ms) display durations can be determined by the initial shrinkage of relevant receptive fields, i.e., the spatial filters (Bredfeldt and Ringach 2002, Frazor et al. 2004, Ruksenas et al. 2007). Longer observation time enables (due to active eye movements, narrowing of the spatial extent of attention, etc.) accumulation of information indicating inaccuracy of the initial perception, and the illusion gradually weakens because the higher-level neural processing provides corrected assessment of spatial relationships of stimulus elements (Coren and Girgus 1972, Predebon 1998, Weidner and Fink 2007).

The presence of a relatively weak O-K effect at the shortest stimulus durations suggests that the neural mechanisms of early spatial filtering can play a certain role in the occurrence of the O-K illusion as well (Bulatov et al. 1997). One may suspect that the deviations from monotonic growth of the illusion magnitude for very short exposures (Fig. 4, subjects EN, KA, and, probably, others) can also be explained by the initial shrinkage of relevant spatial filters, but further studies are needed for more thorough analysis of the reasons of appearance of this illusion magnitude dip.

The illusion magnitude growth with increasing stimulus duration (within approximately 100–700 ms interval, Fig. 5) indicates that some additional time-consuming integration processes are responsible for the full-scaled O-K illusion evolving.

At still longer durations, the illusion slightly weakens (Coren and Hoenig 1972), probably, due to correction of initial judgments by backward information from higher levels of visual processing as in the case of the M-L illusion.

It is noteworthy that the function of time for the O-K illusion is quite similar in shape to the illusion magnitude dependence on the spatial filling density: with an increase in either the density (Bulatov et al. 1997, Bertulis et al 2009, Wackermann and Kastner 2010) or the exposure time (Fig. 5), the magnitude goes up to a maximum and slightly decreases or remains at the saturation level afterwards. This similarity points to a certain symmetry of the illusion manifestation in both the temporal and spatial domain suggesting that the illusion may be associated with the perception of the continuity (Uttal 1975, Smits et al. 1985, Beck et al. 1989) of the filled part of the O-K figure (i.e., with the perception of this part as a single entity during the performance the length comparison task). Each of the filling elements causes a neural activation within the limits of the local spatiotemporal window, and if these windows overlap, individual activations automatically combine into illusory contours (Kojo et al. 1993, Hirsch et al. 1995), which, like the real ones, produce the continuous excitation paths or "associated fields" (Field et al. 1993). The results from different studies (Reynolds 1981, Mather 1988) demonstrate that the perception of continuous illusory contours emerges only after about 80–100 ms of processing time, i.e., consistently with the O-K illusion "starting" duration.

The computational modeling of spatial information integration (Erdfelder and Faul 1994) predicts the behavior of the O-K illusion for different variations of stimulus spatial parameters rather well; however, the modeling proved to be ill-specified because the meaning of "spatial information integration" was not explicitly stated. We assume, the integration takes place along the continuous excitation paths and it is spatiotemporal, rather than just spatial. Although this assumption is not intended to be directly applicable in an adequate quantitative model of the phenomenon, it could help with explanations of the spatial and temporal effects of the filled-unfilled illusion. For instance, the O-K illusion weakens: (1) with shortening of the observation time because of incompleteness of the integration procedure, and (2) with decreasing of the filling density or homogeneity (spacing, height, width, luminance, color) because of the failure of achieving continuity of the excitation paths.

The results of our supplementary experiments at the very least do not contradict the idea that the perception of continuity plays an essential role in the illusion's manifestation. As can be seen from the graph in Figure 8, all five variants of the O-K stimuli have demonstrated practically the same effectiveness probably because of one common structural feature inherent to all these modifications. One may suppose that the horizontal contour components, either real or interpolated, cause quantitatively similar length misjudgments. The filled and outlined rectangles provide the true horizontal borders of the reference part of the stimulus while the sequences of the filling stripes create the illusory ones. The observation made by Mikellidou (2012) demonstrates an outward displacement of the terminal stripe in the filling sequence (a shift of about 0.5% against the total expansion of the filled space of about 5%), which is attributed to the processes of local integration generating repulsion between ultimate and penultimate stripes. The presence of this additional repulsion effect may help in understanding why the stimulus with a certain number of stripes (the optimum) can be slightly more effective than that with the uniform filling.

It is obvious that further studies are needed to check the assumption on the perception of the filled part of the O-K figure as a single entity, e.g., to verify whether time courses of the illusion effects are similar or different for various modifications of the O-K pattern. In addition, the experimental testing ought to be continued with applications of other methods, e.g., varying masking conditions and stimuli presentations.

CONCLUSIONS

The experimental data represent the stimulus observation time as a weighting determinant of the Oppel-Kundt illusion magnitude.

At the early stages of visual processing, which is assessed to 80–100 ms of stimulus observation, the Oppel-Kundt illusion is relatively weak. Given a longer duration, the illusion increases in strength, and the 700–1000 ms exposure durations are sufficient for the Oppel-Kundt illusion complete performance under present experimental conditions.

On the other hand, the Müller-Lyer illusion appears to be strongest at early stages of visual processing and gradually decreases with the elongation of the stimulus observation time.

A regular sequence of stripes in the Oppel-Kundt stimulus superimposed upon filled or outlined rectangles induces illusions approximately equal in strength to those caused by the stripes or rectangles separately.

The data obtained support a suggestion that overestimations of the filled interval in the Oppel-Kundt stimulus can be related to spatiotemporal integrating along the continuous paths of excitations evoked by the real or illusory contours of the filling.

ACKNOWLEDGMENT

We are grateful to Brian Marmion for his kind assistance throughout the preparation of this manuscript.

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