PERGAMON

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Vision Research 43 (2003) 1667–1674

Vision Research

www.elsevier.com/locate/visres

Spatial localization precedes temporal determination in visual perception

Junghyun Park *, Madeleine Schlag-Rey, John Schlag

Department of Neurobiology, UCLA School of Medicine (CHS), Los Angeles, CA 90095-1763, USA

Received 20 June 2002; received in revised form 6 February 2003

Abstract

The temporal order of two spots of light successively appearing in the dark, just before a saccade, influences their perceived spatial relation. Both spots are mislocalized in the saccade direction—the second more so than the first—because mislocalization grows as time elapses from stimulus to saccade onset. On the other hand, the perceived order of the two spots may be altered if the second spot is at the focus of spatial attention. How would these illusory perceptions of space and time interact when they are brought to play together? Could they be independent or could one perception depend on the other? Here we show that perceived location of stimuli is not affected by illusory temporal order, whereas perceived temporal order is affected by misperceived location. The results suggest that the brain processes spatial location of visual stimuli before processing their temporal order.

Keywords: Saccadic eye movement; Spatial localization; Attention; Temporal order

1. Introduction

When attention is focused in a region of space, visual processing of an object in that region could be accelerated so that it reaches perceptual awareness prior to other objects in unattended regions (Posner, Nissen, & Ogden, 1978; Sternberg & Knoll, 1973; Titchener, 1908). Compelling evidence for this 'prior entry' effect comes from studies showing an illusory judgment of the temporal order of two successive dots (Shore, Spence, & Klein, 2001; Stelmach & Herdman, 1991; Stelmach, Herdman, & McNeil, 1994) and an illusion of motion from a line (Hikosaka, Miyauchi, & Shimojo, 1993a, 1993b) caused by directed attention. Furthermore, the temporal order among stimuli successively presented at the same location has been shown to be affected by the attention (Reeves & Sperling, 1986).

Often, a shift of attention is followed by a rapid shift of gaze, a saccadic eye movement, to place the site of interest on the fovea (Posner, 1980). Because saccades have a relatively long latency ($\geqslant 150$ ms), it is conceivable that the visual processing at the saccade goal could be accelerated even before the eyes move. This is supported by several observations: superior letter detection (Hoffman & Subramaniam, 1995) and more accurate letter identification (Kowler, Anderson, Dosher, & Blaser, 1995) at the location of a saccade target shortly before the saccade, and strong illusory line-motion propagating from the saccade target location immediately after the saccade (Park, Lee, & Lee, 2001).

Before saccades, visual perception undergoes another kind of modulation: the apparent position of an object briefly flashed just before a saccade in the dark tends to be shifted in the direction of the saccade even though both the eyes and the object are still (e.g., Bockisch & Miller, 1999; Boucher, Groh, & Hughes, 2001; Dassonville, Schlag, & Schlag-Rey, 1992; Honda, 1989, 1991; Jordan & Hershberger, 1994; Matin, 1972; Matin & Pearce, 1965; Schlag & Schlag-Rey, 1995). In the presence of visual reference near the time of the saccade, mislocalization toward the saccade goal has been reported (Lappe, Awarter, & Krekelberg, 2000; Ross, Morrone, & Burr, 1997). The amount of the localization error is tightly related to the time of stimulus presentation relative to saccade onset. The error begins at least 100 ms before a saccade and increases until its onset. Thus, if a pair of stimuli is flashed in succession just before a saccade, the second stimulus would be more

---

* Corresponding author. Tel.: +1-310-825-9852; fax: +1-310-825-2224.

E-mail address: jhpark@ucla.edu (J. Park).

0042-6989/03/$ - see front matter © 2003 Elsevier Science Ltd. All rights reserved.
doi:10.1016/S0042-6989(03)00217-7

mislocalized than the first (Cai, Pouget, Schlag-Rey, & Schlag, 1997; Morrone, Ross, & Burr, 1997) although an allocentric information may interfere with the separation of relative position to a certain degree (Sogo & Osaka, 2001, 2002).

In the phenomenon of saccadic mislocalization, localization in space depends on localization in time (i.e., stimulus timing relative to saccade onset). But the fact that our perception of the timing of visual events can be altered, for instance, in the case of 'prior entry', raises a question: *does saccadic mislocalization depend on the physical timing of stimuli or on their perceived timing*? Reciprocally, in the phenomenon of illusory temporal order, localization in time depends on localization in space (i.e., stimulus location relative to focus of attention). But the fact that our perception of the location of visual stimuli can be altered, for instance, in the case of saccadic mislocalization, raises another question: *does the illusion of temporal order depend on the physical location of stimuli or on their perceived location*? Stated differently, does focused attention facilitate the perception of a stimulus according to its physical location or to its perceived location?

To answer these questions, we devised an experimental situation promoting illusory perceptions of both the temporal order and the location of stimuli, and we investigated the interaction between these perceptions. We report here that the amount of localization error depends on the physical temporal order of stimuli, not on their perceived order, while the illusion of temporal order depends on the perceived location of stimuli, not on their physical location.

2. Methods

2.1. Stimulus

All visual stimuli were 0.1° diameter blue–green spots generated on an oscilloscope (Tektronix TAS 220) except for the fixation point that was a small yellow light-emitting diode (LED) (0.2° diameter, 2.90 cd/m^2). Stimulus intensity was reduced to 0.98 cd/m^2 with a neutral density filter to decrease visual persistence. The room was completely dark except for the visual stimuli. Viewing was binocular at a distance of 57 cm.

2.2. Eye movement recording

With the head immobilized by a bite plate, movements of the dominant eye were recorded with a SMI EyeLink gaze tracker (SR Research Ltd., Canada) at 250 Hz. This system had a data transit delay of 10 ms that was considered in on-line calculation of saccade latency.

2.3. Procedure

Each trial started with the appearance of a fixation point 10° left of straight ahead (Fig. 1A). In saccade trials of Experiment 1, after 800–1300 ms of initial fixation, a saccade target appeared straight ahead for 50 ms. Subjects were instructed to make a saccade toward this target as soon as the fixation point was extinguished (300–500 ms after the target presentation). This delay was introduced to prevent possible visual interactions between the saccade target and the subsequent stimuli. After the extinction of the fixation point, two successive 3-ms dots were flashed 50 ms apart. These time parameters were chosen, after extensive pilot experiments, as a compromise between two opposite demands: one for inducing an illusory temporal order and the other for differentiating the localization error of each dot. The location of the bottom dot was always the same as the saccade target; the top dot was 3° above it, at one of six possible horizontal locations (Fig. 1B). The temporal order of the two dots and the horizontal location of the top dot were pseudo-randomized between trials. Subjects were requested to judge the temporal order of the two dots as well as their relative location and to give their responses, after the saccade, by pressing the appropriate combination of UP/DOWN and LEFT/RIGHT keys. To maximize the probability of presenting the two dots as late as possible before the saccade, the timing of the dots was adjusted trial by trial by averaging on-line the saccade latencies of the last four trials. In addition to saccade trials, subjects were given fixation trials and no-cue trials. In fixation trials, subjects were instructed to maintain their gaze on the fixation point throughout trials despite the presentation of a light spot, identical to the saccade target in saccade trials. The timing of the test spots was randomized within a range equivalent to that of saccade trials. In no-cue trials, the locations and the timing of all visual stimuli were the same as in a fixation trial but no light spot, that could direct attention to the location of the bottom dot, was presented. Saccade, fixation, and no-cue trials were run in separate blocks.

In Experiment 2, the two dots were separated by 3° horizontally (see Fig. 5A) and 20 ms temporally. The right dot was at the same location as the saccade target (or its equivalent in fixation trial). The reason to reduce the temporal gap to 20 ms was to minimize the difference between the localization errors for each dot while increasing the sensitivity of the temporal order test. Subjects reported only the temporal order of two dots that was varied randomly. Except for these changes, other procedures were the same as for Experiment 1. In additional sessions of Experiment 2, the perceived locations of the two dots were measured from all the subjects in two ways: ocular targeting and perceptual judgment test. In the ocular targeting test, subjects were instructed

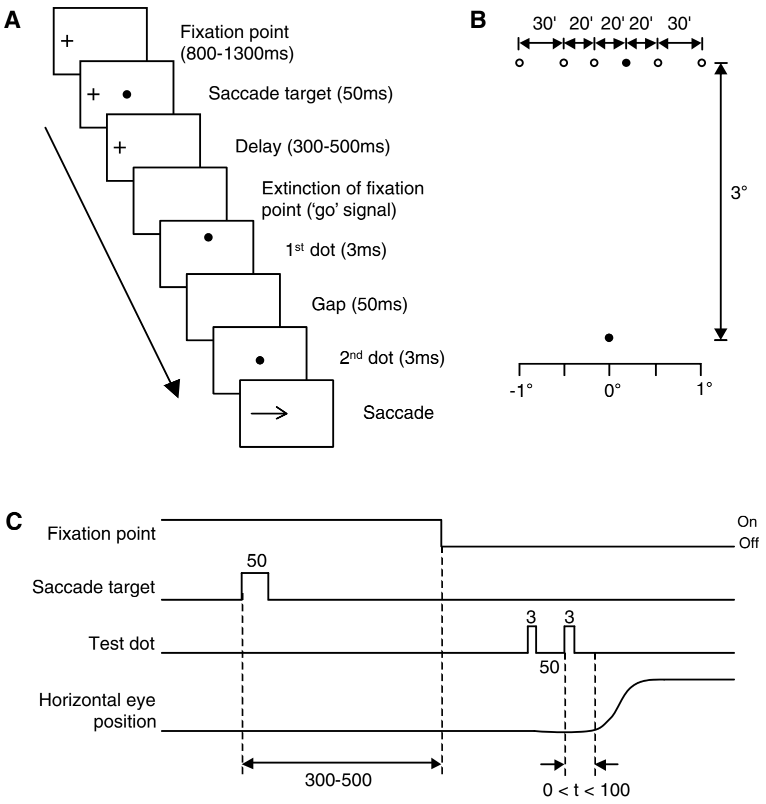

Fig. 1. Schematic representation of the events in Experiment 1. A. Stimulus sequence. Fixation point (an LED, shown as a cross) was 10° left of straight ahead. Rightward arrow represents a 10° rightward saccade. After completing the saccade, subjects reported the perceived temporal order and the perceived relative position of the dots by pressing appropriate keys. B. Location of test dots drawn to scale. C. Temporal structure of a trial.

to direct their eyes, as accurately as possible, to the location of one of the vanished test dots after the main saccade to the target in saccade trials, and directly from the location of the fixation point in fixation trials. Each dot was tested in a separate block. In the perceptual judgment test, a visual reference composed of three dots separated by 3° horizontally with the middle dot at the saccade target position was presented 500 ms after the saccade offset. Subjects were asked to indicate which pair of the three dots—left or right—was at the same location as the two test dots by pressing a key (see Fig. 5C).

2.4. Data analysis

For saccade trials of Experiments 1 and 2, only the trials that fulfilled the following 2 conditions were retained for analysis: the second dot had to be presented within 0–100 ms before saccade onset (not sooner, not later) and the target had to be reached in a single saccade. About 50% of saccade trials passed this criterion.

2.5. Subjects

The same three subjects (2 naïve) participated in each experiment. All had normal or corrected to normal vision and were 25–35 years old. Before data collection, subjects were trained on the saccade task for several days.

3. Results

Experiment 1 tested whether saccadic mislocalization depends on the physical or the perceived temporal order of stimuli. In principle, as we combined a temporal order test with a two-dot vernier test, we expected two kinds of illusions to occur. First, the bottom dot that is presented at the location of the saccade target would be perceived as first. Second, the second of two successive dots would appear more displaced than the first in the direction of the saccade.

Fig. 2 shows the percentages of correct temporal order response in saccade, fixation, and no-cue conditions. In all conditions, the judgment on the temporal order of two dots was almost always correct when they were presented in 'bottom-first' order. In contrast, when stimuli were presented in 'top-first' order, temporal judgments considerably varied between conditions. Temporal judgments on stimuli in 'top-first' order were correct in 11.7% of saccade trials and in 27.3% of fixation trials. A similar pattern of results has been reported

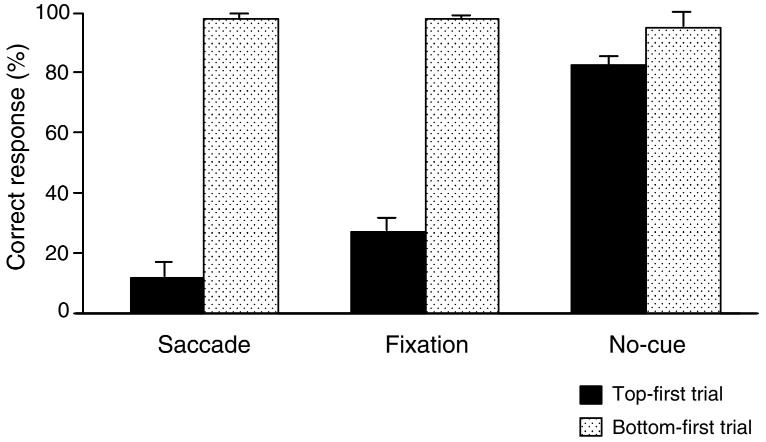

Fig. 2. The temporal order judgment in three conditions of Experiment 1. The facilitatory effects of attention, reflected by the decreased correct response to 'top-first' order stimuli, are strongest in the saccade condition (saccades to the bottom dot location), but these effects almost disappeared in the no-cue condition where attention was not explicitly directed. Data from all three subjects were averaged. Error bars indicate 1 s.e.m.

in a letter identification task using a central cue to direct attention endogenously (Kowler et al., 1995). However, the chance of a correct judgment was considerably increased in the no-cue condition (82.4%). These results suggest that focal attention was deployed at the location of saccade target.

For those trials where the bottom dot was perceived as first, we analyzed the subjects' perception of relative location of the two dots. If the *perceived* order were relevant to the peri-saccadic mislocalization, the top dot (which is perceived as second) should appear shifted more than the bottom dot in the direction of the saccade, regardless of the physical order. However, this was not the case. The upper row of Fig. 3 shows vernier curves for two dots presented shortly before a 10° rightward saccade. The curves were systematically shifted as a function of the *physical* presentation order, and the direction of the shift was such that the second dot appeared to be displaced further in the direction of the saccade than the first one. The point of subjective equality (PSE) was calculated as the horizontal offset corresponding to the 50% point of each vernier curve. The PSE values of three subjects for 'bottom-first' and 'top-first' saccade trials were −5.2 and 7.7 (SK), −7.5 and 13.6 (JP), and −7.1 and 6.9 (YK) minute of arc, respectively. A paired *t*-test showed that the PSE values for 'bottom-first' and 'top-first' trials were significantly different ($t = 6.132$, $p < 0.03$). However, in fixation trials (Fig. 3, lower row), the PES value did not change in relation to the actual order of stimuli ($t = -0.401$, $p > 0.72$). Two of the subjects were tested further in a complementary situation: the fixation point was to the right and 10° leftward saccades were made. Again, the direction of the vernier curve shift was related to the

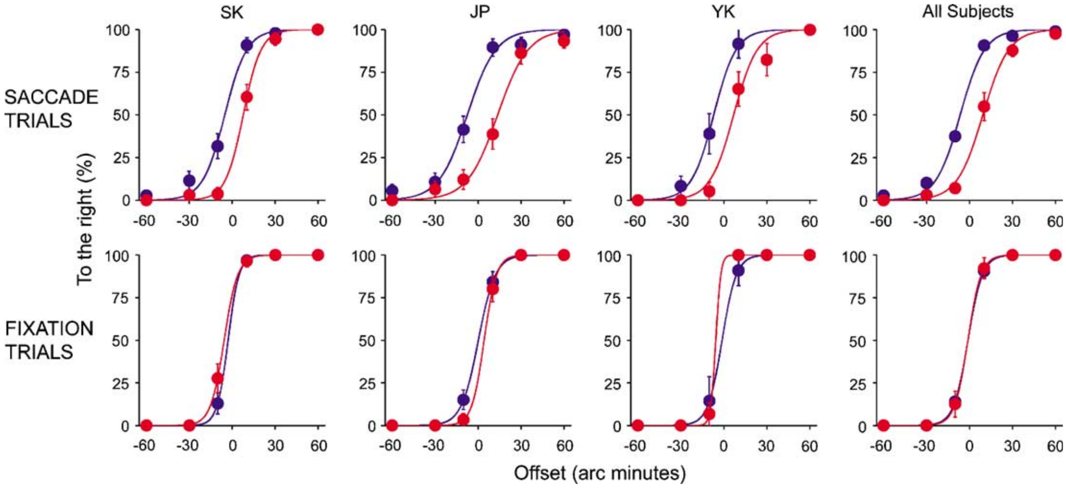

Fig. 3. Vernier judgment as a function of horizontal offset of the top dot from the bottom dot for all three subjects. The ordinate represents the percentage of seeing the top dot to the right of the bottom dot. All curves are based on the trials in which perceived order was 'bottom-first'. Note that, in saccade trials (upper row), vernier curves are systematically shifted according to the order of dot presentation (blue: 'bottom-first', red: 'top-first'), but they are not shifted in fixation trials (lower row). Error bars indicate 1 s.e.m.

physical presentation order. In all cases, the direction of the shift indicates that saccadic mislocalization depends on the *physical* order of stimuli.

The amount of vernier curve shift obtained in Experiment 1 is smaller than what we can expect from the literature where absolute—not relative—localization was tested. Could this small vernier shift be explained by a saccadic compression (i.e., mislocalization toward the saccade target)? This possibility does not seem to be plausible for the following reason. That is, if the dots were mislocalized toward the saccade target position, the change of the temporal order would result in a change of the slope of vernier curve without affecting the PSE value. However, the result shows a shift of the PSE instead of a change of its slope, as expected if both dots were mislocalized in the direction of the saccade. The relative position of temporally adjacent stimuli may be determined not only by egocentric localization of each stimulus, but also by allocentric information (Dassonville, Schlag, & Schlag-Rey, 1995; Sogo & Osaka, 2001, 2002). Thus it would be reasonable to interpret the small amount of vernier shift obtained in Experiment 1 as an influence of allocentric information that resists relative mislocalization. For the purpose of the current study, what is important is the direction of this shift (i.e., would it shift according to real or perceived temporal order?), not its size.

The result of Experiment 1 showed that the localization of the stimulus does not depend on its perceived timing. Two hypotheses can be postulated to explain this result. One is that the brain processes the location and the timing of visual stimuli *in parallel* and the mechanism for timing perception can be selectively affected by attention. This 'parallel-processing' hypothesis predicts that the illusory temporal order would depend on the physical location of stimuli. The 'serial-processing' hypothesis assumes that visual processing is modulated by attention *after* localization is completed. Therefore, this hypothesis predicts that the illusory temporal order would depend on the perceived (not physical) location of stimuli.

Experiment 2 was designed to differentiate these hypotheses. Two dots were horizontally aligned 3° apart, the right dot being at the center of the screen (see Fig. 5A). Fig. 4 shows the judgments of temporal order made by three subjects in saccade trials compared to fixation trials. In fixation trials, the right dot, which was presented at the center of the screen (focus of attention), was almost always perceived as preceding the other dot whatever the real order. In contrast, when these dots shortly preceded a 10° rightward saccade, the perceived temporal order was reversed: now it was the left dot that appeared to come first in most trials. What has caused this dramatic reversal of temporal order? Because the location of focal attention, which is centered on the target, in saccade trials should be the same as that in fixation trials, it would be reasonable to attribute this reversal of temporal order to the changed spatial relation of the two dots with respect to the focus of attention. To test this, the perceived locations of the two dots in Experiment 2 were measured from all subjects with ocular targeting and perceptual judgment test.

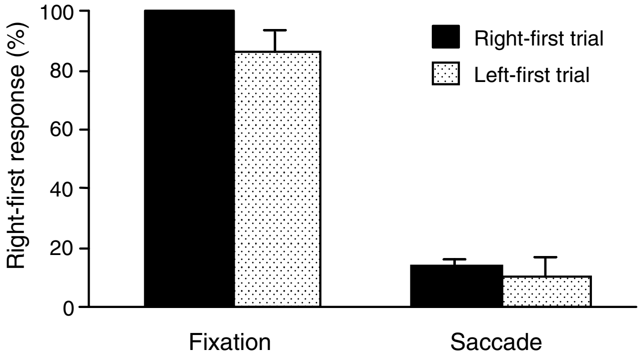

Fig. 4. The temporal order judgment in the fixation and the saccade conditions of Experiment 2. A strong illusion of temporal order was found in both conditions but in the opposite directions. Data from all three subjects were averaged. Error bars indicate 1 s.e.m.

Fig. 5A and B illustrate the results of oculomotor localization from three subjects in two ways: the averaged final eye position attained after the saccade(s) to each of the dots (Fig. 5A) and the mean amplitude of the second saccade (Fig. 5B). The targeting errors expressed in both ways clearly show that the perceived locations of the two dots were displaced to the right (i.e., in the saccade direction) by a similar amount. As expected, mislocalization toward the saccade target position (i.e., saccadic compression) did not occur. Although targeting errors have been shown not to be different from perceptual errors (Bockisch & Miller, 1999; Dassonville, 1995; Dassonville et al., 1992; Honda, 1985; Schlag & Schlag-Rey, 1995), it was recently reported that pointing errors are different from verbal reports in the phenomenon of saccadic compression (Burr, Morrone, & Ross, 2001). To address the possibility of the dissociation between the oculomotor and the perceptual localizations in this study, we collected data on perceptual localization from the same subjects. In this perceptual judgment test, subjects reported the perceived location of the dots with respect to a visual reference presented 500 ms after the saccade (see Fig. 5C). The location of the three dots serving as a reference was chosen to differentiate three possibilities: (1) if there is no mislocalization at all, regardless of the type of the trial (i.e., fixation or saccade), the response 'left-pair' is expected, (2) if the dots are mislocalized toward the saccade target position, the response 'left-pair' is also most likely in saccade trials, (3) if the dots are mislocalized in the direction of the saccade as indicated by targeting errors, the response 'right-pair' is expected in many of saccade trials. Fig. 5D shows that all subjects *perceptually* mislocalized the two dots in the direction of the saccade in agreement with

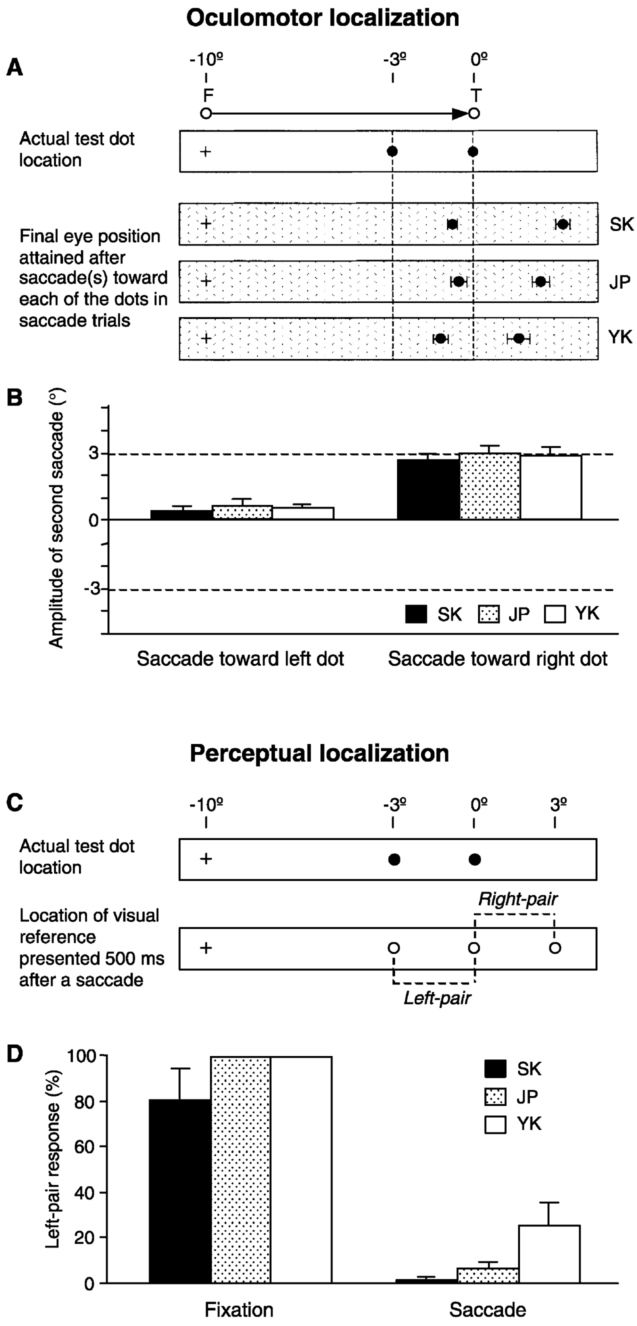

Fig. 5. Perceived location of the two dots in Experiment 2 measured with ocular targeting (A, B) and perceptual judgment test (C, D). A. Top panel: physical location of the two dots. Lower three panels: averaged final horizontal eye position of each subject in saccade trials. F, fixation point; T, saccade target. B. Mean amplitude of second saccade made to each of the two dots. C. Upper panel: physical location of the two dots. Lower panel: location of the three dots composing the visual reference used in perceptual localization experiment. Subjects reported either 'left-pair' or 'right-pair' in a 2AFC. D. The percentage of 'right-pair' response in fixation and saccade trials. Note that, for all subjects, oculomotor localization and perceptual localization agree that both dots, whether at the saccade goal or not, are mislocalized in the direction of the saccade. Error bars indicate 1 s.e.m.

oculomotor localization. Note that the two dots were displaced to the right so that the dot that now appeared to be closest to the saccade target was the left one. That is, the spatial relationship between the two dots and the focus of attention was reversed in saccade trials.

The results of Experiment 2 strongly suggest that the perception of the timing of stimuli depends on their perceived location, rejecting the 'parallel-processing' hypothesis. As predicted by the 'serial-processing' hypothesis, attention accelerates the perception of a stimulus when its perceived location—as distinct from its physical location—is within the focus of attention.

4. Discussion

How does the brain process spatial and temporal properties of visual stimuli? By presenting a pair of stimuli in rapid succession in the dark during a presaccadic period, we could evoke illusory perceptions of both relative timing and relative location of stimuli at the same time. In Experiment 1, we found that the perception of relative location of stimuli is not affected by their illusory temporal order. In Experiment 2, on the other hand, we found that the perception of temporal order of stimuli is strongly affected by their illusory location. These two findings combined lead to the conclusion that the brain analyzes spatial location before the temporal order of visual stimuli (Fig. 6).

To account for saccadic mislocalization, it has been postulated that the brain integrates the retinal signal of the object with an internal eye position (or eye displacement) signal (EPS) to calculate the position of the object in space (MacKay, 1973; Matin, 1972; von Helmholtz, 1866; von Holst & Mittelstaedt, 1950), and that there is a temporal mismatch between a visual signal and its contemporary EPS at the summing junction where these two signals are combined, due to the long afferent delay of the visual pathway (Brenner, Smeets, & van den Berg, 2001; Hazelhoff & Wiersma, 1924; Schlag & Schlag-Rey, 1995).

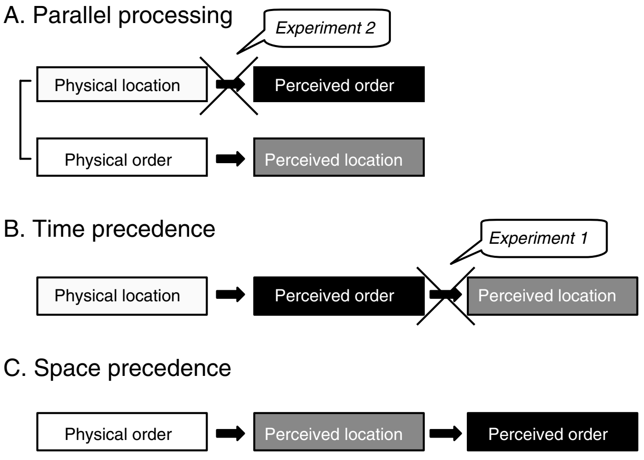

Fig. 6. Three hypotheses for space-time interaction. The result of Experiment 1 rejected 'time precedence' hypothesis and the result of Experiment 2 rejected 'parallel-processing' hypothesis.

The present result showing that the localization mechanism is not affected by perceived (illusory) order suggests that the reversal of temporal order does not take place before visual signals reach this summing junction.

We showed that an illusion of temporal order occurs at the saccadic goal before the eyes start to move. Together with previous reports of enhanced accuracy in the letter detection (Hoffman & Subramaniam, 1995) and discrimination tasks (Kowler et al., 1995), the prior entry effect observed here clearly demonstrates that a saccadic eye movement can shift attention to the target location prior to the actual execution of a saccade, making perception faster and more accurate.

Where does this acceleration of visual processing take place? How early is it? Showing that the illusory line-motion, which is another good example of prior entry effect of attention, can be obtained in dichoptic condition, Hikosaka and colleagues hypothesized that attention acts between visual cortical areas V1 and MT (Hikosaka et al., 1993a, 1996). Although the present results do not provide direct evidence about the place of attentional modulation, they do add a constraint: this modulation should be *after the summing junction* where the retinal input is combined with the EPS. Neuronal activities correlated with eye movement or eye position have been reported throughout the visual pathway (from LGN to higher visual cortical areas) (for example, Andersen, Essick, & Siegel, 1985; Lee & Malpeli, 1998; Park & Lee, 2000; Toyama, Komatsu, & Shibuki, 1984; Weyand & Malpeli, 1993). However, it is not known which of those are utilized for visual localization.

Recently, it was suggested that the recurrent or feedback processing in the visual system is critical for visual awareness and attention (Lamme & Roelfsema, 2000; Pascular-Leone & Walsh, 2001; Super, Spekreijse, & Lamme, 2001). Thus, it is possible that much of visual analysis could be accomplished through the feedforward sweep before attention exerts its effects through the feedback pathway. This seems to be consistent with the present psychophysical results showing that the localization of visual stimulus is completed before its processing is accelerated by attention.

Acknowledgement

This research was supported by USPHS grant EY05879.

References

Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science, 230*, 456–458.

Bockisch, C., & Miller, J. M. (1999). Different motor systems use similar damped extraretinal eye position information. *Vision Research, 39*, 1025–1038.

Brenner, E., Smeets, J. B. J., & van den Berg, A. V. (2001). Smooth eye movements and spatial localisation. *Vision Research, 41*, 2253–2259.

Boucher, L., Groh, J. M., & Hughes, H. C. (2001). Afferent delays and the mislocalization of perisaccadic stimuli. *Vision Research, 41*, 2631–2644.

Burr, D. C., Morrone, M. C., & Ross, J. (2001). Separate visual representations for perception and action revealed by saccadic eye movements. *Current Biology, 11*, 798–802.

Cai, R. H., Pouget, A., Schlag-Rey, M., & Schlag, J. (1997). Perceived geometrical relationships affected by eye-movement signals. *Nature, 386*, 601–604.

Dassonville, P. (1995). Haptic localization and the internal representation of the hand in space. *Experimental Brain Research, 106*, 434–448.

Dassonville, P., Schlag, J., & Schlag-Rey, M. (1992). Oculomotor localization relies on a damped representation of saccadic eye displacement in human and nonhuman primates. *Visual Neuroscience, 9*, 261–269.

Dassonville, P., Schlag, J., & Schlag-Rey, M. (1995). The use of egocentric and exocentric location cues in saccadic programming. *Vision Research, 35*, 2191–2199.

Hazelhoff, F., & Wiersma, H. (1924). Die Wahrenhmungszeit. *Zeitschrift fur Psychologie, 96*, 171–188.

Hikosaka, O., Miyauchi, S., & Shimojo, S. (1993a). Focal visual attention produces illusory temporal order and motion sensation. *Vision Research, 33*, 1219–1240.

Hikosaka, O., Miyauchi, S., & Shimojo, S. (1993b). Voluntary and stimulus-induced attention detected as motion sensation. *Perception, 22*, 517–526.

Hikosaka, O., Miyauchi, S., & Shimojo, S. (1996). Orienting of spatial attention—its reflexive, compensatory, and voluntary mechanisms. *Cognitive Brain Research, 5*, 1–9.

Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception and Psychophysics, 57*, 787–795.

Honda, H. (1985). Spatial localization in saccade and pursuit eye movement conditions: A comparison of perceptual and motor measures. *Perception and Psychophysics, 38*, 41–46.

Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception and Psychophysics, 45*, 162–174.

Honda, H. (1991). The time courses of visual mislocalization and of extraretinal eye position signals at the time of vertical saccade. *Vision Research, 31*, 1915–1921.

Jordan, J. S., & Hershberger, W. A. (1994). Timing the shift in retinal local signs that accompanies a saccadic eye movement. *Perception and Psychophysics, 55*, 657–666.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*, 1897–1916.

Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neuroscience, 23*, 571–579.

Lappe, M., Awarter, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. *Nature, 403*, 892–895.

Lee, D., & Malpeli, J. G. (1998). Effects of saccades on the activity of neurons in the cat lateral geniculate nucleus. *Journal of Neurophysiology, 79*, 922–936.

MacKay, D. M. (1973). Central processing of visual information. In R. Jung (Ed.), *Handbook of sensory physiology VII* (pp. 307–331). Berlin: Springer-Verlag.

Matin, L. (1972). Visual psychophysics. In D. Jameson, & L. M. Hurvich (Eds.), *Handbook of sensory physiology VII* (pp. 311–380). Berlin: Springer-Verlag.

Matin, L., & Pearce, D. G. (1965). Visual perception of direction for stimuli during voluntary saccadic eye movements. *Science, 148*, 1485–1488.

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*, 7941–7953.

Park, J., & Lee, C. (2000). Neural discharge coupled to saccade offset in the cat visual cortex. *NeuroReport, 11*, 1661–1664.

Park, J., Lee, J., & Lee, C. (2001). Non-veridical motion perception immediately after saccades. *Vision Research, 41*, 3751–3761.

Pascular-Leone, A., & Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science, 292*, 510–512.

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32*, 3–25.

Posner, M. I., Nissen, N. J., & Ogden, W. C. (1978). Attended and unattended processing models: The role of set for spatial location. In H. L. Picks, & I. J. Saltzman (Eds.), *Modes of perceiving and processing information* (pp. 137–157). Hillsdale: Lawrence Erlbaum.

Reeves, A., & Sperling, G. (1986). Attention gating in short-term memory. *Psychological Review, 93*, 180–206.

Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature, 386*, 598–601.

Schlag, J., & Schlag-Rey, M. (1995). Illusory localization of stimuli flashed in the dark before saccades. *Vision Research, 35*, 2347–2357.

Shore, D. I., Spence, C., & Klein, R. M. (2001). Visual prior entry. *Psychological Science, 12*, 205–212.

Sogo, H., & Osaka, N. (2001). Perception of relation of stimuli locations successively flashed before saccade. *Vision Research, 41*, 935–942.

Sogo, H., & Osaka, N. (2002). Effects of inter-stimulus interval on perceived locations of successively flashed perisaccadic stimuli. *Vision Research, 42*, 899–908.

Stelmach, L. B., & Herdman, C. M. (1991). Directed attention and perception of temporal order. *Journal of Experimental Psychology: Human Perception and Performance, 17*, 539–550.

Stelmach, L. B., Herdman, C. M., & McNeil, K. R. (1994). Attentional modulation of visual processes in motion perception. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 108–121.

Sternberg, S., & Knoll, R. L. (1973). The perception of temporal order: Fundamental issues and a general model. In S. Kornblum (Ed.), *Attention and performance IV* (pp. 629–685). New York: Academic Press.

Super, H., Spekreijse, H., & Lamme, V. A. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience, 4*, 304–310.

Titchener, E. B. (1908). *Lectures on the elementary psychology of feeling and attention*. New York: MacMillan.

Toyama, K., Komatsu, Y., & Shibuki, K. (1984). Integration of retinal and motor signals of eye movements in striate cortex cells of the alert cat. *Journal of Neurophysiology, 51*, 649–665.

von Helmholtz, H. (1866). *Handbuch der Physiologischen Optik*. Leipzig: Voss, English translation, from ed. 3, 1925. In J. P. C. Southall (Ed.), *A treatise on physiological optics: Vol. 3* (pp. 242–246). New York: Dover.

von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. *Naturwissenschaften, 37*, 464–476.

Weyand, T. G., & Malpeli, J. G. (1993). Responses of neurons in primary visual cortex are modulated by eye position. *Journal of Neurophysiology, 69*, 2258–2260.