Research paper

Acta Neurobiol Exp 2017, 77: 157–167

ACTA NEUROBIOLOGIÆ EXPERIMENTALIS

An effect of continuous contextual filling in the filled-space illusion

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In the filled-space (or Oppel-Kundt) illusion, the filled part of the stimulus for most observers appears longer in comparison with the empty one. In the first two experimental series of the present study, we investigated the illusory effect as a function of continuous filling (by a shaft-line segment) of the reference spatial interval of the three-dot stimulus. It was demonstrated that for the fixed length of the reference interval, the magnitude of the illusion increases non-linearly with the shaft length. For the fixed length of the shaft, the illusion magnitude gradually decreases with the lengthening of the reference interval. In the third series, psychophysical examination of the conventional Oppel-Kundt stimulus with different number of equally spaced elements (dots) subdividing its filled part was performed. Based on the analysis of the functional dependencies established, we have proposed a simple computational model that was successfully applied to fit the experimental data obtained in the present study.

Key words: length misjudgment, filled-space illusion, Oppel-Kundt figure

INTRODUCTION

In the filled-space (or Oppel-Kundt) illusion, the filled part of the stimulus for most observers appears longer in comparison with the empty one (Fig. 1A). This illusion represents one of the most striking manifestations of the misperception of spatial extent, which has been systematically investigated for more than one-and-half century after Oppel (1855) originally reported simple drawings comprised of a series of dots. During this period, various modifications of stimuli have been used in a great number of investigations aimed to identify the principal parameters governing the effect of the illusion. The studies resulted in a more or less broad consensus that the most relevant factors determining the illusion magnitude are the uniformity of the contextual filling elements (fillers) and the density of their distribution (Obonai 1933, Coren et al. 1976, Noguchi et al. 1990, Bulatov et al. 1997, Deregowski and McGeorge 2006, Wackermann and Kastner 2010, Giora and Gori 2010). It has been demonstrated that a stimulus with a certain number of evenly allocated identical fillers induces a considerably stronger illusion than that with an irregular distribution (Lewis 1912, Noguchi 2003) or with many fillers fused into one continuous unit (Bailes 1995, Bertulis and Bulatov 2001). At the same time, the region of the illusion maximum was relatively flat and

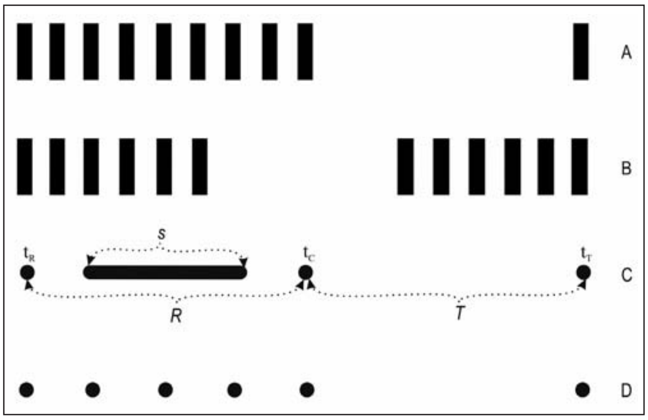

Fig. 1. Filled-space (Oppel-Kundt) illusion. (A) The conventional Oppel-Kundt figure made up of vertical stripes; the filled half of the figure for most observers appears longer than the empty one. (B) The three-part Oppel-Kundt figure. (C) The three-dot (t_R, t_C, and t_T) stimulus with contextual horizontal shaft-line segment, *s* centered in the reference interval, *R*; the length of the test stimulus interval designated as *T*. In the first series of experiments, the length, *s* was altered from 0 to 60 min of arc; the length, *R* was fixed at 60 min of arc. In the second series, the length of the shaft-line was fixed at 45 min of arc, and the length of the reference interval was changed in a range from 45 to 90 min of arc. (D) The dotted version of the Oppel-Kundt stimulus; the length of the reference interval, *R* was fixed at 60 min of arc, the number of filling dots varied from 0 to 55. In experiments, white stimuli (luminance 75 cd/m^2) were presented against a dark round-shaped background (5° in diameter and 0.4 cd/m^2 in luminance).

Received 5 January 2017, accepted 9 May 2017

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varied between studies: the greatest effect was found for the number of fillers from 11 to 23 (Spiegel 1937), 9 to 14 (Piaget and Osterrieth 1953), 4 to 13 (Bulatov et al. 1997), 11 to 13 (Wackermann and Kastner 2010), and 8 to 12 (Mikellidou and Thompson 2014). If the stimulus elements differed in shape or size then the effect of the illusion was substantially diminished (Obonai 1954, Wackermann and Kastner 2009, Wackermann 2012a).

Nonetheless, many other factors to a certain extent influence the illusion's manifestation, thus confirming the need of the multivariate approach to a deeper understanding of the phenomenon under investigation (Wackermann and Kastner 2010). For instance, an increase of the absolute luminance contrast between the stimulus parts has resulted in a significant weakening of the illusion (Bulatov and Bertulis 2005). The strength of the Oppel-Kundt illusion increased with the figure/background luminance contrast (Long and Murtagh 1984, Dworkin and Bross 1998) and was higher for light figures against a dark background than *vice versa* (Wackermann 2012b); changes of the color contrast under isoluminant conditions also affected the illusion magnitude (Surkys 2007). The results of different studies of the Oppel-Kundt illusion demonstrated that the illusion magnitude varies with the duration of stimuli presentation (Bailes 1995, Dworkin and Bross 1998, Bertulis et al. 2014); however, these data contradict each other for short presentations, therefore issues concerning the changes in the illusion manifestation still remain open. A significant decrease of the illusion magnitude was registered for subjects making voluntary saccadic eye movements during the stimulus observations (Coren and Hoenig 1972). Some additivity of illusory effects was revealed in experiments with the three-part Oppel-Kundt figure (one empty interval flanked by two filled ones, Fig. 1B), which induced an illusion about a quarter stronger than that caused by the conventional two-part figure (Bertulis et al. 2009).

Although different modifications of the filled-space illusion have been rather well studied experimentally, at present there is as yet no generally accepted explanation for the occurrence of this visual phenomenon. Along with a purely phenomenological modeling (Erdfelder and Faul 1994, Wackermann and Kastner 2010), a number of various theoretical approaches has been tried out in order to account for the data obtained in psychophysical experiments. For instance, the methods of the potential theory in physics have been used to explain the illusion by the interactions between the stimulus elements in a two-dimensional perceptual field (Eriksson 1970). According to another (more physiological) approach (Bertulis et al. 2014), the illusion may be associated with the perception of the continuity of the filled part of the stimulus (Uttal 1975, Smits et al. 1985, Beck et al. 1989). It was assumed that individual filling elements evoke a neural activation within relevant spatiotemporal windows, and these windows (if overlap) merge into a continuous array of "associated fields" of excitation (Field et al. 1993, Kojo et al. 1993, Hirsch et al. 1995). According to the "contour density" hypothesis (Craven and Watt 1989, Watt 1990), the number of zero-crossings of the spatial profile of neural excitation caused by the filled part of the Oppel-Kundt figure can be one of the most important factors determining the illusion magnitude. A rather adequate description of illusory effects was obtained from the computational model seeking to explain the misperception of extent in terms of physiological (i.e., based on the spatial properties of the receptive fields of neurons in the primary visual cortex) spatial-frequency filtering (Bulatov et al. 1997, Bulatov and Bertulis 1999, 2005), as well as from the quantitative approach that explains the illusion occurrence by internal noises in the neural networks (Fermüller and Malm 2004).

It should be pointed out that in most studies, both experimental and theoretical, stimuli with regularly distributed discrete fillers have received more attention from researchers, whereas questions concerning the illusion parameters for stimuli with the continuous filling still remain open; none of the investigations, at least among those known to us, have addressed this topic directly. Therefore, we think that a more thorough comparison of the illusion characteristics for both continuous and discrete filling can shed additional light on the issues concerning the features of the effect under study, and can be helpful for the development of its unified theoretical (possibly quantitative) description. For this purpose, in the present study we have performed a psychophysical examination of the illusory effects induced by figures comprising a contextual line segment (shaft-line) continuously filling the reference part of the horizontal three-dot stimulus (Fig. 1C). In the first series of experiments, the length of the shaft-line varied, whereas in the second series, the length of the shaft-line was constant, and the length of the reference interval was changed. In order to collect data for the conventional Oppel-Kundt stimulus (Fig. 1D) comprising a varying number of equally spaced discrete filling elements (dots), the third series of experiments was performed with the same group of observers. The use of figures comprising elements (dots and thin line segments) concentrated along a single stimulus axis enables to consider only the simplest one-dimensional effects of the filled-space illusion; this, in turn, significantly facilitates the subsequent theoretical interpretation of the experimental results.

The main goals of the present study were to establish the functional dependencies of the illusion magnitude on the degree of filling of the reference part of the stimulus, and to try to develop a preliminary quantitative model capable to account for the illusory effects induced by stimuli both with continuous and with discrete fillers.

METHODS

Apparatus

The experiments were carried out in a dark room (the surrounding illumination<0.2 cd/m^2). A Sony SDM-HS95P 19-inch LCD monitor (spatial resolution 1280×1024 pixels, frame refresh rate 60 Hz) was used for the stimuli presentations. A Cambridge Research Systems OptiCAL photometer was applied to the monitor luminance range calibration and gamma correction. A chin and forehead rest was used to maintain a constant viewing distance of 330 cm (at this distance each pixel subtended about 0.3 min of arc); an artificial pupil (an aperture with a 3 mm diameter of a diaphragm placed in front of the eye) was applied to reduce optical aberrations.

Stimuli were presented in the center of a round-shaped background of 5° in diameter and 0.4 cd/m^2 in luminance (the monitor screen was covered with a black mask with a circular aperture to prevent observers from being able to use the edges of the monitor as a vertical/horizontal reference). For all the stimuli drawings, the Microsoft GDI+ antialiasing technique was applied to avoid jagged-edge effect.

Stimuli

The stimuli used in the experiments consisted of three horizontally arranged dots (diameter, 1 min of arc; luminance, 75 cd/m^2), which were considered as terminators (t_R, t_C, and t_T, Fig. 1C) specifying the ends of the reference and test stimulus intervals. In the first two series of experiments, a contextual horizontal line segment (shaft-line with the thickness and luminance 1 min of arc and 75 cd/m^2, respectively) was centered in the reference interval (Fig. 1C). In the first series, the length, s (the independent variable) of the shaft-line was altered in a pseudo-random fashion from 0 to 60 min of arc; the length of the reference interval, R was fixed at 60 min of arc. In the second series, the length of the shaft-line was fixed at 45 min of arc, and the length of the reference interval was pseudo-randomly changed in a range from 45 to 90 min of arc. In the third series of experiments, the reference interval (length, 60 min of arc) was filled with a set of equally spaced dots (diameter, 1 min of arc; luminance, 75 cd/m^2) according to the conventional Oppel-Kundt pattern (Fig. 1D), and the number of the filling dots was pseudo-randomly varied from 0 to 55.

Procedure

In order to establish the functional dependences of the illusion magnitude on different spatial parameters of the stimuli, we used the method of adjustment. During the experimental run, the subjects were asked to manipulate the keyboard buttons "←" and "→" to move the lateral dot (terminator t_T, Fig. 1C) of the test interval into a position that makes both stimulus parts perceptually equal in length; the physical difference between the lengths of the test and reference intervals, $T–R$, was considered as the value of the illusion magnitude. A single button push varied the position of the terminator by one pixel corresponding approximately to 0.3 min of arc. The initial length differences between the test and reference stimulus intervals were randomized and distributed evenly within a range of ±10 min of arc.

The subjects were encouraged to maintain their gaze on the central stimulus terminator, however, observation time was not limited, and subjects' eye movements were not registered. A combination of two types of stimulus presentation conditions was used in each experimental run. In the first condition, the reference (i.e., the filled) interval was presented on the left side of the stimulus, whereas in the second one, it was on the right side. Trials from different conditions were pseudo-randomly interleaved in order to minimize (by averaging subjects' responses) effects of the left/right visual field anisotropy and reduce stimulus persistence. An experimental run comprised 84 (or 72 in the third series) stimulus presentations, i.e., 21 (or 18 in the third series) different values of the independent variable for each stimulus condition were taken (in a pseudo-random order) twice. Each observer carried out at least five experimental runs on different days. Ten trials went into each data point analysis, and in the data graphs, the error bars depict ±one standard error of the mean (SEM).

Subjects

Twelve University students, 19–23-year-old five males and seven females, took part in the experiments. All subjects reported normal or corrected-to-normal vision, and were *naïve* with respect to the goal of the study. In order to maintain more strict experimental conditions (i.e., to reduce a number of potential interfering factors related to binocular viewing), the right eye was always tested irrespective of whether it was the leading eye or not. All subjects gave their informed consent before taking part in the experiments performed in accordance with the ethical standards of the Declaration of Helsinki.

Experimental data modeling

Unfortunately, now there are insufficient neurophysiological data to discuss specific neuronal structures responsible for the emergence of the effects of the filled-space illusion. However, based on a *post hoc* analysis of the present experimental results, a relatively simple scheme of the functional organization of some hypothetical visual subsystem can be considered. One can suppose that the comparison of the lengths of stimulus intervals is reduced to neural calculations based on visual information about spatial coordinates of relevant terminators, and that these coordinates are encoded by the magnitude of the subsystem response, which increases with terminators' retinal eccentricity (Bulatov et al. 2005). The latter feature of the subsystem necessarily requires the normalization of its input values (to provide initial amplitude-independent conditions); it is worth mentioning here that the normalization of neural activity plays an important role in information processing at different levels of the nervous system (Reynolds and Heeger 2009, Olsen et al. 2010, Carandini and Heeger 2012, Vokoun et al. 2014). In turn, the output of the subsystem can be generated by means of the mechanism similar to that of a weighted spatial pooling of the neural excitation within Gaussian-shaped attentional windows (which linearly increase in width with visual eccentricity), proposed earlier to account for procedures of automatic centroid extraction in length illusions of the Müller-Lyer type (Bulatov et al. 2010). Then, the contextual filling of the stimulus interval can be considered as a source of an additional distorting signal that induces (due to the increased cumulative response of the subsystem) perceptual biases in the assessment of the coordinates of relevant terminators, and thereby causes misjudgments in a length-matching task. In an imaginary case of an observer's gaze fixation on the central stimulus terminator, the bias evoked by the continuous filling can be interpreted as being proportional to the spatial integral of the normalized (i.e., with amplitude equals to 1) excitation within the attentional window centered with the lateral terminator of the reference interval (Fig. 2A):

$$\tau(d,R) \approx k\int_{-0.5(R+d)}^{-0.5(R-d)} e^{-\frac{1}{2}\left(\frac{x+R}{\sigma}\right)^2} dx = k\sigma\sqrt{\frac{\pi}{2}}\left[erf\left(\frac{R+d}{2\sqrt{2}\sigma}\right) - erf\left(\frac{R-d}{2\sqrt{2}\sigma}\right)\right], \tag{1}$$

where k is the coefficient of proportionality; R and d represent the length of the reference interval and extent of the filling, respectively; σ is a linear function of R, and represents the standard deviation of the Gaussian function of attentional window; *erf*(x) is the error function encountered in integrating the normal distribution. For simplicity, we consider only one-dimensional functions, and disregard the contribution from the relatively small foveated attentional window.

However, this simple algorithm of calculations is not directly suitable in the case of the Oppel-Kundt stimulus shown in Fig. 1D, because of the uncertainty in determining the length of a discrete contextual filling. In order to resolve this issue, it seems reasonable to suppose that, due to lateral interactions, the neural representation of the original stimulus pattern can be obtained through its convolution with a Gaussian function (Bocheva and Mitrani 1993, Bulatov et al. 2009), the width of which in general is eccentricity-dependent. If one assumes, for the sake of simplicity, a Gaussian function with σ equal to that of the attentional window (Bulatov et al. 2010), then for the stimulus with equally spaced dots in the reference interval (Fig. 1D) the corresponding one-dimensional profile of neural excitation can be described using the following formula:

$$P_D(x,n,R) = \sum_{i=0}^{i=n+1} e^{-\frac{1}{2}\left(\frac{(n+1)(x+R)-iR}{(n+1)\sigma}\right)^2}, \tag{2}$$

where R is the length of the interval; n represents the number of filling dots.

In a similar way, for the stimulus with the contextual line segment (Fig. 1C), the profile of excitation can be calculated as follows:

$$P_L(x,s,R) = e^{-\frac{1}{2}\left(\frac{x+R}{\sigma}\right)^2} + \sigma\sqrt{\frac{\pi}{2}}\left[erf\left(\left(x+\frac{R+s}{2}\right)\frac{1}{\sqrt{2}\sigma}\right) - erf\left(\left(x+\frac{R-s}{2}\right)\frac{1}{\sqrt{2}\sigma}\right)\right] + e^{-\frac{1}{2}\left(\frac{x}{\sigma}\right)^2}, \tag{3}$$

where s represents the length of the shaft-line.

Next, in order to determine the effective length of excitation profiles (i.e., extent of the filling in formula 1), the method of an amplitude-independent assessment of the signal width (Sharpless and Melamed 1976, Hoffman 2009) can be considered. According to the method, the width can be estimated by calculating the ratio of the signal area to its peak height; a noteworthy feature of the method is that this ratio calculation certainly satisfies the above-mentioned requirement for the normalization of the inputs to the subsystem.

Hence, the effective lengths, l_D and l_L, of the contextual filling made up of equally spaced dots or line-segment can be evaluated as follows:

$$l_D(n,R)=\frac{\int_{-\infty}^{\infty}P_D(x,n,R)\,dx}{mP_D(n,R)}\text{, and } l_L(s,R)=\frac{\int_{-\infty}^{\infty}P_L(x,s,R)\,dx}{mP_L(s,R)}\text{,} \tag{4}$$

where the numerators and denominators are the areas under the curves (corresponding to functions 2 or 3) and their peak values, respectively.

Unfortunately, a direct assessment of peak values for functions (2) and (3) can be performed only numerically; therefore, it is assumed that a quite satisfactory (Fig. 2B) analytical approximation of $mP_D(n, R)$ can be obtained using the following empirically derived formula:

$$mP_D(n,R)\approx 1+2\sum_{i=2}^{i=N+1}e^{-\frac{1}{2}\left(\frac{R(i-1)}{\sigma(n+1)}\right)^2}\text{,} \tag{5}$$

where N represents the maximum number of filling dots used in experiments (e.g., equal to 55 in the third series).

In a similar way, the peak values for function (3) can be calculated (Fig. 2C) using the following empirical formula:

$$mP_L(s,R)\approx\sigma\sqrt{2\pi}\,erf\left(\frac{s}{2\sqrt{2}\sigma}\right)+e^{-\frac{1}{2}\left(\frac{s}{0.001\sigma}\right)^2}\text{,} \tag{6}$$

and for relatively long (in comparison with σ) shaft-line of the fixed length, the peak value of the function is very close to $\sigma\sqrt{2\pi}$.

Thus, the magnitude of the illusion (i.e., the overestimation of the length of the filled stimulus interval in comparison with that of the empty one) as a function of the number, n of discrete filling dots can be calculated as follows:

$$\delta_D(n,R)\cong\tau(l_D(n,R),R)-\tau(l_D(0,R),R)\text{,} \tag{7}$$

where $\tau(l, R)$ represents the function (1).

In the case of the continuous contextual filling (with shaft-line of the length s), the illusion magnitude can be evaluated using the following formula:

$$\delta_L(s,R)\cong\tau(l_L(s,R),R)-\tau(l_L(0,R),R)\text{,} \tag{8}$$

In the model calculations, we have considered only the simplest way of viewing the stimulus by focusing on the central terminator, whereas under real experimental conditions the observations occur without any strict limitations regarding the direction of gaze fixation, saccades, attentional shifts, etc. Since the value of the perceptual bias caused by contextual filling of the reference interval depends (the value of σ in formulas 1–3) on retinal eccentricity of the interval terminators, the illusion

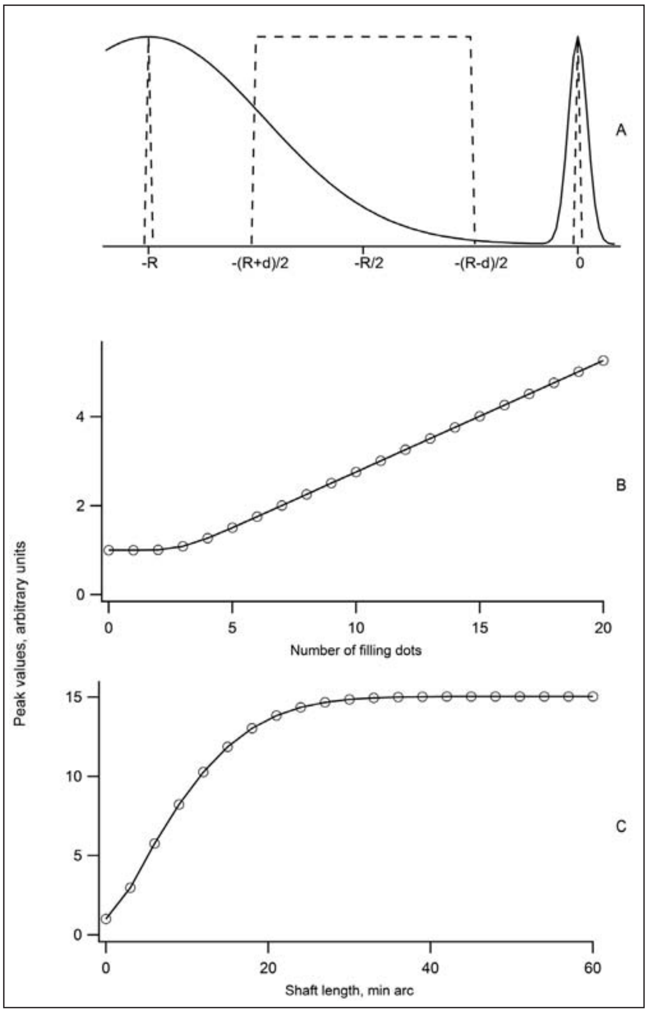

Fig. 2. Diagrams illustrating experimental data modeling. (A) Solid line represents one-dimensional Gaussian profiles of attentional windows corresponding to the lateral (located at −*R*) and the central (located at 0) stimulus terminators. Dashed line, schematic representation of the luminance profile of the reference part of the stimulus (the extent of continuous filling, *d*). (B) Solid curve represents the function (5) used for approximation of the results of numerical calculations (circles) of peak values of the function (2). (C) Solid curve represents the function (6) used for approximation of the results of numerical calculations (circles) of peak values of the function (3). In approximations, the standard deviation, σ of the Gaussian function of the attentional window was equal to 6 min of arc.

magnitude may vary depending on the actual direction of the observer's gaze. Nonetheless, on average, a certain correspondence between the model calculations and measured values of the illusion magnitude can be expected.

RESULTS

Experimental data

The aim of the first series of experiments was to quantitatively determine the magnitude of the filled-space illusion as a function of the length of the contextual shaft-line. As can be seen from the upper graph in Fig. 3, despite a rather large inter-individual difference (e.g., at least two observers reported considerable negative values of the illusion magnitude for the shaft-line shorter than 50 min of arc), the experimental results from all subjects yielded curves of similar shape. The illusion magnitude varies relatively little with lengthening of the shaft-line up to about 40 min of arc. Afterwards, the magnitude rapidly increases and indicates a maximum value (about 5–15 min of arc or 8–25% overestimation of the reference interval length for different subjects) at completely filled reference interval of the stimulus. We suppose that significant inter-individual variability of the results can be explained mainly by the inherent inaccuracy of the method of adjustment used in the present study, e.g., errors due to the impossibility to control the subjects' attention and gaze fixation during stimulus observations, or because of decisional biases (observers can set individual criteria for determining whether the stimulus parts are different in length) in judgment and decision-making (Morgan et al. 2013). In order to assess the general tendency of the results for the entire group of the observers, the overall (grand)

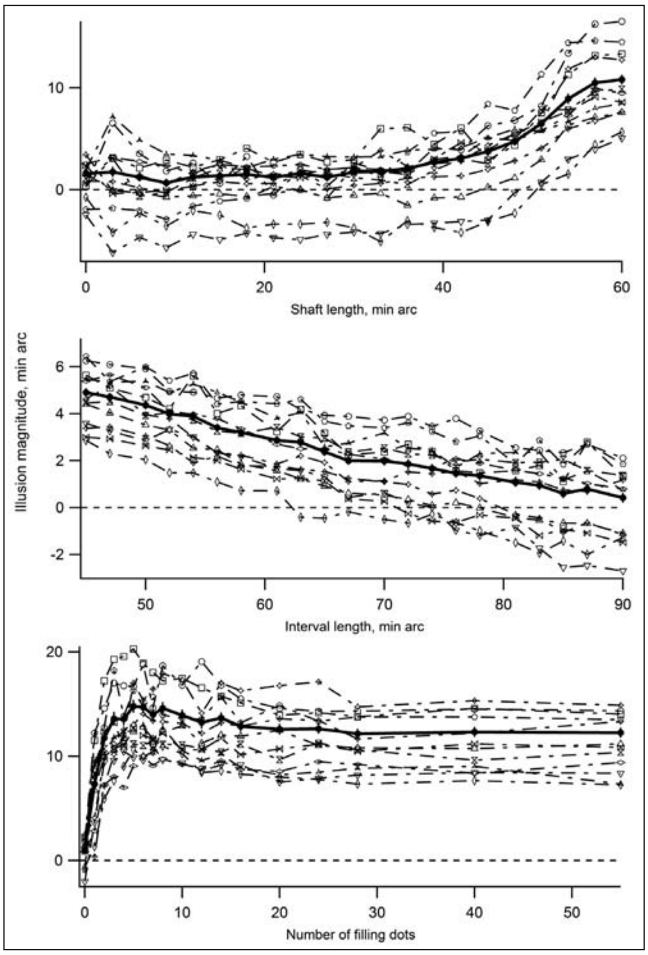

Fig. 3. Dependency of the illusion magnitude on the degree of filling of the reference part of the stimulus. In the graphs, dashed curves with different symbols represent the individual effects for all twelve subjects as functions of the length of the contextual shaft-line (upper), length of the reference interval (middle), and number of filling dots in the reference part of the Oppel-Kundt figure (lower), respectively. Thick solid curves represent grand-means of the individual data.

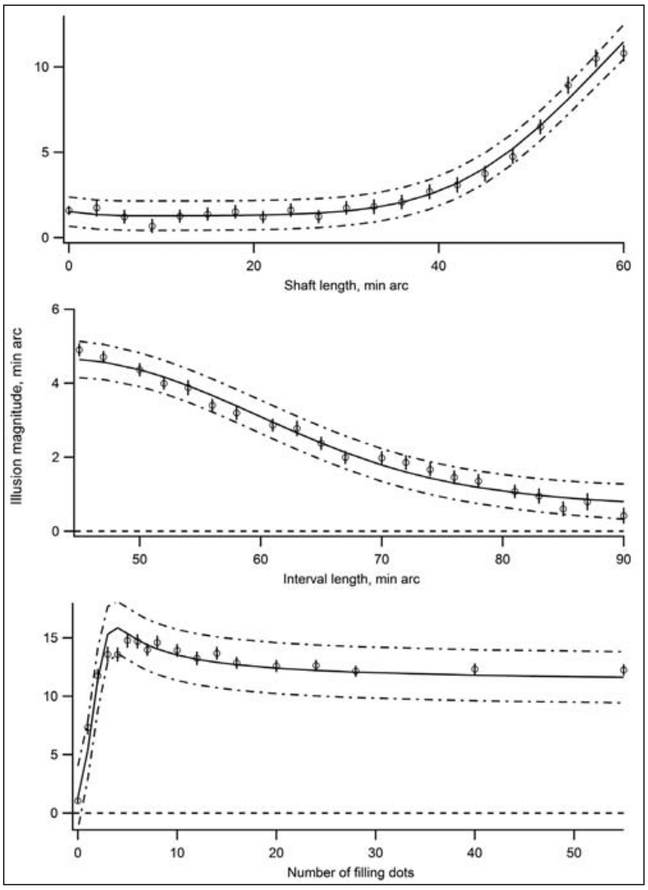

Fig. 4. The results of the fittings of the model function to the experimental data. In the graphs, *circles* represent grand-means (from Fig. 3) of the individual data for all twelve subjects as functions of the length of the contextual shaft-line (upper), length of the reference interval (middle), and number of filling dots in the reference part of the Oppel-Kundt figure (lower), respectively. Solid curves represent the least squares fittings of the function (9) to the experimental data; dash-dot curves, confidence intervals of the fitting. Error bars, ±one standard error of the mean (SEM).

mean curve (Fig. 3, upper graph, solid line) was calculated from the individual experimental data. We believe that a rather small values of SEM (not exceeding 0.52 min of arc) for the grand-mean indirectly confirms our assumption regarding the similarity of the individual curves shape.

In the second series of experiments, the length of the shaft-line was fixed at 45 min of arc, and the length of the reference interval was randomly changed in a range from 45 to 90 min of arc. As can be seen from the middle graph in Fig. 3, for all the subjects the illusion magnitude gradually diminishes with increase the length of the interval. As well as in previous series of experiments, quite large inter-individual variability of the experimental results presented, however, the values of SEM calculated for the grand mean curve (Fig. 3, middle graph, solid line) do not exceed 0.63 min of arc. It should be noted that for the same set of the stimulus parameters (s=45 min of arc, and R=60 min of arc) in experiments with different independent variables, quite comparable values of the illusion magnitude were obtained (3.75±0.46 min of arc and 3.2±0.19 min of arc for grand-means from the first and second series of experiments, respectively; paired t-test: t_{119}=1.471, P=0.144; the Shapiro-Wilk test: W_{119}=0.986, P=0.234). We think that this fact may serve as an additional argument in favor of a rather good precision of the experimental measurements.

In order to establish the dependence of the filled-space illusion magnitude on the number of discrete filling elements, the third series of experiments with the same group of observers was performed. The length of the reference interval of the Oppel-Kundt stimulus (Fig. 1D) was set to 60 min of arc; the number of filling dots (the independent variable) was randomly changed in a range from 0 to 55. The results gathered in experiments of the third series show curves (Fig. 3, lower graph), which are similar to those demonstrated in most of previous studies of the Oppel-Kundt illusion (Coren et al. 1976, Bulatov et al. 1997, Deregowski and McGeorge 2006, Wackermann and Kastner 2010, Wackermann 2012a, 2012b). With increasing number of dots up to about 4–8 (the data differ somewhat for different subjects), the illusion magnitude steeply reaches a relatively flat region of maximum, and thereafter decreases slowly to an almost constant level (about 8–14 min of arc or 13–23% overestimation of the reference interval length) with further increasing of subdivision density. It is noteworthy that for the same stimulus conditions (i.e., for complete continuous filling of the reference interval) in experiments from different series, quite comparable values of the illusion magnitude were obtained (10.8±0.49 min of arc and 11.2±0.49 min of arc for data from the first and third series, respectively; paired t-test: t_{119}=1.133, P=0.259; the Shapiro-Wilk test: W_{119}=0.993, P=0.799).

Data fitting

In order to check the model predictions quantitatively, we have fitted the experimental data presented in Fig. 3 with the following function (in the fitting of the data from the second series of experiments, the interval length, R was considered as the independent variable):

$$I(x, R) = C + AF(x, R, B), \tag{9}$$

where C refers to a constant shift along the ordinate axis, and A is a coefficient of proportionality; $F(x, R, B)$ corresponds to function (7) or (8) with additional argument $B=0.5\sigma^{-2}$, where σ refers to the standard deviation of the Gaussian profile of the attentional window.

To fit the experimental data, the method of least squares with three free parameters (C, A and B) was used. A good resemblance between the computational and experimental results was obtained (Fig. 4, solid curves); the values of the coefficient of determination R^2 in all the cases were higher than 0.9 (Table I).

Table I. The parameters (the significance level, α=0.05) of fitting Eq. 9 to experimental data

Parameters	Independent variable		
	Shaft length	Interval length	Dots number
A	1.132±0.142	1.194±0.461	0.882±0.133
C	1.528±0.251	0.722±0.277	1.328±1.681
σ	6.394±0.747	8.052±0.504	6.113±0.478
R^2	0.986	0.981	0.919
W	0.962 (df=20)	0.957 (df=20)	0.917 (df=17)
P_w	0.559	0.451	0.129

A and C (min of arc), proportionality coefficient and a constant component, respectively; σ (min of arc), standard deviation of the Gaussian profile of the attentional window; R^2, coefficient of determination; W, the Shapiro-Wilk test statistic; P_w, the p-value for Shapiro-Wilk test.

With the aim of a more thorough examination of the goodness-of-fit, statistical analysis of the data with the Shapiro-Wilk test (assessment of normality of residuals) was performed (Table I). For each calculated curve, a matrix of partial derivatives (Jacobian) of the model's function was multiplied by the residual mean square. These data allowed an additional evaluation of the goodness-of-fit by calculating confidence intervals for predicted values at each point along the range of the independent variable (Fig. 4, dash-dot curves).

DISCUSSION

The striking non-monotonic dependence of the effect of the filled-space illusion on the number of the subdividing discrete elements was probably the key feature that has diverted the attention of most researchers away from the fact that the illusion survives when many fillers form one uninterrupted unit. Therefore, our primary goal in the present study was to perform psychophysical experiments with aim to establish functional dependences of the illusion magnitude on the spatial parameters of the continuous filling of the reference part of the stimulus. The *post hoc* analysis of the data gathered in these experiments has enabled to propose a simplified quantitative description of the illusion phenomenon based on the assumption that an integrated context-evoked neural excitation induces biases in perceptual localization of stimulus terminators. The data from the entire group of observers have demonstrated that the model calculations properly fit (Fig. 4, upper and middle graphs, solid curves; Table I) all variations of the illusion magnitude caused by the changes in the completeness of the continuous filling. The model was also applied quite successfully (Fig. 4, lower graph, solid curve; Table I) to account for the data collected in the experiments with the conventional Oppel-Kundt figures comprising a varying number of discrete fillers. Therefore, it seems reasonable to assume that the results obtained in the present study at least do not contradict the explanation based on the idea that the perceptual displacement of stimulus terminators can be one of the main causes of the filled-space illusion. It needs to be emphasized here that this putative perceptual displacement arises due to the increased cumulative response of the visual subsystem supposed, therefore, it should not be confused with the localization errors caused by processes of lateral inhibition, which specifically alter the profile of neural excitation. As suggested by Ganz (1966), these profile changes can result in a perceptual repulsion of adjacent stimulus elements, thereby inducing the Oppel-Kundt illusion. Recently, however, it was demonstrated experimentally (Mikellidou and Thompson 2014) that the effect of repulsion is too small and can account for only about 10% of the total illusion magnitude.

It is evident that the proposed theoretical approach is highly simplistic, and represents only an initial step towards a more comprehensive quantitative description of the phenomenon under study. For instance, formula (1) gives a rather rough assessment of perceptual biases induced by the contextual filling because only one-dimensional profiles of the putative neural excitation were taken for calculations and the same holds true for the derivation of subsequent formulas (2) and (3). The other essential drawback in a quantitative interpretation of the present experimental data is associated with uncertainty concerning the gaze-fixation pattern during stimulus observation. Under real experimental conditions, the subjects were not constrained in moving their eyes; thus, the illusion magnitude could vary depending on the actual direction of the observer's gaze (some initial biases in eye movements or attentional shifts could also contribute significantly to the illusory effect). According to the model, the illusion magnitude depends on the size (which grows linearly with visual eccentricity) of terminators-related attentional windows and convolution kernels in excitation profiles; however, accounting for these changes significantly complicates calculations and requires too many free parameters for fittings to experimental data. Therefore, for the sake of simplicity, we have considered only a single way of the stimulus observation with gaze fixation on the central terminator, and in the model fittings the experimental data points were judged as representing some averaged values of the illusion magnitude. Consequently, when trying to assess the width of relevant attentional window (the parameter B in formula 9), it was assumed that this putative window is located at a certain averaged distance from the fovea center.

A great variety of the accompanying neural processes has not been taken into account in the model, and this circumstance could also be the reason of substantial imperfection in the estimates of the parameters of the filled-space illusion. For instance, the model was not concerned with issues related to earlier spatial-frequency filtering, which is an inherent feature in even the lowest levels of the visual system; as well, the influence of any top-down control from higher-order visual processing was not considered. Nevertheless, a quite good agreement between the theoretical and experimental results for different stimuli modifications confirms that the suggested approach offers a rather simple unified explanation of the effects of the illusion, and thereby provides a potentially fruitful way to proceed. Furthermore, the results of the fitting of the experimental data yielded physiologically quite reasonable parameters. It has been shown (Sagi and Julesz 1986, Nakayama and Mackaben 1989, Intriligator and Cavanagh 2001) that the size of the "spotlight of attention" is about 3–5 min of arc at the fovea center and increases with retinal eccentricity to about 25–40 min of arc in 1°

periphery. If one assumes that this scaling is also applicable for our putative attentional windows, then their averaged size (Table I, $\sigma \times 4$: 25.6±3.0, 32.2±2.0, and 24.5±1.9 min of arc for results from the first, second, and third series of experiments, respectively) seems to be rather consistent with that from the literature data. It should be pointed out that the model calculations for the experimental data from the second series yielded the size of attentional window, which is approximately 1.3 times greater than that from the first and third ones. In our opinion, this result additionally supports the validity of the model assumptions because, on average, the size of the stimuli used in the second series of experiments was also larger than that of the stimuli used in the other series ((45+90)/2=67.5 min of arc against 60 min of arc). It is worth mentioning here that the estimates for the size of attentional windows obtained in the present work are quite consistent with those from our recent studies of various modifications of illusions of the Müller-Lyer type (Bulatov et al. 2009, 2010, 2013, 2015a, 2015b).

We think, the hypothesis on "continuity perception" (Bertulis et al. 2014) can be considered, to some extent, as a possible alternative explanation of the results obtained in the present study. The explanation operates with the overlapping spatiotemporal windows, which form the continuous paths of "associated fields" of neural activity (Uttal 1975, Field et al. 1993, Kojo et al. 1993, Hirsch et al. 1995) that in some respects are similar to the profiles of excitation within the limits of attentional windows used in our modeling. Unfortunately, it was merely declared in the explanation that an overestimation of the filled interval in the Oppel-Kundt stimulus could be related to a spatiotemporal integration along the real or illusory contours of the filling, without providing any methodological description of computational algorithms for the quantitative assessment of the illusion effects.

The computational modeling of "logarithmic information-integration" proposed by Erdfelder and Faul (1994) can be considered as another potential alternative explanation. According to the model, the perceived length of the filled interval of the Oppel-Kundt stimulus is equal to the subjective length of a single subdivision multiplied by the subjective number of subdivisions. Although this analytical approach offers rather adequate predictions for different variations of parameters of the Oppel-Kundt illusion, the meanings of the basic theoretical definitions (like "information-integration") were not stated explicitly, and it makes the modeling to be highly formal (also, without any neurophysiological substantiation). In addition, the model functions are not intended to be directly applicable in the case of continuous contextual filling of the stimulus intervals. On the contrary, in our current approach, for both types of filling (i.e., discrete and continuous) we have used the same unified procedure of spatial integration of the normalized neural excitation within the limits of attentional windows of the same type (i.e., a Gaussian function, the parameters of which depend only on retinal eccentricity).

Neither the analysis of the results from the previous studies with the conventional Oppel-Kundt figures nor the data obtained in the present experiments with stimuli comprising of continuous filling do not allow us to speculate more or less definitely regarding the localization of brain mechanisms responsible for the occurrence of the filled-space illusion. In our previous seeking of underlying principles behind the misperception of extent (Bulatov et al. 1997, Bulatov and Bertulis 1999, 2005), the main attention was drawn to the cortical processes of spatial-frequency filtering. Since the computational procedures of the current model represent some calculations of convolution and spatial integration, it can be considered as a further development of the "filtering" hypothesis. However, the model parameters obtained in the present study incline us towards the assumption that the illusion effects to a greater extent can be related to visual information processing in the superficial layers of the superior colliculus. It is known (Klier et al. 2001, Bergeron et al. 2003, Nakahara et al. 2006, Krauzlis et al. 2013, Vokoun et al. 2014) that these brain structures are important for gaze control, and that elevated neural activity at an appropriate locus in their map represents a real-time estimate of the retinotopic distance to the target.

Stimuli used in the present experiments were composed of elements (dots and thin line segments) concentrated along a single stimulus axis, thereby allowing to consider and modeling only the simplest one-dimensional effects of the filled-space illusion; therefore, the results obtained cannot be immediately extended to more general conditions. It is obvious that further studies are needed to verify whether the same principles in the interpretation of perceptual misjudgments can be used in the case of more sophisticated filling of two-dimensional stimuli. We expect that the results of these studies can contribute to a better understanding of the multi-factorial neurophysiological basis of the illusion.

CONCLUSIONS

In the present study, psychophysical examination of different variants of the filled-space illusion was performed. It was demonstrated in experiments with the continuous contextual filling that the magnitude of the illusion increases non-linearly with the lengthening of the shaft-line centered in the reference part of the horizontal three-dot stimulus. For the constant length of the shaft-line, the illusion magnitude gradually decreases with the increase of the reference interval length. The data for the discrete contextual filling were collected in experiments with the conventional Oppel-Kundt stimulus comprising different number of equally spaced dots. Based on a *post hoc* analysis of the experimental data, a simple computational model was developed. It was demonstrated that the model calculations adequately follow all the variations of the illusion magnitude for both types (i.e., discrete and continuous) of the contextual filling. A good correspondence between the experimental results and the predictions of our computational model supports the suggestion that perceptual positional biases induced by additional context-evoked neural excitation can be considered as one of the main causes of the filled-space illusion.

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