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Interactions Between Shape Perception and Egocentric Localization

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1 Introduction

Neuropsychological studies of patients with damage to either the temporal or parietal region have suggested that these areas can be broadly divided into two functionally different pathways, a ventral “what” pathway for feature-related object vision and a dorsal “where” pathway for motor-oriented spatial vision (Milner and Goodale 1995; Mishkin and Ungerleider 1982). This is a reasonable separation since humans must resolve what an object is regardless of where it is to achieve object recognition, and vice versa to plan body actions in relation to the object. Neuroanatomical studies in the monkey cerebral cortex have demonstrated that parietal and temporal cortical areas are heavily connected with each other (Felleman and Van Essen 1991). Given the similarity between human and monkey cortical architecture (Van Essen 2003), it is expected that human temporal and parietal areas also have similar inter-connections. Such inter-connections would imply potential interactions between the temporal and parietal areas. However, it remains unclear how deeply these areas actually interact with each other. Concerning this question, we report recent studies suggesting that illusory perception of an object location called “saccadic compression of visual space” affects the perception of object shapes.

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2 Saccadic Compression of Visual Space

2.1 Localization of a Flash near the Time of Saccade Execution

In daily life, humans frequently make a voluntary rapid eye movement called a saccade. Although the retinal location of an object changes quickly when doing a saccade, we usually do not perceive this change as a movement of the object. A widely accepted explanation for this fact is that the object location that we perceive is represented with respect to the head (Bridgeman et al. 1994). It is necessary to calculate the head-centered representation to integrate retinal location of the object image to eye position. Denoting head-center representation, retinal image location and eye position as T , R and E , respectively, this calculation can be represented as $T = R + E$ (Fig. 1a). Neurophysiological and neural network simulation studies have suggested that this calculation is performed in parietal cortical areas (Andersen and Zipser 1987). For example, strength of visual responses of neurons in Brodmann area 7a of monkey brain is modulated by eye position (Andersen et al. 1985, see Fig. 1b). Such property is typically found in the intermediate layer of a feed-forward neural network that calculates head-centered representation from retinal image and eye position signal (Zipser and Andersen 1988). Generally, representation of object location with respect to a body part of the observer such as head-center representation is called “egocentric representation”. Egocentric representation of an object location is important for control of visually guided body actions, and integration of visual input with idiothetic or self-motion information (e.g., vestibular, motor efference copy and proprioception) is a common prerequisite for all kinds of egocentric representation.

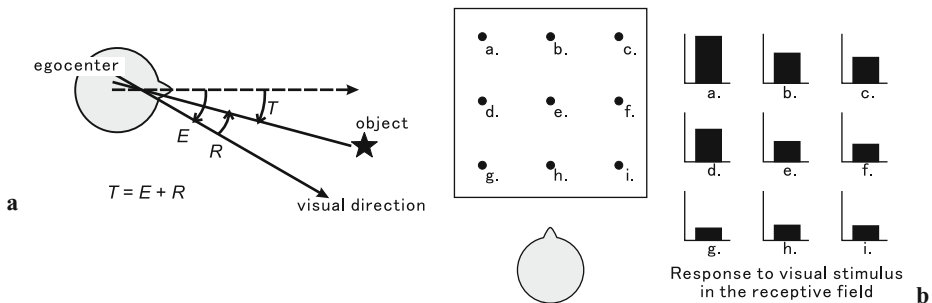


FIG. 1. Head-center representation of object location. Left: Head-centered representation of a visual object (T). T is the invariant of change in eye position when the object and head are fixed. Right: Eye-position modulation of visual responses of neurons in area 7a of the monkey brain. Visual responses during fixating on a ~ i are schematically shown in bar plots. Response of this model cell is enhanced when the monkey fixates on the top left. Head-center representation can be built up from this sort of eye-position-modulated visual response

Although head-center localization works well in daily life, it is known that the apparent location of a stimulus flashed within tens of milliseconds before, during or after saccade onset changes drastically depending on stimulus onset time relative to saccade onset time (Honda 1989, 1990, 1991; Matin et al. 1969, 1970). In general, localization error is in the same direction as the saccade when the flash is presented before saccade onset, and opposite to the saccade when the flash is presented after saccade. These results are interpreted as indicating that eye position signal changes more slowly compared to the actual change of eye position during saccade execution (Honda 1990). If this interpretation is correct, we could assume that localization error will be independent of the physical properties of a flash. However, previous studies showed that the presence of a luminous background causes dependency of the mislocalization size on retinal location of the flash (Bischof and Kramer 1968; Honda 1995; O'Regan 1984; Ross et al. 1997). Among these studies, Ross et al. (1997) reported that mislocalization strongly depended on the location of a flash when a green stimulus was flashed on an equiluminant red background. Figure 2 schematically shows the procedure and the results of their experiment. The subject made a horizontal saccade from F to T, while a vertical bar was presented for 10 ms before, during or after the saccade onset. Possible bar locations were -10 deg, 0 deg or 10 deg. The subject was asked

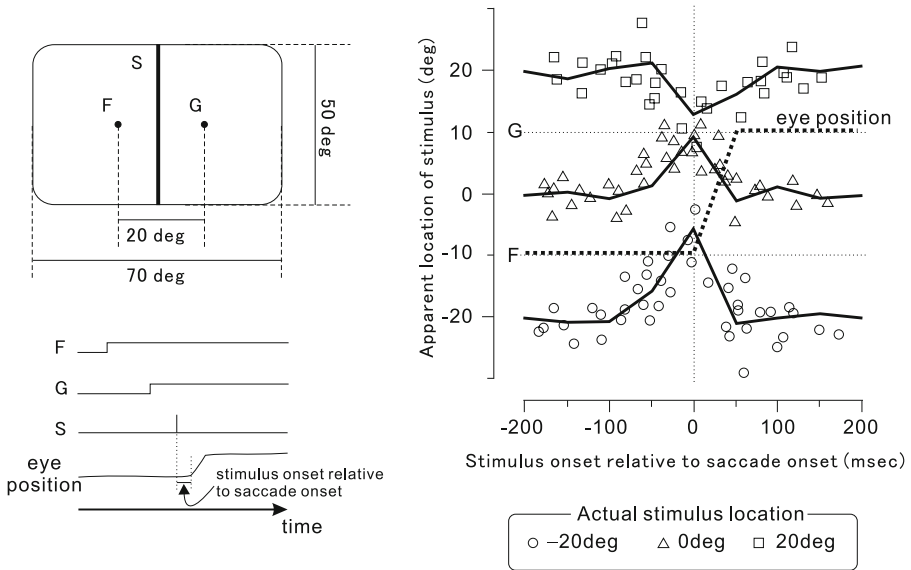


FIG. 2. Saccadic compression of visual space. Left: Spatial configuration of the stimulus and the time course of stimulus presentation. The subject made a saccade from F to G and reported the apparent location of the vertical bar (S). Right: Apparent position of vertical bars, plotted against stimulus onset time relative to saccade onset time. Each symbol (circle, triangle or square) corresponds to the result of a single trial

to report verbally where the vertical bar was perceived after saccade termination by indicating a horizontal ruler presented on the screen. The right panel of Figure 2 plots the apparent location of the vertical bar against the stimulus onset time relative to saccade onset. Each symbol corresponds to a single trial. This plot shows that the vertical bar was mislocalized as if visual space was compressed toward the goal of the saccade near the time of saccade onset (Ross et al. 1997). Ross et al. called this phenomenon “saccadic compression of visual space”. Hereafter, we will abbreviate this “saccadic compression”.

To date, it has been shown that saccadic compression also occurs in a luminance-modulated stimulus (Morrone et al. 1997). The effect of saccadic compression becomes stronger when stimulus contrast decreases (Michels and Lappe 2004). Compression in the direction orthogonal to the saccade is also observed, but the amount of compression is much smaller in comparison to that in the direction parallel to the saccade (Kaiser and Lappe 2004). Lappe et al. (2000) examined the dependence of perisaccadic mislocalization on the availability of visual spatial references at various times around a saccade. Their results showed that presaccadic compression occurs only if visual references are available immediately after, rather than before or during, the saccade. This finding indicates the importance of the time course of visual input on the generation of saccadic compression, while it is known that rapid displacement of a visual frame of reference simulating saccadic eye movement does not produce localization error similar to saccadic compression (Honda 1995; Morrone et al. 1997). These results suggest that saccade execution also plays an essential role in generating the compression effect.

2.2 Neural Correlates of Saccadic Compression

Krekelberg et al. (2003) suggested that the middle temporal (MT) and medial superior temporal (MST) areas may be concerned with the generation of saccadic compression. Initially, they measured the conditional probability of a particular firing rate for MT, MST, LIP and ventral intraparietal (VIP) neurons given the presentation of a flash at a particular location during fixation (this conditional probability was called “codebook”). The flash was presented during fixation or within ± 200 ms from saccade onset, with “fixation codebook” obtained from data in the former condition and “perisaccadic codebook” obtained from the latter. They then examined how precisely the flash location can be estimated by translating the firing rate of neurons into stimulus location using these codebooks. The results indicate that MT and MST neurons can reliably encode retinal location of the flash with the fixation codebook. Performance of the perisaccadic codebook was no better than that of the fixation codebook even for decoding the location of perisaccadic flash. Most importantly, retinal location of the flash estimated using the fixation codebook was widely mislocalized in a manner similar to saccadic compression. From these findings, Krekelberg et al. suggested that dorsal downstream areas relying on MT and MST for retinal location information would inherit this mislocalization.

3 Saccadic Compression and Shape Perception

3.1 Effects of Saccadic Compression on Shape Perception

Ross et al. (1997) performed several experiments to argue that the illusion that they found results from compression of the neural representation of visual space. In one of these experiments, they presented some photographs of natural scenes 25 ~ 0 ms before saccade execution, and asked the subjects to report verbally how the shape of objects in the scene were perceived. The result was that 11 of 13 subjects reported shape distortion of objects. Santoro et al. (2002) examined the effect of saccadic compression on the detection of a Glass pattern, i.e., a moiré pattern constructed from spatially random dots by duplication and displacement (Glass 1969). The subject made a horizontal saccade of 19 deg amplitude and a stimulus was presented 25 ~ 0 ms before saccade onset. The upper or bottom half of the stimulus was a horizontal or vertical Glass pattern, and the other half was random dots. Duration of the stimulus presentation was 5 ms. The subjects reported which of the upper or bottom half was a Glass pattern. In the control condition, the subject judged the same stimulus without making a saccade. The results showed that detection of the horizontal Glass pattern was improved when it was presented before saccade onset, while there was no such improvement for the vertical Glass pattern (Fig. 3). Santoro et al. (2002) discussed that saccadic compression apparently shortened the horizontal dot separation resulting in

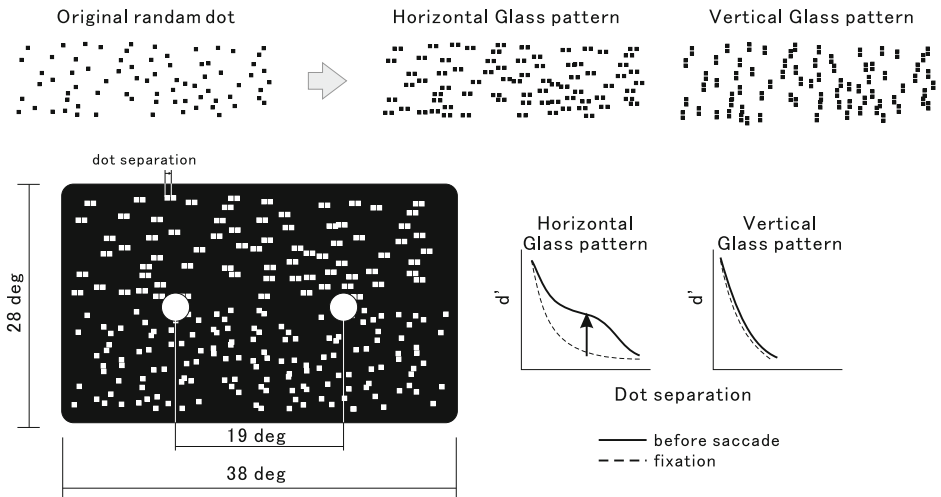


FIG. 3. Saccadic compression improves detection of Glass patterns. The subject made a horizontal saccade of 19 deg amplitude and a dot pattern was flashed for 5 ms. The subject then judged whether the top or bottom half of the dot pattern was a Glass pattern. They reported that performance of detection of the Glass pattern (d') was improved when a horizontal Glass pattern was flashed immediately before saccade onset

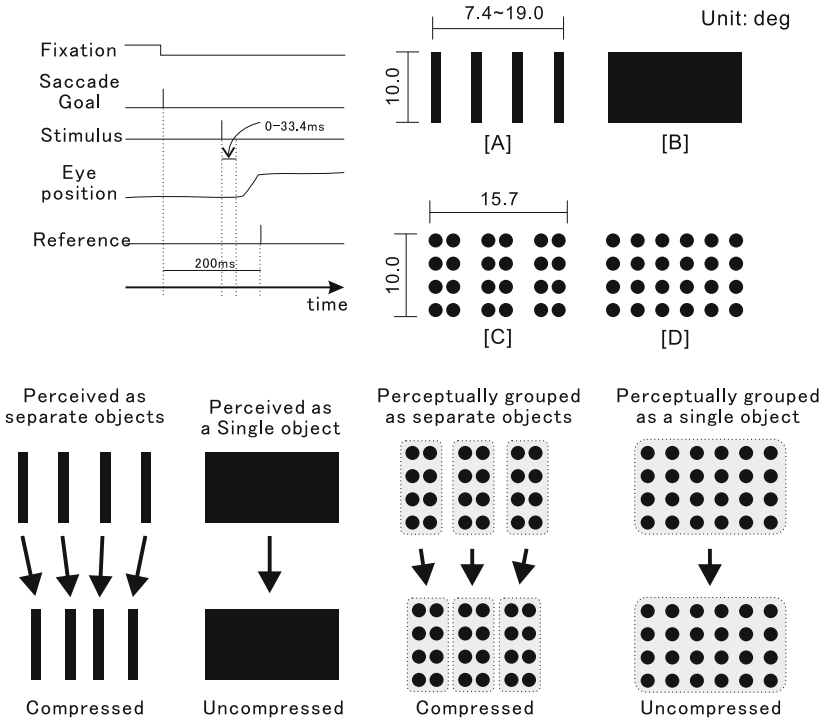


FIG. 4. Saccadic compression did not affect the apparent width of rectangle and proximity-grouped object. Top: The stimuli used in the experiment and the time course of stimulus presentation. Bottom: summary of the results and explanations by Matsumiya and Uchikawa (2001). A perceptually-grouped single object is uncompressed in the same manner as a solid object

improved detection of the horizontal Glass pattern. Considering the involvement of MT/MST in saccadic compression (Lappe et al. 2000), these findings suggest that transient changes in neural responses in MT/MST affect perception of object shape and global patterns as well as perception of object locations.

Contradictory to this suggestion, Matsumiya and Uchikawa (2001) reported that the apparent width of a rectangle presented before saccade onset was not compressed. Figure 4 shows their stimuli and procedure. At first, they compared the apparent widths of multiple bars (Fig. 4a) and solid rectangles (Fig. 4b) briefly presented before saccade onset. The subjects made a horizontal saccade to the location at which the saccade target was presented (20 deg right from the fixation point), and the stimulus was presented for one video frame (15.0 ~ 16.7 ms) so that the stimulus onset relative to saccade onset was 33.4 ~ 0 ms. The center of the stimulus was on the goal of the saccade. Two hundred milliseconds after the saccade goal was extinguished, a reference triangle was presented for one video frame. The subject judged whether the stimulus was smaller or larger than the

reference. In control trials, the subject observed the same sequence of visual stimuli without making a saccade. The results showed that the apparent width of multiple bars was compressed compared to that in control trials, while the apparent width of a rectangle remained unchanged. In addition, they examined the apparent width of figures shown in Figure 4c,d. The procedure was the same as described above except that the width of the stimulus was fixed and the width of the reference rectangle was changed between trials. The results were that the apparent width of Figure 4c was compressed while that of Figure 4d remained unchanged. Based on these results, Matsumiya and Uchikawa (2001) suggested that shape perception of a single object is not distorted by saccadic compression. The “single object” need not be a solid, but a global pattern of multiple elements that is perceptually grouped as a single object (see the bottom part of Fig. 4) also defends against saccadic compression. This suggestion conflicts with the finding of saccadic compression of objects in a natural scene reported by Ross et al. (1997). Concerning this point, they speculated that there was no distortion of the object images in natural scenes, but the apparent location of each object image in the natural scenes shifted toward the saccade goal just before the saccades. The impression that the natural scene had become deformed would result from an apparent shift of each object image (Matsumiya and Uchikawa 2001).

3.2 Does Kanizsa Figure Defend against Saccadic Compression?

The suggestion by Matsumiya and Uchikawa (2001) further implies that perception of an object shape may be protected from transient changes in neural responses in MT/MST. Considering the theory of two visual pathways for “what” and “where” vision, this is an attractive hypothesis. However, Matsumiya and Uchikawa (2001) only showed that a solid object and a set of multiple objects organized by the so-called “Gestalt law of proximity” are uncompressed. To demonstrate that shape perception is truly protected from saccadic compression, it is necessary to show that other shape perception processes are also unaffected by saccadic compression. To investigate this point, Sogo and Osaka (2005) examined whether a Kanizsa-type subjective figure is protected against saccadic compression. The top left of Figure 5 shows the stimuli used in our experiment. “Disks” and “Pacmen” were expected to be apparently compressed. “Real Contour” and “Filled” were expected to remain uncompressed because these figures contained a single wide rectangle. Our question is whether the “Illusory contour” of a rectangle defined by a Kanizsa-type subjective contour (Kanizsa 1979) would be compressed or not.

The top right of Figure 5 shows the spatial configuration of the stimuli used in our experiment. The subject fixated on F at the beginning of a trial and a cross (G) was flashed for 20ms 20deg right to the F. The subject made a horizontal saccade as quickly as possible to the location where G was flashed. At a random time within 120 ~ 240ms from the onset of G, one of the target stimuli shown in the top left of Figure 5 was presented for 10ms. Width of the target was 16deg

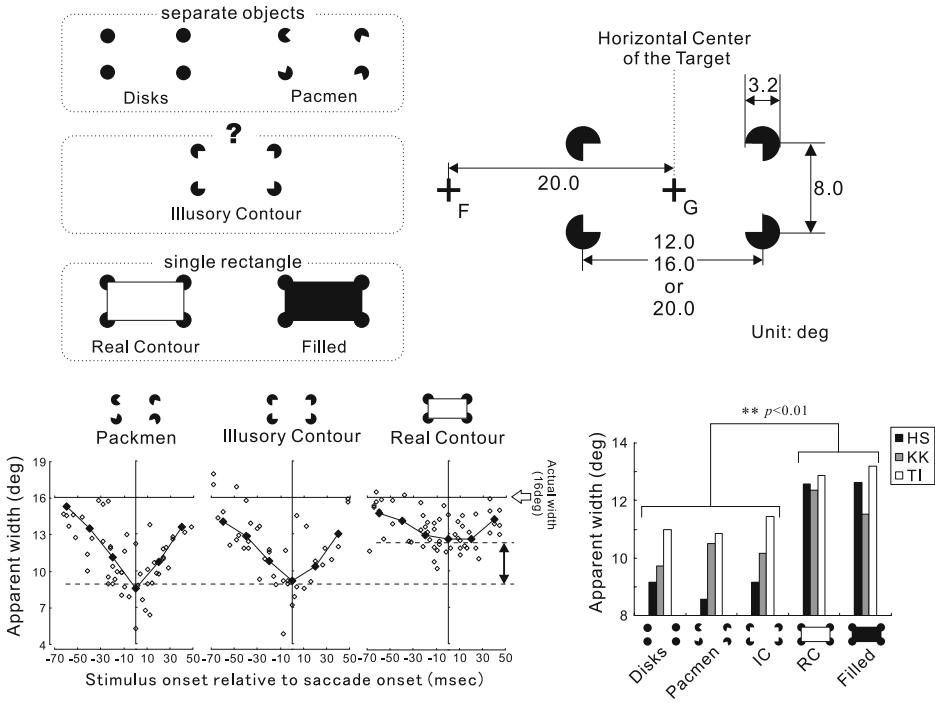


FIG. 5. Effect of saccadic compression on the apparent width of a Kanizsa figure. Top: The stimuli used in the experiment and spatial configuration of the stimuli. Bottom left: Representative results from a single subject. Bottom right: The minimal apparent width (average of the results of four subjects). The result for “Illusory Contour” was clearly similar to those for “Disks” and “Pacmen”

for 83% of the trials and 12deg and 20deg for the rest of the trials. A probe appeared approximately 1500ms after onset of the saccade goal. The probe was the same shape and height as the target but the width of the probe was either wider or narrower than the target. The subject reported the apparent width of the target by adjusting the width of the probe using a joystick. Representative data are shown at the bottom left of Figure 5. The apparent width of all stimuli was narrowest when they were presented near the time of saccade onset. As expected, the minimum apparent width of “Pacmen” was narrower than that of “Real Contour”. The result for “Illusory Contour” was clearly similar to that of “Pacmen”. The bottom right of Figure 5 compares the minimal apparent widths of five targets (the mean from four subjects). The minimal apparent widths of “Disks”, “Pacmen” and “Illusory Contour” were significantly narrower than those of “Real Contour” and “Filled”. This finding indicates that Kanizsa-type illusory contour does not protect against saccadic compression. However, it is also possible to speculate that the horizontal distance between inducers (i.e., pacmen in the “Illusory Contour”) might be too long to provoke a strong impres-

sion of illusory rectangle. To investigate this possibility, we examined whether the apparent width of a Kanizsa rectangle was compressed even when the horizontal distances between inducers were much shorter. The result was, interestingly enough, that minimal apparent width of “Illusory Contour” was not different from that of “Disks” for all distances examined (Sogo and Osaka 2005). Thus, we did not find any sign that perception of a Kanizsa figure is protected against saccadic compression.

3.3 Does a Line-Drawing of a Triangle Defend against Saccadic Compression?

An unexpected finding in the experiment shown in Figure 5 is that the apparent width of the “Real Contour” was also slightly compressed. This may be because this stimulus was not a single object in the strict sense but a compound of a rectangle and four disks. If the rectangle and four disks were perceived as separate objects and the apparent horizontal distance between disks was compressed, the overall width of the stimulus would be slightly compressed while the width of the rectangle was correctly perceived. Another possibility is that compression of the rectangle width was too small to detect with the method used by Matsumiya and Uchikawa (2001). To investigate this possibility, we examined the effect of saccadic compression on shape perception of a single object in a manner different from asking the subject to indicate the apparent width of the object (Sogo and Osaka 2007). Top left of Figure 6 shows the stimulus. The experiment consists of two conditions, “triangle” and “bar” condition. In the triangle condition, the subject fixated on F at the beginning of the trial and G was flashed for 20 ms. As quickly as possible, the subject made a horizontal saccade to the location where G had flashed. A triangle was flashed for 10 ms near the time of saccade onset. The triangle was randomly upright or upside-down, and the top or bottom vertex was offset from the horizontal center of the triangle. The task of the subject was to judge whether the top or bottom vertex was shifted to the left or right of the horizontal center of the rectangle. Under the “bar” condition, a vertical bar was flashed for 10 ms instead of the triangle. The location of the bar was randomly selected from three possible locations, indicated by B_L , B_R and B_C in Figure 6. The task for the “bar” condition was to point to the apparent location of the bar using a cursor. To compare the results of the “triangle” and “bar” condition, we calculated the distortion of the triangle under the “triangle” condition and the predicted distortion from mislocalization of the vertical bars (bottom left of Fig. 6). Distortion of the triangle in the “triangle” condition was defined as a proportion of the shift of the top or bottom vertex of the subjectively regular triangle (defined by 50% point of the psychometric function) from the horizontal center in proportion to the width of the triangle. The predicted distortion was defined as a shift of B_C location from the center of B_L and B_R in proportion to the distance between B_L and B_R . The right panel of Figure 6 shows the results for four subjects. Solid lines with filled squares show the observed distortion in the “triangle” condition, and dashed lines with open diamonds show the distortion

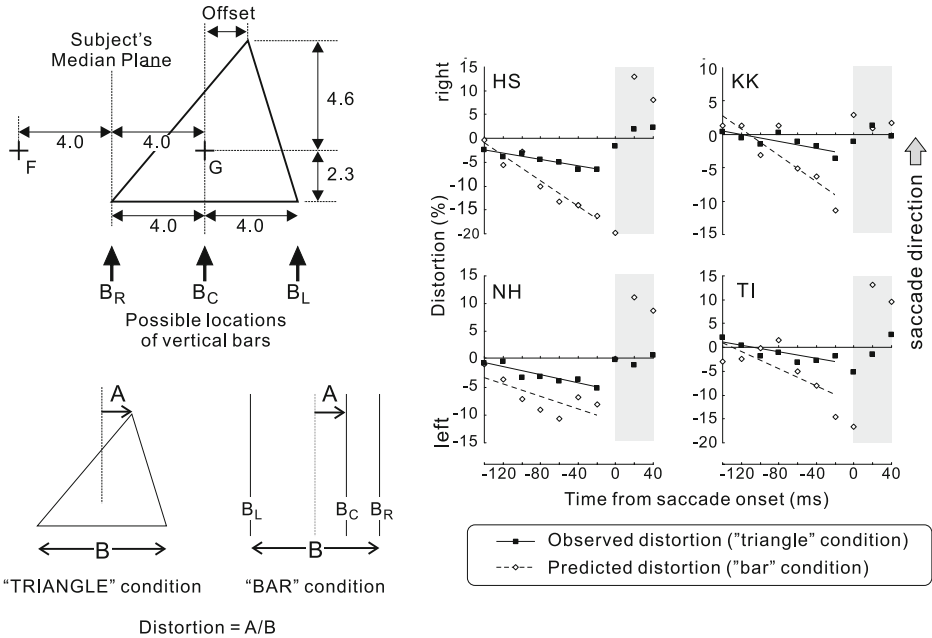


FIG. 6. Effect of saccadic compression on the perception of triangle shape. Top left: Spatial configuration of the stimuli. Bottom left: Definition of distortion. Dashed vertical lines indicates horizontal center of the stimuli. Right: The results from four subjects. Shaded areas indicate that stimulus presentation and eye movement overlapped. These data should be unreliable because retinal image of the triangle was smeared in these trials

predicted from the “bar” condition. In the presaccadic period, both the observed and predicted distortion occurred in the direction opposite to the saccade and increased as the stimulus onset time relative to saccade onset became closer. The amount of the observed distortion was constantly smaller than that of the predicted distortion. These results suggest that the shape perception of a single object was less affected by saccadic compression compared to localization of vertical bars. In this sense, shape perception is protected from saccadic compression. However, this protection is not sufficient to eliminate all distortions of object shape.

3.4 How does Saccadic Compression Distort Shape Perception?

We have reviewed recent studies of saccadic compression and its effect on shape perception. These studies indicate that some figures are hardly affected by saccadic compression (simple geographic object and proximity-grouped objects) while others are affected (Kanizsa figure and Glass pattern). Our tentative expla-

nation for these findings is based on the following data and assumptions. Firstly, saccadic compression probably originates in transient changes of neural responses in the parietal areas (Krekelberg et al. 2003, for MT/MST neurons) and propagates to early visual processing areas through feedback connections (Deco and Lee 2004; Juan and Walsh 2003). Secondly, recognition of Kanizsa figures, Glass patterns and natural objects are processed in recurrent loop between early and higher visual areas (Grill-Spector et al. 2001; Kourtzi and Kanwisher 2001; Larsson et al. 1999; Mendola et al. 1999; Murray et al. 2002) and are somehow time-consuming (Brandeis and Lehmann 1989; Guttman and Kellman 2004; Murray et al. 2002; Ringach and Shapley 1996). Finally, proximity-based perceptual grouping is rapidly processed in early visual areas (Han et al. 1999, 2001). From these assumptions, we speculate that neural representations of single objects and proximity-grouped objects will be built up so quickly that these representations are hardly affected by feedback input from parietal areas where saccadic compression is generated. Compared to these, Kanizsa figures, Glass patterns and natural objects will be more strongly affected by feedback inputs from parietal areas because it takes a longer time to recognize these patterns and objects.

There may be other possible explanations for differences in the strength of compression effect between figures. For example, Sogo and Osaka (2005) pointed out that differences between representations of real and illusory contour in V1 and V2 (Ramsden et al. 2001) may cause stronger compression of a Kanizsa rectangle compared to that of a real rectangle. However, we consider it difficult to explain the effect of saccadic compression on shape perception without assuming that an interaction with the dorsal “where” pathway could have an effect on the ventral “what” pathway.

4 Conclusion

In this chapter, we showed new evidence supporting the interaction between dorsal and ventral pathways by showing that saccadic compression affects the shape perception process in the ventral pathway. The functional significance of such interaction is not clear at present. We speculate that this interaction may support building and maintaining representations of object shape under dynamic change of retinal images due to body actions, although a possible model showing how dorsal-ventral interaction achieves stable object representation could be advanced in the future.

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