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Kanizsa figure does not defend against saccadic compression of visual space

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Abstract

Recent studies have suggested that the apparent shape of a perceptually organized object flashed immediately before saccade is not distorted although a perisaccadic flash is mislocalized as if the visual space is compressed toward the goal of the saccade. We report that the apparent width of a Kanizsa illusory rectangle flashed in the perisaccadic period was compressed as much as that of a control stimulus that did not induce illusory rectangle, while that of a rectangle with real contour was less compressed. Our results imply that the process of saccadic compression of visual space completes faster than the interpolation process of illusory contours. © 2004 Elsevier Ltd. All rights reserved.

Keywords: Saccade; Visual space; Illusory contour; Shape perception

1. Introduction

When we perform a saccade while viewing objects, the retinal locations of the object images change quickly. The brain compensates for this change to achieve stable visual space using information such as eye position signal and the retinotopic relation between object images (Bridgeman, Van der Heijden, & Velichkovsky, 1994; Helmholtz, 1866). This compensation functions correctly in most cases, however, previous studies have been demonstrated that stimuli are erroneously located when briefly presented near the time of saccade execution (Honda, 1989; Lappe, Awater, & Krekelberg, 2000; Mateeff, 1978; Ross, Morrone, & Burr, 1997). This illusion can be decomposed into two components, i.e., "shift" and "compression" (Lappe et al., 2000). "Shift" referred to the apparent shift of the location of a stimulus in a direction parallel to the saccade. Direction and amount of shift is considered to reflect an error of ext-

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raretinal eye position signal (Honda, 1989; Mateeff, 1978). "Compression" referred to the apparent shift of the location of a stimulus toward the goal of saccade as if visual space is compressed. This component is also called "saccadic compression of visual space" (Lappe et al., 2000; Ross et al., 1997).

Recently, it is reported that the apparent shape of a single object is not distorted even when it is briefly presented immediately before saccade onset (Matsumiya & Uchikawa, 2001). They presented a solid rectangle of 10 deg height and 15 deg width immediately before executing a saccade of 20 deg amplitude (Fig. 1A). The centre of the stimulus was aligned with the goal of saccade. The results showed that the apparent width of the stimulus was not significantly decreased although the apparent total width of four thin vertical bars (Fig. 1B) was decreased. They also tested the apparent total width of rectangular arrays of disks (Fig. 1C and D). The results were that the apparent width of Fig. 1C was not decreased; however, the apparent Fig. 1D was decreased. From these results, they concluded that both a single object and multiple objects that are perceptually organized into a single object are uncompressed

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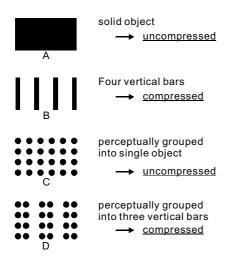


Fig. 1. Summary of the results of Matsumiya and Uchikawa (2001). They interpreted these results as indicating that a solid object (A) and a set of multiple elements perceptually organized into a single object (C) are not affected by saccadic compression of visual space.

even if they were briefly presented near the time of saccade execution. Interestingly, their conclusion raises a question about interaction (or separation) between object shape perception and compensation for the location of perisaccadic stimuli. That is, what kinds of "perceptually organized" single objects are uncompressed by saccade execution? The results of Matsumiya and Uchikawa (2001) seem only to indicate that objects organized by so-called "the Gestalt law of proximity" (Wertheimer, 1923) are uncompressed. The answer to this question will tell us at which stage of the visual information processing saccadic compression of visual space occurs and how perception of object shape and object location interacts or separates.

To investigate this question, we compared the apparent width of a Kanizsa-type illusory rectangle (Kanizsa, 1979) with control figures such as a solid rectangle when they briefly flashed near the time of saccade execution. If the apparent width of a Kanizsa rectangle is uncompressed as a solid rectangle, it is considered that the interpolation process of a Kanizsa rectangle does not affect compensation for object locations around the time of saccade execution.

2. Experiment 1

2.1. Methods

Three male subjects participated voluntarily in the experiment. One of the subjects was an author of the present paper, while the others did not know the purpose of the experiment. All subjects had normal or corrected-to-normal visual acuity.

A CRT used to present stimuli was placed in front of the subject at a distance of 25cm. Frame rate of the CRT was 100 Hz. A $68 \times 56 \text{ deg } 14 \text{ cd/m}^2$ rectangle was presented throughout the experimental session as a background. Left panel of Fig. 2 shows the spatial arrangement of the stimuli. An initial fixation point and a saccade goal was placed 10 deg left and 10 deg right of the centre of the background, respectively. A target stimulus, consisting of disks, packmen and rectangles, was placed on the saccade goal. The diameter of the disks and the pacmen at the vertices was 3.2 deg. Distance between the centre of disks and pacmen was 8 deg vertically and 12 deg, 16 deg or 20 deg horizontally. To avoid difficulty due to dependency of saccadic compression of visual space on stimulus location (Morrone, Ross, & Burr, 1997; Ross et al., 1997), only the 16deg wide targets were selected for analyses. The targets of 12 deg and 20 deg width were used to prevent the subjects from remembering actual width of the target and being biased toward the remembered width. The vertical and horizontal center of the target was always aligned with the saccade goal. Luminance of the initial fixation point, the saccade goal and the target was 0.5 cd/m^2 .

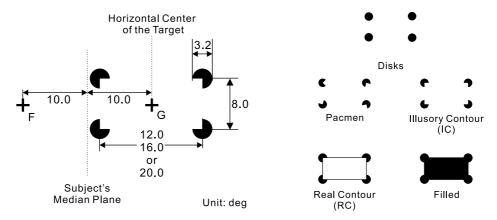


Fig. 2. Left panel: spatial arrangement of the stimuli in Experiment 1. F and G indicate the initial fixation point and the saccade goal, respectively. Right panel: five types of targets used in Experiment 1.

The Right panel of Fig. 2 shows the five types of target stimuli used in Experiment 1. "Illusory contour" (IC) is a Kanizsa figure that yields an illusory rectangle. "Filled" is a target whose apparent width is not compressed (Matsumiya & Uchikawa, 2001). "Disks" is a target whose apparent width is compressed. "Real contour" (RC) and "pacmen" are control targets to confirm whether solidness of the target and replacing disks with pacmen does not affect the apparent width of the target.

The subject sat in a dark room (luminance was less than 0.01 cd/m^2) with the head stabilized by a headrest and a chin rest. Horizontal eye movement was recorded by DC-EOG. At the beginning of each trial, the initial fixation point was presented for 1000-1500 ms. Immediately after the offset of the fixation point, the saccade goal appeared for 20ms. The subject was required to make a saccade from the fixation point to the saccade goal. At a random time within 120-240 ms from the onset of the saccade goal, one of the targets shown in Fig. 2 was presented for 10ms. Width of the target was 16deg for 83% of the trials and 12 deg or 20 deg for the rest of the trials. A probe appeared approximately 1500 ms after onset of the saccade goal. The probe was the same shape and size as the target except that the width of the probe was 0-4 deg wider or narrower than the target in random order. The horizontal center of the probe was randomly shifted 0-2 deg to the left or right of that of the target. The subject could change the width and horizontal center of the probe using a joystick. The task of

the subject was to adjust the probe to the apparent width and location of the target. When the subject finished adjustment and pressed a button on the joystick, one trial finished and the next trial started after a 2s interval. One experimental session included 24 trials. To avoid fatiguing the subject, the duration of the experiment was restricted to less than 1 h per day. The experiment was continued until sufficient data were obtained for statistical analysis.

Output of the EOG recorder was analyzed off-line to determine saccade onset. We defined saccade onset as the time when the angular velocity of horizontal eye rotation exceeded 40 deg/s. We discarded trials in which latency of the saccade was more than 360 ms or less than 100 ms, and when the subject made leftward saccades or the subject made another saccade within 200 ms after the first saccade. To avoid difficulty due to dependency of saccadic compression of visual space on stimulus location (Morrone et al., 1997; Ross et al., 1997), only trials in which the width of the target was 16 deg were selected for analyses.

2.2. Results and discussion

Fig. 3 shows raw data obtained from a single subject. In this figure, the apparent widths of targets are plotted against the time of stimulus onset relative to saccade onset. The responses depended strongly on the time of stimulus onset relative to saccade onset for "disks"

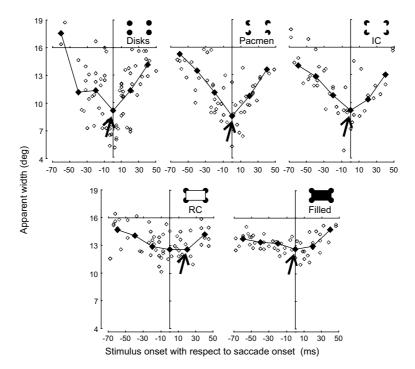


Fig. 3. Apparent widths of the targets were plotted against the time of stimulus onset relative to saccade onset (real width = 16 deg, results a single subject). Each open diamond corresponds to a single trial. Filled diamonds connected with solid lines show mean apparent widths within 20 ms intervals. Arrows indicate the minimal mean apparent width.

target. However, this dependency was much weaker for "filled" target. These tendencies are consistent with the results reported by Matsumiya and Uchikawa (2001), although they reported that no significant compression was observed for a filled rectangle. The responses to "IC" target, which we are interested in, were obviously similar to "disks" and "pacmen" targets rather than "RC" and "filled" targets. To confirm this observation, we split the data into 20ms intervals in terms of the target onset time relative to saccade onset and selected an interval at which the mean apparent width was minimized (indicated by arrows in Fig. 3). We examined the effects of subject and target on these selected data by two-way analysis of variance (ANOVA). ANOVA showed that the effects of subject (F(2,210) = 8.10,p < 0.01) and target were significant (F(4, 210) = 16.5, p < 0.01), while their interaction was insignificant (F(8,210 = 1.17), p > 0.05). Post hoc analysis showed that the apparent width of "disks", "pacmen" and "IC" were significantly narrower than "RC" and "filled" (Fig. 4). In summary, apparent width of a rectangle with a real contour was the same as that of a solid rectangle. However, a rectangle with an illusory contour was perceived as narrow as stimuli that do not induce illusory contours.

There seem to be two possible interpretations of this finding. Firstly, Kanizsa-type illusory rectangle cannot withstand the effect of saccadic compression of visual space. Secondly, inducers of "IC" target were separated too far to induce a strong illusory rectangle. As for the second possibility, Ringach and Shapley showed that perception of illusory contours was scale invariant in the range of 5.72-13.17 deg gaps between inducers (Ringach & Shapley, 1996). Horizontal gap of our "IC" target was within this range when the actual width of the target was 16 deg (16.0-3.2 deg = 12.8 deg). How-

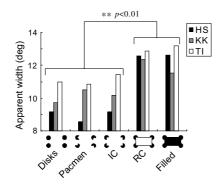


Fig. 4. Minimal apparent widths of targets with a 16 deg width, which was obtained by splitting the data in 20 ms intervals in terms of the target onset time relative to saccade onset and comparing the mean apparent width at these intervals (indicated by arrows in Fig. 3). Two-way ANOVA showed that effects of subjects and target type were significant (p < 0.01) and that their interaction was insignificant (p > 0.05).

ever, it is uncertain whether the results by Ringach and Shapley are applicable to stimuli that are briefly presented in the peripheral visual field near the time of saccade execution. In the next experiment, we examined whether the apparent width of an illusory rectangle is compressed even when horizontal gaps between inducers are much smaller.

3. Experiment 2

The purpose of Experiment 2 is to examine the effect of gap sizes between inducers. Here we must pay attention to the fact that the size and direction of compression strongly depend on stimulus location (Morrone et al., 1997; Ross et al., 1997). This makes it difficult to compare the compression effect across stimuli of different widths. To avoid this problem, we fixed locations of the left and the right end of the stimuli and changed the gap sizes by inserting additional inducers in between the left-end and the right-end inducers.

3.1. Methods

The subjects and the apparatus were the same as those in Experiment 1. The left panel of Fig. 5 shows the spatial arrangement of the stimuli. The initial fixation point was shifted toward the subject's median plane so that subjects could fixate on it effortlessly. Vertical of the target was 12.0 deg. Horizontal size of the target was 16.0, 20.0 or 24.0 deg. For the same reason described in Experiment 1, only the 20.0 deg wide targets were selected for analysis. The right panel of Fig. 5 shows the target stimuli used in Experiment 2. As in Experiment 1, "Illusory contour (IC)" category is a Kanizsa figure that yields an illusory rectangle. To examine the effect of horizontal gap sizes between inducers, we prepared five subtypes that have different numbers of columns of inducers. Centers of the left and right end column were always aligned to the left and the right end of the illusory rectangle. Other columns were placed so that horizontal gaps between adjoining columns were equal. In the case of target of 20 deg width, horizontal gaps between inducers were 17.0, 7.0, 3.67, 2.0 and 1.0 deg for 2, 3, 4, 5 and 6 column targets, respectively. Support ratio, denoting the ratio between the sum of the length of the horizontal side of the inducers and the horizontal length of the illusory Kanizsa rectangle, were 0.25, 0.30, 0.45, 0.60, and 0.75, respectively. The "disks" category is obtained by replacing pacmen and half disks of "IC" targets with disks. "Real contour (RC)" is obtained by replacing illusory contours of "IC" targets with real contours.

The time course of stimulus presentation and task of the subjects were the same as those of Experiment 1 except for the following points. Firstly, width of the target

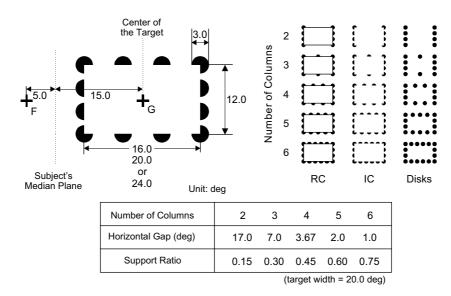


Fig. 5. Left panel: spatial arrangement of the stimuli in Experiment 2. F and G indicate the initial fixation point and the saccade goal, respectively. Right panel: Targets used in Experiment 2. Bottom table: Horizontal gap between inducers and support ratio (the ratio between the sum of the length of the horizontal side of the inducers and the horizontal length of the illusory Kanizsa rectangle) associating with each number of columns. The probe shape was "IC-2 columns" for "RC" and "IC" targets, and "disks-2 columns" for "disks" targets.

was 20 deg for 83% of the trials and 16 deg or 24 deg for the rest of the trials. Only trials in which the width of the target was 20 deg were selected for analyses. Target type and number of columns were randomly selected per session, and fixed throughout a single session. Lastly, shape of the probe was "IC-2 columns" for "RC" and "IC" targets, and "disks-2 columns" for "disks" targets. This was done to avoid the subjects judging width of the stimuli only from local features of the target, i.e., gap size between inducers.

3.2. Results and discussion

We selected trials in which the target onset was -10 to 30 ms with respect to saccade onset because apparent

width was minimized within this period. Fig. 6 shows mean apparent width of 20 deg wide targets within this period. Although considerable individual differences were observed, it can be seen that apparent widths of "IC" and "disks" targets became narrower as the number of columns decreased in comparison with those of "RC" targets. We performed two-way ANOVA separately for each subject to examine the effects of target types and number of columns (Table 1). A significant interaction was revealed for all subjects. Results of post hoc analysis are shown in Fig. 6 (for simplicity, significant differences only between stimuli of the same number of columns were indicated). Apparent width of "IC" and "disks" were not significantly different when the number of the columns was the same. When the

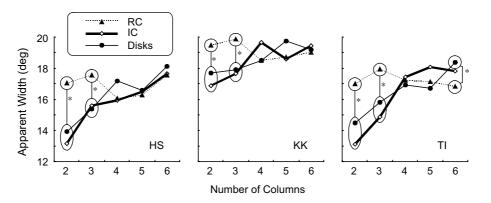


Fig. 6. Mean apparent width of the target (actual width = 20 deg). In all subjects, interaction between target type and number of columns was significant (Table 1). Asterisks indicate a significant difference on post hoc analysis (for simplicity, significant differences only between stimuli of the same number of columns are presented). In all subjects, "IC" and "disks" targets were perceived narrower than "RC" targets when number of columns was 2 or 3.

 $F(4, 113) = 13.61^*$

 $F(2, 113) = 4.88^*$

 $F(8, 113) = 5.65^*$

| Two-way ANOVA (Experiment 2) | | |
|------------------------------|--|---|
| Subject | Effect | F value |
| HS | No. of columns Target type Interaction | $F(4, 183) = 12.34^*$ $F(2, 183) = 5.29^*$ $F(8, 183) = 3.82^*$ |
| КК | No. of columns Target type Interaction | F(4, 170) = 2.19 F(2, 170) = 1.85 $F(8, 170) = 2.56^{**}$ |

No. of columns

Target type

Interaction

Table 1

ΤI

number of columns was 2 or 3, "IC" and "disks" were perceived as significantly narrower than "RC" targets. In summary, "IC" targets were compressed as much as "disks" targets for all numbers of columns tested in this experiment.

In the discussion of Experiment 1, we speculated that "IC" target of Experiment 1 was compressed because inducers were separated too far to induce strong illusory contour. The results of Experiment 2 did not support this interpretation. It can be concluded that Kanizsa rectangle is not included in the class of perceptually organized objects that remain unaffected by saccadic compression of visual space.

It remains unclear whether Kanizsa rectangle is compressed because illusory contours have no effect of withstanding against saccadic compression or simply because illusory contours are not perceived. To answer this question, we need to evaluate the strength of perceived illusory contours in a direct way. Previous studies successfully evaluated the strength of illusory contours (Guttman & Kellman, 2004; Ringach & Shapley, 1996). However, their paradigms are difficult to introduce into experiments of saccadic compression of visual space for the following reasons. Firstly, the duration of Kanizsa figure presentation reaches 100ms or longer. Such a long duration of presentation causes a terrible smear of retinal image. Secondly, a mask stimulus has to follow the presentation of a Kanizsa figure. It is difficult to align perceptual location (not actual location) of the Kanizsa figure and subsequent mask because of the mislocalization of perisaccadic flashes. Thirdly, to prove strictly that the subject sees a strong illusory contour even when the Kanizsa figure is compressed, subjects have to indicate both target shape and apparent width in a single trial. We performed a pilot experiment and found that this "dual task" was too difficult to perform consistently. Moreover, subjects frequently made saccades to inducers rather than the saccade target so that a large part of the data had to be discarded. In conclusion, we think that a new task of evaluating the strength of illusory contour of briefly presented perisaccadic Kanizsa figure has to be invented. This problem remains a subject for future investigation.

4. General discussion

Matsumiya and Uchikawa (2001) reported that the apparent width of a dense array of multiple objects as well as a single solid object is not affected by saccadic compression of visual space. Based on these results, they suggested that a set of multiple objects that are perceptually organized into a single object is uncompressed. However, present results showed that the apparent width of Kanizsa-type illusory rectangle is compressed as well as those of control targets. Here we discuss the implication of these results on the relationship between interpolation of illusory contour and saccadic compression of visual space.

To begin with, let us discuss where of the human visual system perceptual grouping of dense array of multiple objects is processed. As described in Section 1, the results of Matsumiya and Uchikawa (2001) seem to indicate that perceptual grouping by the proximity law can stand against saccadic compression of visual space. Interestingly, a psychophysical study showed that grouping by proximity is perceived as fast as grouping by connecting elements with lines and faster than grouping by similarity (Han, Humphreys, & Chen, 1999). An electroencephalographic study showed that shortlatency (110-120 ms) modulation of event related potential (ERP) is observed over the medial occipital cortex when the subjects are discriminating proximity-grouped stimuli (Han, Song, Ding, Yund, & Woods, 2001). They also showed that this component was not observed while discriminating similarity-grouped stimuli. These results suggest that grouping by proximity is processed at early stages in the visual information pathway (bottom of Fig. 7). Concerning interpolation of illusory contour, neuroimaging studies suggested that lateral occipital (LO) complex in the ventral visual pathway plays an important role in recognition of Kanizsa figure (Larsson et al., 1999; Mendola, Dale, Fischl, Liu, & Tootell, 1999; Murray et al., 2002). PET study showed that V1 and V2 are also sensitive to Kanizsa figure (Larsson et al., 1999). In the monkey brain, neurons that respond to both illusory and real contours are found in V2 (Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989) and V1 (Lee & Nguyen, 2001; Leventhal, Wang, Schmolesky, & Zhou, 1998). LO complex is considered to cooperate with earlier visual areas in object recognition and to represent higher level shape information rather than simple image features such as contours (Doniger et al., 2000; Doniger et al., 2001; Grill-Spector, Kourtzi, & Kanwisher, 2001; Kourtzi & Kanwisher, 2001; Murray, Kersten, Olshausen, Schrater, & Woods, 2002; Murray & Wojciulik, 2004). From these results, it

p < 0.01. *p* < 0.05.

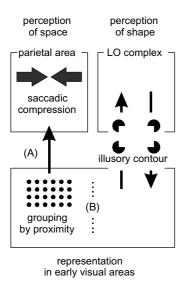


Fig. 7. Hypothetical relationship between processing of grouping by proximity, contour interpolation and saccadic compression of visual space. To explain the present results, saccadic compression of visual space must be completed faster than contour interpolation; otherwise contour interpolation and saccadic compression must be separated at the level of early visual areas (dashed line (B)).

is expected that interpolation of illusory contours require higher-level information processing than grouping by proximity (top right part of Fig. 7). Finally, where in the human visual system does saccadic compression of visual space occur? The answer to this question is not well confirmed at present. In the human brain, fMRI study showed that the fronto-parietal system is involved in egocentric representation of object location (Galati et al., 2000). In monkey brain, electrophysiological studies have demonstrated that posterior parietal neurons integrate visual and eye position information to represent egocentric location of visual stimulus (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990; Andersen, Essick, & Siegel, 1985; Andersen & Zipser, 1987). Duhamel et al. reported that visual receptive field of lateral intraparietal (LIP) neurons in monkey brain jump in an anticipatory manner before saccade execution (Duhamel, Colby, & Goldberg, 1992). It has been discussed that such anticipatory activity of LIP neurons might cause illusory perception of perisaccadic flashes including saccadic compression of visual space (Lappe et al., 2000; Ross, Morrone, Goldberg, & Burr, 2001). From these results, it seems rational to assume that saccadic compression of visual space occurs at the parietal cortical areas (top left part of Fig. 7). Because grouping by proximity can defend against saccadic compression of visual space as a solid object can, it is considered that saccadic compression of visual space occurs after grouping by proximity (arrow (A) in Fig. 7).

Now we shall discuss the relationship between illusory contour and saccadic compression of visual space. The present results demonstrate that illusory contours cannot defend against saccadic compression of visual space although primary visual areas respond to illusory contours (Fig. 7). We think that the simplest hypothesis is that saccadic compression is completed faster than interpolation of illusory contours. Although it is unclear how long it takes to complete saccadic compression of visual space, a previous study showed that presenting a second flash following a perisaccadic flash backwardly affects the apparent location of the first flash (Sogo & Osaka, 2002). This effect becomes weaker as the interstimulus interval (ISI) between two flashes becomes longer. This ISI can be considered to reflect how long it takes until apparent location of perisaccadic stimulus is not affected by a subsequent stimulus. Sogo and Osaka (2002) showed that this effect was observed when ISI was up to approximately 120ms if the stimuli were presented in a dark room. Ross et al. (1997) demonstrated that this effect was not observed even when ISI was 80ms if the stimuli were presented on a luminous background like our Experiments 1 and 2. Therefore, apparent location of perisaccadic stimulus is considered to be completed faster than 80ms or at latest approximately 120ms. As for interpolation of illusory contours, psychophysical studies revealed that there are two different phases of contour interpolation. The first phase takes 100-120 ms to interpolate illusory contours of Kanizsa figure (Guttman & Kellman, 2004; Ringach & Shapley, 1996). Moreover, another 140–200 ms is necessary to recognize the shape of Kanizsa figure (Ringach & Shapley, 1996). These results may correspond with an ERP study showing that modulation of ERP occurred twice (approximately 100-250 ms and 300-450ms) when a Kanizsa figure was presented. The second phase of interpolation is probably later than localization of perisaccadic flashes. Although time differences between localization of perisaccadic flashes and the first phase of contour interpolation are subtle, localization of perisaccadic flash does not seem to be slower than the second phase of interpolation. These results are consistent with the hypothesis that the process of saccadic compression of visual space completes faster than the interpolation process of illusory contours. Interestingly, ERP modulation occurred only once around the latter half of 200ms when Kanizsa figure was presented in the lateral visual field (Brandeis & Lehmann, 1989; Murray et al., 2002). This result favors our hypothesis if this result indicates delay or lack of the first phase of contour interpolation. In summary, previous results seem consistent with the hypothesis that saccadic compression of visual space is completed faster than interpolation of illusory contours.

If we assume interpolation of illusory contours is faster than saccadic compression of visual space, another hypothesis is necessary to explain why neuronal responses to illusory contours in primary visual areas do not prevent saccadic compression of visual space. One of the possible hypotheses is that representation of illusory contours may be separated from those of real contours within early visual areas (dashed line (B) in Fig. 7). It has shown that orientation selectivity to illusory contours is the inverse of that to real contours in V1 neurons (Ramsden, Hung, & Roe, 2001), while orientation selectivity to real and illusory contours in V2 are highly correlated with each other (von der Heydt & Peterhans, 1989). Ramsden et al. discussed that this multiple representation of contours allows humans to distinguish and identify real and illusory contours as the occasion demands. We can speculate that parietal networks may utilize only representation of real contours when perceiving perisaccadic Kanizsa figure. However, we do not know of any results directly supporting this speculation.

In conclusion, Kanizsa-type illusory contours do not defend against saccadic compression of visual space, while real contours do. Taking account of previous psychophysical and neuroscientific studies, we think that the simplest hypothesis for the present results is that the process of saccadic compression of visual space completes faster than the interpolation process of illusory contours.

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References

- Andersen, R. A., Bracewell, R. M., Barash, S., Gnadt, J. W., & Fogassi, L. (1990). Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of Macaque. *Journal of Neuroscience*, 10(4), 1176–1196.
- Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science*, 230(4724), 456–458.
- Andersen, R. A., & Zipser, D. (1987). The role of the posterior parietal cortex in coordinate transformations for visual-motor integration. *Canadian Journal of Physiology and Pharmacology*, 66, 488–501.
- Brandeis, D., & Lehmann, D. (1989). Segments of event-related potential map series reveal landscape changes with visual attention and subjective contours. *Electroencephalography and Clinical Neurophysiology*, 73(6), 507–519.
- Bridgeman, B., Van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A theory of visual stability across saccadic eye movements. *Behavioral Brain Research*, 17, 247–292.
- Doniger, G. M., Foxe, J. J., Murray, M. M., Higgins, B. A., Snodgrass, J. G., Schroeder, C. E., et al. (2000). Activation timecourse of ventral visual stream object-recognition areas: high density electrical mapping of perceptual closure processes. *Journal* of Cognitive Neuroscience, 12(4), 615–621.
- Doniger, G. M., Foxe, J. J., Schroeder, C. E., Murray, M. M., Higgins, B. A., & Javitt, D. C. (2001). Visual perceptual learning in human

object recognition areas: a repetition priming study using highdensity electrical mapping. *Neuroimage*, *13*(2), 305–313.

- Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, 255(3), 90–92.
- Galati, G., Lobel, E., Vallar, G., Berthoz, A., Pizzamiglio, L., & Le Bihan, D. (2000). The neural basis of egocentric and allocentric coding of space in humans: a functional magnetic resonance study. *Experimental Brain Research*, 133(2), 156–164.
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, 41(10–11), 1409–1422.
- Guttman, S. E., & Kellman, P. J. (2004). Contour interpolation revealed by a dot localization paradigm. *Vision Research*, 44(15), 1799–1815.
- Han, S., Humphreys, G. W., & Chen, L. (1999). Uniform connectedness and classical Gestalt principles of perceptual grouping. *Perception and Psychophysics*, 61(4), 661–674.
- Han, S., Song, Y., Ding, Y., Yund, E. W., & Woods, D. L. (2001). Neural substrates for visual perceptual grouping in humans. *Psychophysiology*, 38(6), 926–935.
- Helmholtz, H. v. (1866). Handbuch der Physiologischen Optik (translated by Southall, J.P.C., Helmholtz's, Treatise on physiological optics. Bristol: Thoemass Press, 2000).
- Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception and Psychophysics*, 45(2), 162–174.
- Kanizsa, G. (1979). Organization in vision. New York: Praeger.
- Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science*, 293(5534), 1506–1509.
- Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature*, 403, 892–894.
- Larsson, J., Amunts, K., Gulyas, B., Malikovic, A., Zilles, K., & Roland, P. E. (1999). Neuronal correlates of real and illusory contour perception: functional anatomy with PET. *European Journal of Neuroscience*, 11(11), 4024–4036.
- Lee, T. S., & Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. *Proceedings of National Academy of Sciences USA*, 98(4), 1907–1911.
- Leventhal, A. G., Wang, Y., Schmolesky, M. T., & Zhou, Y. (1998). Neural correlates of boundary perception. *Visual Neuroscience*, 15(6), 1107–1118.
- Mateeff, S. (1978). Saccadic eye movements and localization of visual stimuli. *Perception and Psychophysics*, 24(3), 215–224.
- Matsumiya, K., & Uchikawa, K. (2001). Apparent size of an object remains uncompressed during presaccadic compression of visual space. *Vision Research*, 41(23), 3039–3050.
- Mendola, J. D., Dale, A. M., Fischl, B., Liu, A. K., & Tootell, R. B. (1999). The representation of illusory and real contours in human cortical visual areas revealed by functional magnetic resonance imaging. *Journal of Neuroscience*, 19(19), 8560–8572.
- Morrone, M. C., Ross, J., & Burr, D. C. (1997). Apparent position of visual targets during real and simulated saccadic eye movements. *Journal of Neuroscience*, 17(20), 7941–7953.
- Murray, M. M., Wylie, G. R., Higgins, B. A., Javitt, D. C., Schroeder, C. E., & Foxe, J. J. (2002). The spatiotemporal dynamics of illusory contour processing: combined high-density electrical mapping, source analysis, and functional magnetic resonance imaging. *Journal of Neuroscience*, 22(12), 5055–5073.
- Murray, S. O., Kersten, D., Olshausen, B. A., Schrater, P., & Woods, D. L. (2002). Shape perception reduces activity in human primary visual cortex. *Proceedings of National Academy of Sciences USA*, 99(23), 15164–15169.
- Murray, S. O., & Wojciulik, E. (2004). Attention increases neural selectivity in the human lateral occipital complex. *Nature Neuroscience*, 7(1), 70–74.

- Peterhans, E., & von der Heydt, R. (1989). Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *Journal of Neuroscience*, 9(5), 1749–1763.
- Ramsden, B. M., Hung, C. P., & Roe, A. W. (2001). Real and illusory contour processing in area V1 of the primate: a cortical balancing act. *Cerebral Cortex*, 11(7), 648–665.
- Ringach, D. L., & Shapley, R. (1996). Spatial and temporal properties of illusory contours and amodal boundary completion. *Vision Research*, 36(19), 3037–3050.
- Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature*, 386(10), 598–601.
- Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neuroscience*, 24, 113–121.
- Sogo, H., & Osaka, N. (2002). Effects of inter-stimulus interval on perceived locations of successively flashed perisaccadic stimuli. *Vision Research*, 42(7), 899–908.
- von der Heydt, R., & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *Journal of Neuroscience*, 9(5), 1731–1748.
- Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt II. Psychologische Forschung, 4, 301–350.