Psychological Research (2011) 75:272–278
DOI 10.1007/s00426-010-0305-4

ORIGINAL ARTICLE

Bottom-up effects modulate saccadic latencies in well-known eye movement paradigm

**Saskia van Stockum · Michael R. MacAskill ·
Tim J. Anderson**

Received: 1 April 2010 / Accepted: 11 August 2010 / Published online: 21 August 2010

Abstract A well-known eye movement paradigm combines saccades (fast eye movements) with a perceptual discrimination task. At a variable time after the onset of a central arrow cue indicating the target direction [the stimulus onset asynchrony (SOA)], discrimination symbols appear briefly at saccade target and non-target locations. A previous study revealed an unexpected effect of SOA on saccadic latencies: latencies were longer in trials with longer SOAs. It was suggested that this effect reflects a top-down process as observers may wait for the discrimination symbol to appear before executing saccades. However, symbol onsets may also modulate saccade latencies from the bottom-up. To clarify the origin of the SOA effect on latencies in this paradigm, we used a simplified version of the original task plus two new symbol onset conditions for comparison. The results indicate that the modulation of saccadic latencies was not due to a top-down strategy, but to a combination of two opposing bottom-up effects: the symbol onsets at the target location shortened saccade latencies, while symbol onsets at non-target locations lengthened saccade latencies.

S. van Stockum (✉) · M. R. MacAskill · T. J. Anderson
Van der Veer Institute for Parkinson's and Brain Research,
Christchurch, New Zealand
e-mail: vanev008@student.otago.ac.nz

S. van Stockum · M. R. MacAskill · T. J. Anderson
Department of Medicine, University of Otago,
Christchurch, New Zealand

T. J. Anderson
Department of Neurology, Christchurch Hospital,
Christchurch, New Zealand

Introduction

Saccades are fast eye movements, which align the fovea with objects or locations of interest in the visual field. The selection of a target for an upcoming saccade is accompanied by a shift of the focus of visual attention to the intended location (Awh, Armstrong, & Moore, 2006; Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Rizzolatti, Riggio, Dascola, & Umilta, 1987). Such a shift of visual attention can be a reflexive response to a sudden change in the visual field, or a voluntary process driven by the intention of the observer. Shifting visual attention to a future point of fixation in the visual field increases perceptual efficiency at the saccadic target location and is thought to help maintain visual stability across saccades [for a review see (Wurtz, 2008)].

A well-known experimental paradigm, designed to investigate the time course of pre-saccadic shifts of visual attention, combines a saccadic task with a perceptual discrimination task (Deubel, 2008). The primary task in this paradigm is the execution of a saccade to a peripheral target location, cued by the appearance of a central arrow. During the preparation of the saccade (the saccadic latency), while the eyes are still focused on the central arrow cue, symbols appear briefly at the cued target location as well as at uncued non-target locations. After each saccade, participants are asked to indicate the identity of the discrimination symbol that was displayed during the trial. The timing of the onset of the discrimination symbol relative to the onset of the cue [the stimulus onset asynchrony (SOA)] affects the performance of the discrimination task. Visual attention is shifted after cue onset and before saccade initiation to the intended saccadic target location, so that perceptual discrimination performance is better on trials with longer SOAs than on trials with short SOAs. This effect of SOA on perceptual performance reflects the time-course of the pre-saccadic shift of the focus of visual attention to the cued target location. The original study using this paradigm also found, unexpectedly, a clear effect of SOA on saccadic latencies: latencies were longer in trials with longer SOAs (Deubel, 2008). Deubel suggested that a top-down process could account for the effect of SOA if observers used a strategy of waiting for the appearance of the discrimination symbol before executing their planned saccades. However, it is also possible that the symbol onsets modulate saccadic latencies from the bottom-up in this paradigm. On the one hand, a pre-saccadic visual change at the cued target location may facilitate saccade initiation (Edelman & Xu, 2009; Koelewijn, Bronkhorst, & Theeuwes, 2009). On the other hand, visual changes at un-cued locations away from the target location may act as 'remote distractors' and delay saccade initiation (Bompas & Sumner, 2009b; Buonocore & McIntosh, 2008; Edelman & Xu, 2009; Ludwig, Gilchrist, & McSorley, 2005; Walker, Deubel, Schneider, & Findlay, 1997).

The modulation of saccadic latencies was not relevant to the conclusions regarding the time course of pre-saccadic attentional shifts in the original study (Deubel, 2008). However, clarification of the origin of the SOA effect on latencies may be relevant to future users of this paradigm and provide additional insight into the time course of saccadic target selection and saccade initiation.

For the present investigation, two new experimental conditions were devised for comparison with the original version of the task. First, trials without any symbol onsets were included as catch trials. We hypothesised that if the top-down explanation is correct, and observers adopt a strategy to delay the execution of their saccades until after the appearance of the discrimination symbol, then saccade latencies should be longest in trials where no discrimination symbol appears at all. We reasoned that on these catch trials observers would be waiting (in vain) for the appearance of the discrimination symbol and delay the execution of their planned saccades beyond the duration of the longest SOA occurring in trials with symbol onsets. Second, trials with symbol onsets at the target location only (i.e. without symbol onsets at non-target locations) were included for comparison with the original condition. We hypothesised that if the top-down account were not correct, the SOA effect in this paradigm may be due either to the symbol onsets at target or to the symbol onsets at non-target locations, as these onsets may facilitate or suppress saccade initiation, respectively. In summary, we used a simplified version of the original task paradigm with only four potential target locations and measured saccade latencies and discrimination performance in three different trial types: (1) trials with symbol onsets at target and non-target locations as in the original version of the task, (2) trials with symbol onsets at the cued target location only, and (3) catch trials without any symbol onsets.

Methods

Participants

Eight healthy adults (four female) aged between 22 and 31 years were recruited and gave informed consent. All participants had normal or corrected-to-normal vision at a viewing distance of 600 mm.

Apparatus and stimuli

Eye movements were recorded using a video-based iView X Hi-Speed system (SMI, Berlin) at a sampling rate of 1,250 Hz. Stimuli were displayed on a 21 in. CRT screen with a 100 Hz refresh rate and a resolution of 800 × 600 pixels. The computer screen was positioned 600 mm in front of observers, who sat with head supported by the chin and forehead rest of the iView tracking column. Stimuli were presented on a dark-grey background (R50 G50 B50). The fixation point was a red (R255 G0 B0) square (0.6 × 0.6°), targets (1° wide × 1.5° high) were white (R0 G0 B0) and the central cue was a red (R255 G0 B0) arrow (0.6 × 0.6°). If required, each block of trials started with a calibration check and a two dimensional 13-point calibration procedure covering the display area. At the beginning and end of each recording, a sequence of reflexive saccades was recorded to provide data for post hoc assessment and adjustment of the calibration if required. Stimuli were generated using PsychoPy, an open source experimental control software package (Peirce, 2007, 2008).

Procedure

All observers performed voluntary saccades and a two-alternative-forced-choice (2AFC) discrimination task in an experimental paradigm adapted from Deubel (2008). In our version of the paradigm, the primary task was a voluntary saccade to one of four figure `8`s, cued by a central arrow. The arrow pointed to each of the four potential target locations on 25% of trials in randomised order. The secondary task was the discrimination of a symbol (`E` or `3`), which appeared briefly at the cued target location. Each trial started with observers fixating a central fixation point, which was surrounded by four figure `8`s arranged on the four corners of a square, each at 5.38° from the centre (see Fig. 1). After a variable fixation period (1,000–1,400 ms), the central fixation point changed into an arrow pointing to one of the four figure `8`s. This was the cue for observers to

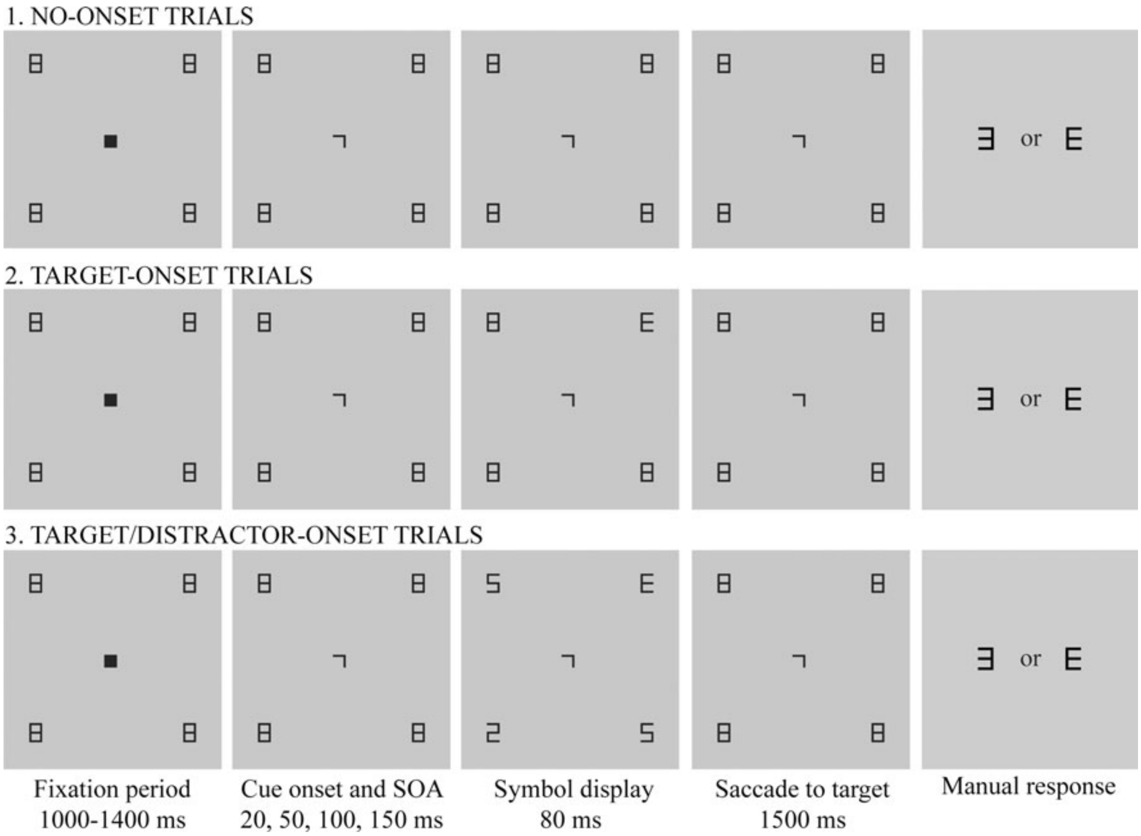

Fig. 1 *Rows* represent the three trial types and *columns* represent the five different stages of the stimulus display. The No-onset trials (*top row*) were interleaved as catch trials in the blocks of Target-onset trials (*second row*) and in the blocks of Target/distractor-onset trials (*third row*). The three trial types differed only during the *symbol display* (*third column*). *First column* Each trial started with the display of a central fixation square and four figure 8s. *Second column* After 1,000–1,400 ms the square changed into an *arrow* cue indicating the target location. *Third column* (*1*) No-onset trials: the stimulus display remains unchanged after cue onset. *2* Target-onset trials: after 20, 50, 100 or 150 ms (SOA) a discrimination symbol (E or 3) appears for 80 ms at the cued target location. *3* Target/distractor-onset trials: after 20, 50, 100 or 150 ms (SOA) a discrimination symbol (E or 3) appears for 80 ms at the cued target location, while 2s or 5s appear at the un-cued non-target locations. *Fourth column* the figure 8s re-appear for 1,500 ms while the saccade to the target is made. *Fifth column* The participant indicates with a *left* or *right* manual button press which symbol was displayed at the target location

move their eyes 'as quickly and accurately as possible' to the figure 8 indicated. Three types of trials were used. 1. *No-onset trials* all four figure 8s remained unchanged throughout the trial. 2. *Target-onset trials* the 8 at the cued target location changed into E or 3 for 80 ms while the figure 8s at un-cued non-target locations remained unchanged. 3. *Target/distractor-onset trials*: the 8 at the cued target location changed into E or 3 for 80 ms while the figure 8s at un-cued non-target locations changed into 2 or 5 (as in the original version of the paradigm). The distractor symbol was always 2 at the top right and bottom left and 5 at the top left and bottom right location. After each trial, observers were asked to indicate which symbol they had seen by responding 'E' or '3' with a right or left manual button press, respectively. Observers were explicitly told to guess if unsure and to push one of the two buttons at random when they thought no discrimination symbol had appeared. To discourage observers from making anticipatory saccades it was stressed that the saccade task was the primary task and the perceptual discrimination was the secondary task. No feedback was provided regarding the discrimination performance between trial blocks. *Target-onset trials* and *Target/distractor-onset trials* were presented in blocks. A block of trials consisted of two trials in each SOA condition (20, 50, 100, or 150) at each target location (top left, top right, bottom left or bottom right) in a random sequence. Interleaved in each block were eight *No-onset trials*, for a total of 40 trials. Each participant performed two blocks of *Target-onset trials* and two blocks of *Target/distractor-onset trials* in balanced order (a total of 160 trials).

Analysis

Latency and gain of the primary saccade (the first saccade following the appearance of the cue) were measured off-line.

Latency was calculated from the onset of the central arrow cue. Gain was defined as the ratio of the Euclidean amplitude of the saccade to the target amplitude (5.38°). The eye position trace was searched to find the first instance where the eye velocity reached 80°/s after cue onset. The beginning and end of a primary saccade were determined by searching backwards and forwards in time from this point for the nearest velocity minimum. Primary saccades with gain smaller than 30% of the target amplitude or with latencies longer than 600 ms, and directional errors (primary saccades not directed at the cued target location) were removed from the analysis (10.5% of the total number of trials). Latency frequencies were calculated separately for each observer and for each trial type (No onset, Target onset and Target/distractor onset). Trials where the eyes reached the target location before the offset of the discrimination symbol were removed from the analysis of the discrimination performance (2% of all saccades). The proportion of correct discriminations was calculated from the total number of remaining saccades in Target-onset and Target/distractor-onset trials for each observer in each SOA condition.

Results

Latencies

Repeated measures ANOVA with trial type (Target-onset and Target/distractor-onset) and SOA (20, 50, 100, and 150) as factors showed a significant effect of SOA on saccade latency; longer SOAs were associated with longer latencies, $F(3, 21) = 20.75$, $p < 0.001$. There was no interaction between trial type and SOA. When the latencies obtained in the No-onset trials were included as another level of SOA in the repeated measures ANOVA with trial block (Target-onset and Target/distractor-onset) and SOA (No onset, 20, 50, 100, and 150) as factors, there was a significant interaction between trial block and SOA, $F(4, 28) = 3.49$, $p = 0.02$ (see Fig. 2). This interaction effect was due to the mean latency in No-onset trials (where no symbols appear at all) being longer than the mean latency in the trials with the longest SOA (150 ms) only in the blocks of Target-onset trials, and not in the blocks of Target/distractor-onset trials. Planned comparisons showed that in the blocks of Target/distractor-onset trials the mean latency in the No-onset trials was actually shorter than the mean latency in the trials with symbol onsets at the longest SOA ($p < 0.05$). The mean saccade latency in No-onset trials did not differ between the trial blocks in which they occurred (288 ms, 28 SD and 289 ms, 24 SD), and they were combined for the following analysis. Repeated measures ANOVA with trial type as factor (No-onset, Target-onset and Target/distractor-onset) showed a significant effect of trial type, $F(2, 14) = 16.3$, $p < 0.001$. The mean saccade latency in Target-onset trials (267 ms, 19 SD) was shorter than the mean latency in Target/distractor-onset trials (296 ms, 27 SD, $p < 0.001$), and than the mean latency in No-onset trials (289 ms, 25 SD, $p = 0.001$).

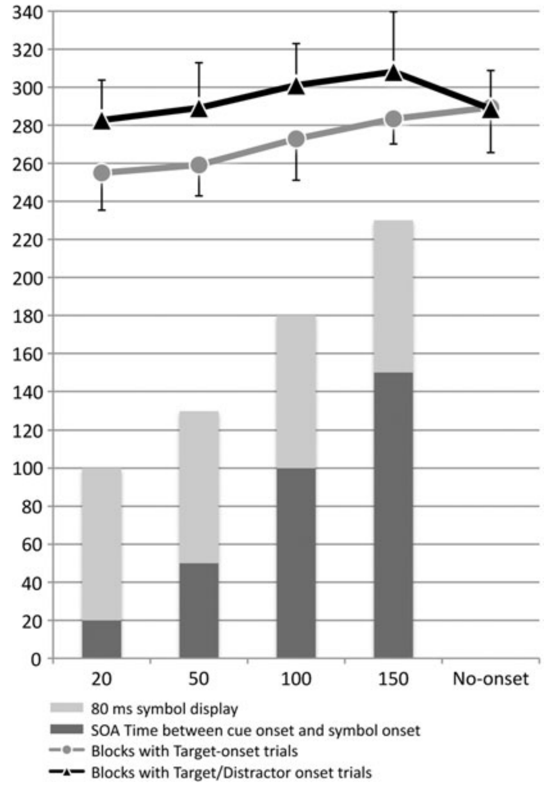

Fig. 2 The duration and timing of the discrimination symbol display and mean saccade latency in Target-onset and Target/distractor-onset trials is shown as a function of SOA (i.e. the time between cue onset and symbol onset). *Dark grey bars* represent the SOA (20, 50, 100, or 150 ms), *light grey bars* represent the duration of the symbol display (80 ms). Trials where no discrimination symbol appears (No-onset trials) are shown at right. *Grey circles* represent mean saccade latencies in the Target-onset blocks and *black triangles* represent mean saccade latencies in the Target/distractor-onset blocks. The *error bars* show 95% confidence intervals

Discrimination performance

The mean proportion of correct discriminations did not differ between the blocks of Target-onset and Target/distractor-onset trials (75 and 78%, respectively). Repeated measures ANOVA with trial type (Target-onset and Target/distractor-onset) and SOA (20, 50, 100, and 150) as factors showed a significant effect of SOA on proportions of correctly identified discrimination symbols, $F(3, 21) = 4.01$, $p = 0.02$. Discrimination was better in trials with longer SOAs than in trials with short SOAs. The mean proportion of correct discriminations in the trials with SOA 20, 50, 100 and 150 ms was 68, 75, 76 and 83%, respectively.

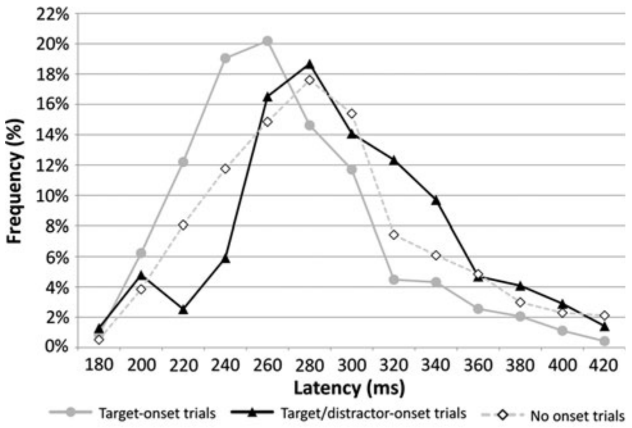

Fig. 3 The proportion of saccades initiated in each latency bin was calculated separately for each observer and for each trial type. The frequency distribution of latencies in the No-onset catch trials (*dashed line*) is shown for comparison with the Target-onset (*solid grey line*) and Target/distractor-onset trials (*solid black line*). The shape of the distributions in the two conditions with symbol onsets was similar. Symbol onsets at non-target locations in the Target/distractor trials delayed the initiation of saccades and shifted the distribution rightwards (compare *solid grey* and *black lines*). Compared to the distribution in the No-onset condition, symbol onsets at the target location promoted the initiation of saccades at short latencies and changed the shape of the distribution (compare *solid grey* and *dashed lines*)

Latency distributions

The proportion of saccades initiated in each 20-ms latency bin in the three trial types was calculated for each observer. Figure 3 shows the mean proportion across observers for each trial type for each latency bin. The distribution of latencies in the Target-onset trials (where symbols appeared at the cued target location only) suggests that the symbol onsets promoted the initiation of saccades at short latencies compared to the No-onset trials (where no symbols appeared). There were few saccades with latencies shorter than 240 ms in the Target/distractor-onset trials (where symbols appeared at target and non-target locations) compared to the Target-onset and No-onset trials, indicating that the symbol onsets at non-target locations acted as distractors and delayed saccade execution.

Discussion

This study was designed to test the proposal that the effect of SOA on saccade latencies in this paradigm is due to subjects adopting a strategy of waiting for the onset of discrimination symbols before initiating saccades in this paradigm. We hypothesised that if subjects adopted this strategy, saccade latencies should be longer on catch trials, where no symbol onsets occur compared to saccade latencies in trials with symbol onsets a the longest SOA, because subjects would wait in vain for the discrimination symbol onset on catch trials. Our results support a bottom-up explanation for the effect of SOA in this task and they are not consistent with a top-down account. Symbols appearing at the cued target location (in the Target-onset trials) shortened mean saccadic latency by 10–34 ms, depending on the SOA. The additional symbol onsets at un-cued, non-target locations (in the Target/distractor-onset trials) increased mean saccade latency by 25–30 ms, irrespective of the SOA.

It has been well documented that abrupt onsets (where a stimulus briefly appears and disappears), or a change in stimulus size, luminance, colour or shape can affect saccade initiation (Bompas & Sumner, 2009a; Edelman & Xu, 2009; Irwin, Colcombe, Kramer, & Hahn, 2000; Koelewijn et al., 2009; Ludwig & Gilchrist, 2002; Mulckhuyse, van Zoest, & Theeuwes, 2008). Generally it is found that visual onsets at or near the intended target location attract attention and facilitate the initiation of saccades, but onsets away from the intended saccadic target location act as distractors and inhibit the initiation of saccades. Our data suggest that when symbols are displayed briefly at both target and non-target locations simultaneously (as is the case in the original version of the paradigm under investigation), saccade latencies reflect the combined effects of facilitatory and inhibitory processes.

The results lead us to three main conclusions. First, the effect of SOA in our version of this paradigm was not due to a top-down strategy. If, as Deubel (2008) proposed, observers adopted a strategy of waiting for a discrimination symbol to appear before executing their planned saccades, latencies should be longest in the catch trials where no symbol appears. In these trials, observers would be waiting beyond the duration of the longest SOA to execute their planned saccades. In contradistinction, we found that in trials without any symbol onsets, the mean latency was shorter than in trials with symbol onsets at target and non-target locations (as in the original version of the task) at the longest SOA. Second, we conclude that the pre-saccadic appearance of symbols at the cued target location shortened latencies by facilitating the saccadic target selection process. The appearance of the discrimination symbols at the cued target location facilitated saccade initiation at all SOAs, but the effect was strongest in trials with short SOAs (when the symbol appeared at the target location early during saccade planning), and weaker in trials with longer SOAs (when the symbol appeared later during saccade planning, see Fig. 2). This observation is consistent with reports that during saccade planning, stimulus onsets can automatically attract attention and facilitate saccade initiation (Edelman & Xu, 2009; Koelewijn et al., 2009; Mulckhuyse et al., 2008) and with studies showing that visual attention is shifted to a future saccadic target location over the first 200 ms after cue onset (Deubel, 2008; Montagnini & Castet, 2007). A visual change occurring early during the planning of a saccade (i.e. at a short SOA) at the target location may attract attention and facilitate the shift of visual attention. However, when a visual change occurs at a later stage during saccade planning (i.e. at a longer SOA), the target selection process and the accompanying shift of attention are already advanced and therefore the facilitating effect would be smaller. This suggests that the time course of pre-saccadic shifts of visual attention is not only reflected in the discrimination performance but also in the facilitatory effect of the symbol onsets at the target location. A change in the shape of the frequency distributions confirms that symbol onsets at the target location promoted the initiation of saccades at short latencies compared to the latency distribution obtained in the catch trials (compare solid grey and dotted lines in Fig. 3). Third, we conclude that the pre-saccadic symbol onsets at non-target locations interfered with saccade planning. The irrelevant visual changes at non-target locations (in addition to the symbol onsets at the target location) delayed saccade initiation by 25–30 ms on average, irrespective of SOA. The symbol onsets at non-target locations shifted the distribution rightwards without changing the shape of the distribution (compare solid grey and black lines in Fig. 3). These observations are consistent with reports that visual onsets remote from the saccade target location transiently interfere with saccade planning and delay the execution of saccades (Bompas & Sumner, 2009b; Buonocore & McIntosh, 2008; Edelman & Xu, 2009; Reingold & Stampe, 2002; Walker et al., 1997). Previous reports showed that a transient change in the stimulus displays results in a dip in the latency distribution reflecting saccadic inhibition during a 30-ms window, starting 70–80 ms after a transient change in the stimulus display. In the present study, the display changed at 20, 50, 100 or 150 ms after cue onset, and the mean saccadic latency was 284 ms (SD 24). This means that, in this paradigm, the expected 30-ms window of saccadic inhibition occurred prior to the earliest saccades being initiated. Under these circumstances the visual change prolonged the mean saccadic latency and delayed the initiation of all saccades irrespective of SOA.

Interestingly, the facilitatory effect of the symbol onsets at the target location and the delaying effect of additional onsets at non-target locations appear to be cumulative, suggesting that the two effects may have affected different stages of saccade planning. Also, the additional onset of irrelevant symbols at non-target locations only delayed saccade initiation and did not affect the performance of the discrimination task. We suggest that this pattern of results is consistent with a model of visual attention that allows a degree of independence between top-down target selection processes and bottom-up influences on saccade planning (Deubel, 2008).

We conclude that, in the paradigm under investigation, symbol onsets modulated the initiation of voluntary saccades from the bottom-up, indicating that the observed effects may originate in a component of the saccadic system where sensory inputs are integrated with oculomotor planning.

Neurophysiology of the effects of visual onsets on saccade initiation

Many studies of the effects of visual onsets on saccade planning suggest that the effects originate in the superior colliculus (SC) (Bompas & Sumner, 2009a; McPeek, 2008; Reingold & Stampe, 2002; Walker et al., 1997). Neural processes associated with target selection and saccade triggering in the SC are well described through studies of the neurophysiology of the oculomotor system in monkeys (Dorris, Olivier, & Munoz, 2007; Li, Kim, & Basso, 2006). Across various layers of the SC, exogenous visual signals are integrated with saccade planning in a topographically arranged map representing the visual field in terms of eye movement coordinates. Levels of neural activity in the SC map reflect the allocation of visual attention to objects and locations in the visual field, and the probability that an eye movement will be made towards a particular object or location (Fecteau, Bell, & Munoz, 2004; Fecteau & Munoz, 2006). Voluntary control over saccade initiation is exerted via inhibitory basal ganglia outputs from the substantia nigra to the SC (Hikosaka, Takikawa, & Kawagoe, 2000). Mutually inhibitory connections between fixation- and saccade-related neurons in the SC help to maintain stable periods of fixation and resolve conflict between incompatible eye movement commands (Isoda & Hikosaka, 2008; Munoz & Istvan, 1998). Tonically active fixation neurons have to be inhibited before a saccade can be executed (Everling, Pare, Dorris, & Munoz, 1998). Competitive integration models of saccade planning (Dorris et al., 2007; Godijn & Theeuwes, 2002; Trappenberg, Dorris, Munoz, & Klein, 2001) explain how the build-up of saccade-related neural activity in the SC can be enhanced or inhibited by bottom-up visual signals. Neural signals evoked by a visual change close to an intended saccadic target location increase the probability of triggering a saccade. In contrast, neural activity evoked by visual changes distant from the intended saccadic target location transiently interferes with the build-up of saccade-related neural activity and inhibits saccade initiation. The results from the present study suggest that the time course of the opposing effects of the simultaneous symbol onsets at target and at non-target locations differs. The facilitating effect of the symbol onsets at the target location is strongest early during saccade planning at short SOAs, but distractor onsets at non-target locations affect saccade initiation irrespective of SOA. After the onset of a central arrow cue, neural activity specifying the intended saccade starts building up. A transient visual response due to symbol onsets at the target location would accelerate this process from the bottom-up if it occurs before the target selection process is complete. The visual response associated with distractor onsets does not appear to interfere with the build-up of activity at the target location, but it may delay the inhibition of fixation neurons required for the execution of a saccade (Boehnke & Munoz, 2008; Edelman & Xu, 2009; Everling et al., 1998).

Conclusion

This study investigated the effect of symbol onsets on saccadic latencies in a well-known eye movement paradigm. The modulation of saccadic latencies reflected the combined effects of two opposing bottom-up processes: target selection was facilitated by symbol onsets at the intended target location, and saccade execution was delayed by symbol onsets at non-target locations.

Acknowledgments This research was supported by a FRST Doctoral Scholarship (SvS) and a New Zealand Lottery Grant.

References

Awh, E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection: Links, causes and implications for spatial attention. *Trends in Cognitive Sciences, 10*(3), 124–130.

Boehnke, S. E., & Munoz, D. P. (2008). On the importance of the transient visual response in the superior colliculus. *Current Opinion in Neurobiology, 18*(6), 544–551.

Bompas, A., & Sumner, P. (2009a). Oculomotor distraction by signals invisible to the retinotectal and magnocellular pathways. *Journal of Neurophysiology, 102*(4), 2387–2395.

Bompas, A., & Sumner, P. (2009b). Temporal dynamics of saccadic distraction. *Journal of Vision, 9*(9), 11–14.

Buonocore, A., & McIntosh, R. D. (2008). Saccadic inhibition underlies the remote distractor effect. *Experimental Brain Research, 191*(1), 117–122.

Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research, 72*(6), 630–640.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research, 36*(12), 1827–1837.

Dorris, M. C., Olivier, E., & Munoz, D. P. (2007). Competitive integration of visual and preparatory signals in the superior colliculus during saccadic programming. *Journal of Neuroscience, 27*(19), 5053–5062.

Edelman, J. A., & Xu, K. Z. (2009). Inhibition of voluntary saccadic eye movement commands by abrupt visual onsets. *Journal of Neurophysiology, 101*(3), 1222–1234.

Everling, S., Pare, M., Dorris, M. C., & Munoz, D. P. (1998). Comparison of the discharge characteristics of brain stem omnipause neurons and superior colliculus fixation neurons in monkey: Implications for control of fixation and saccade behavior. *Journal of Neurophysiology, 79*(2), 511–528.

Fecteau, J. H., Bell, A. H., & Munoz, D. P. (2004). Neural correlates of the automatic and goal-driven biases in orienting spatial attention. *Journal of Neurophysiology, 92*(3), 1728–1737.

Fecteau, J. H., & Munoz, D. P. (2006). Salience, relevance, and firing: A priority map for target selection. *Trends in Cognitive Sciences, 10*(8), 382–390.

Godijn, R., & Theeuwes, J. (2002). Programming of endogenous and exogenous saccades: Evidence for a competitive integration model. *Journal of Experimental Psychology: Human Perception and Performance, 28*(5), 1039–1054.

Hikosaka, O., Takikawa, Y., & Kawagoe, R. (2000). Role of the basal ganglia in the control of purposive saccadic eye movements. *Physiological Reviews, 80*(3), 953–978.

Irwin, D. E., Colcombe, A. M., Kramer, A. F., & Hahn, S. (2000). Attentional and oculomotor capture by onset, luminance and color singletons. *Vision Research, 40*(10–12), 1443–1458.

Isoda, M., & Hikosaka, O. (2008). A neural correlate of motivational conflict in the superior colliculus of the macaque. *Journal of Neurophysiology, 100*(3), 1332–1342.

Koelewijn, T., Bronkhorst, A., & Theeuwes, J. (2009). Auditory and visual capture during focused visual attention. *Journal of Experimental Psychology: Human Perception and Performance, 35*(5), 1303–1315.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*(13), 1897–1916.

Li, X., Kim, B., & Basso, M. A. (2006). Transient pauses in delay-period activity of superior colliculus neurons. *Journal of Neurophysiology, 95*(4), 2252–2264.

Ludwig, C. J., & Gilchrist, I. D. (2002). Stimulus-driven and goal-driven control over visual selection. *Journal of Experimental Psychology: Human Perception and Performance, 28*(4), 902–912.

Ludwig, C. J., Gilchrist, I. D., & McSorley, E. (2005). The remote distractor effect in saccade programming: Channel interactions and lateral inhibition. *Vision Research, 45*(9), 1177–1190.

McPeek, R. M. (2008). Reversal of a distractor effect on saccade target selection after superior colliculus inactivation. *Journal of Neurophysiology, 99*(5), 2694–2702.

Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision, 7*(14), 1–16.

Mulckhuyse, M., van Zoest, W., & Theeuwes, J. (2008). Capture of the eyes by relevant and irrelevant onsets. *Experimental Brain Research, 186*(2), 225–235.

Munoz, D. P., & Istvan, P. J. (1998). Lateral inhibitory interactions in the intermediate layers of the monkey superior colliculus. *Journal of Neurophysiology, 79*(3), 1193–1209.

Peirce, J. W. (2007). PsychoPy–Psychophysics software in Python. *Journal of Neuroscience Methods, 162*(1–2), 8–13.

Peirce, J. W. (2008). Generating stimuli for neuroscience using PsychoPy. *Frontiers in neuroinformatics, 2*, 10.

Reingold, E. M., & Stampe, D. M. (2002). Saccadic inhibition in voluntary and reflexive saccades. *Journal of Cognitive Neuroscience, 14*(3), 371–388.

Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia, 25*, 31–40.

Trappenberg, T. P., Dorris, M. C., Munoz, D. P., & Klein, R. M. (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience, 13*(2), 256–271.

Walker, R., Deubel, H., Schneider, W. X., & Findlay, J. M. (1997). Effect of remote distractors on saccade programming: Evidence for an extended fixation zone. *Journal of Neurophysiology, 78*(2), 1108–1119.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research, 48*(20), 2070–2089.