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The parallel programming of voluntary and reflexive saccades

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Abstract

A novel two-step paradigm was used to investigate the parallel programming of consecutive, stimulus-elicited ('reflexive') and endogenous ('voluntary') saccades. The mean latency of voluntary saccades, made following the first reflexive saccades in two-step conditions, was significantly reduced compared to that of voluntary saccades made in the single-step control trials. The latency of the first reflexive saccades was modulated by the requirement to make a second saccade: first saccade latency increased when a second voluntary saccade was required in the opposite direction to the first saccade, and decreased when a second saccade was required in the same direction as the first reflexive saccade. A second experiment confirmed the basic effect and also showed that a second reflexive saccade may be programmed in parallel with a first voluntary saccade. The results support the view that voluntary and reflexive saccades can be programmed in parallel on a common motor map.
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1. Introduction

Converging evidence from behavioural, physiological and neuroimaging studies have provided great insights into how the brain transforms a sensory input into a motor output. Our understanding of this process of sensorimotor transformation is especially high for the oculomotor system and it has proved possible to relate specific behavioural effects to the underlying neural activity (McPeek, Han, & Keller, 2003; McPeek & Keller, 2002a; Munoz & Wurtz, 1992). A small number of behavioural studies have provided intriguing evidence indicating that the oculomotor (saccadic) system may be able to programme two consecutive responses in parallel (Godijn & Theeuwes, 2002; McPeek, Skavenski, & Nakayama, 2000; Theeuwes, Kramer, Hahn, & Irwin, 1998). Although the suggestion of parallel programming of consecutive saccades is not new (Becker & Jürgens, 1979), it remains to be accounted for by

models of saccade generation and is, moreover, incompatible with models based on a 'winner-take-all' account of saccade target selection processes (Findlay & Walker, 1999; Trappenberg, Dorris, Munoz, & Klein, 2001). Recently, the parallel programming of consecutive saccades has been related to a distinction between so-called stimulus-elicited (or 'reflexive') and endogenous (or 'voluntary') saccades that are thought to rely on different neural pathways for their generation. The conceptual distinction between voluntary and reflexive saccades[1] has received support from dissociations in their basic behavioural characteristics (Everling & Fischer, 1998; Hallett, 1978; Walker, Walker, Husain, & Kennard, 2000) and from functional imaging studies that have revealed differential activation in the underlying neural circuit involved in their generation

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[1] Although a similar distinction is often made between the exogenous and endogenous orienting of covert attention (Jonides, 1981; Müller & Rabbitt, 1989; Posner, 1980), the analogy is somewhat misleading in the oculomotor domain as saccades are in a sense all voluntary in nature (Carpenter, 1988)—see final discussion.

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(Connolly, Goodale, Menon, & Munoz, 2002; DeSouza, Menon, & Everling, 2003; Mort et al., 2003).

Evidence of parallel programming of saccades was revealed using the 'double-step paradigm' (Becker & Jürgens, 1979) in which saccades were made to a stimulus onset that could step to a new location following a delay period. On occasions, two accurate saccades were made which were separated by inter-saccadic intervals that were much shorter (0–100 ms) than the normal saccade latency period (of 150–250 ms—Carpenter, 1988). Becker and Jürgens (1979) proposed that the short inter-saccadic intervals were a consequence of the second saccade being programmed in parallel (pipelined) with the first saccade. More recent reports of short inter-saccadic intervals (ISIs) have typically involved behavioural paradigms in which a voluntary (endogenous) saccade is required (e.g., anti-saccade and visual search paradigms). For example, in the anti-saccade task where subjects are required to make a saccade in the direction opposite to a peripheral stimulus onset (Hallett, 1978). On a small proportion of anti-saccade trials (around 10–15%) subjects make erroneous reflexive saccades ('pro-saccade errors') to the peripheral stimulus, and on occasions a secondary corrective saccade can be initiated after a brief fixation interval (0–100 ms) (Amador, Schlag-Rey, & Schlag, 1998; Mokler & Fischer, 1999; Weber, Dürr, & Fischer, 1998). Similarly, in visual search paradigms, in which the desired response is a target defined in terms of stimulus characteristics (such as colour and shape), subjects occasionally make an erroneous saccade to a distractor, which may be followed by a corrective saccade to the target after a short ISI (Findlay, Brown, & Gilchrist, 2001; Godijn & Theeuwes, 2002; Hooge & Erkelens, 1996; McPeek et al., 2000; Theeuwes et al., 1998; Viviani & Swensson, 1982). The short inter-saccadic intervals can be taken as evidence for the parallel programming of two consecutive responses.

One suggestion is that parallel programming of consecutive saccades in such situations may involve a first erroneous reflexive (error) saccade being made, which is then followed by a second corrective saccade that is more voluntary in nature (Godijn & Theeuwes, 2002; Theeuwes et al., 1998). This account is intuitively appealing as it appears consistent with the differential activation observed in the underlying neural structures involved in voluntary (endogenous) and reflexive (stimulus-elicited) saccade generation in functional imaging studies (Mort et al., 2003), and also with the possibility that separate neural pathways exist for their generation (Schiller, True, & Conway, 1980). The generation of stimulus-elicited reflexive saccades is thought to involve a cortico-tectal pathway from the parietal eye fields, located in the intra parietal sulcus, which project to the superior colliculus (SC), which projects to the brain stem saccade generator (Schall, 1995; Schiller, 1998; Sparks & Hartwich-Young, 1989). By contrast, voluntary endogenous saccades are thought to rely more heavily on structures located in the frontal lobe, such as the frontal and supplementary eye fields (FEFs and SEFs) (Connolly et al., 2002; Mort et al., 2003). The frontal eye fields project to the superior colliculus (Schlag-Rey, Schlag, & Dassonville, 1992) and may also have a direct projection to the brainstem (Schiller, Sandell, & Maunsell, 1987) (although this has since been questioned—Hanes & Wurtz, 2001). Differential activation within the underlying neural circuit involved in saccade generation, or the involvement of separate pathways, are important considerations for the parallel programming of consecutive saccades. One possibility is that the first stimulus-elicited saccade may be mediated by the parieto-collicular pathway, while the second voluntary response may depend on the fronto-collicular pathway. An alternative possibility is that the second voluntary response depends on a separate pathway from the FEFs to the brainstem that bypasses the SC (Schiller et al., 1980, but see Hanes & Wurtz, 2001).

To date the evidence advanced to support the idea of parallel programming has typically relied on an examination of a small sub-population of trials on which an erroneous response is followed, after a short ISI period, by a secondary corrective response. As a result, there are relatively few trials on which parallel programming may be observed and a detailed examination of these saccades has not yet been possible. The present study used a novel two-step saccade paradigm designed to mimic the situation where a first reflexive saccade can be followed by a second voluntary response in parallel. The paradigm required a reflexive saccade to be made to a stimulus-onset that was followed by a second voluntary saccade made on the basis of a central symbolic directional cue (Mort et al., 2003; Walker et al., 2000). The cue was presented along with the peripheral stimulus and the timing sequence meant that the second saccade could be programmed in parallel with the first response. Single reflexive (stimulus-elicited) and voluntary (arrow-cued—endogenous) saccades were made as the critical control measure. The critical behavioural measure of interest was the inter-saccadic interval (or fixation duration) between the end of a first reflexive saccade and the initiation of the second voluntary saccade made on the basis of a symbolic arrow-cue.

2. Experiment 1

2.1. Method

2.1.1. Participants

Seven normal observers, four females and three males, (age range from 19 to 39 years) participated in the experiment.

2.1.2. Apparatus

A Pentium II computer with a 17 in. colour monitor was used to present the stimuli and a second computer, interfaced by a local ethernet link, was used to control the recording of eye movements. Eye movements were recorded using a video-based eye tracker (Eyelink I, Sensomotoric

Instruments) with a temporal resolution of 250 HZ and spatial accuracy of less than 0.5°. A chin rest was used to minimise head movements and maintain a viewing distance of 57 cm from the computer screen. Eyelink software identified saccade start and endpoints using a 22 deg/s velocity and 8000 deg/s² acceleration criterion. The latency of the saccade was calculated as the time from the presentation of the peripheral target (reflexive) or cue (voluntary) until the eye started to move. The latency of voluntary saccades in the two-step condition was taken as the time interval from the end of the first saccade until the start of the second saccade.

2.1.3. Stimuli

Fig. 1 shows the stimulus display for each trial sequence. All stimuli were white presented on a black background (0.2 cd/m²). At the start of each trial participants viewed a central fixation stimulus (1.5 cd/m²) consisting of a cross overlaid with a diamond (0.5° diameter) along with two circular 'marker' stimuli (0.5° diameter, 1.2 cd/m²) located along a horizontal axis (at ±10°) that served as goals (targets) for the voluntary saccades. After a random fixation foreperiod of 800–1300 ms the second frame was presented during which time a response (one or two saccades) was required. The reflexive saccade target (2.2 cd/m²) appeared at 5°, to the left or right of fixation, in a direction of 45° in either the upper or lower field. Voluntary saccade targets (marker stimuli) were indicated by an arrow-cue at central fixation which was formed by the offset of two lines from the fixation stimulus (see Walker et al., 2000). The second frame was presented for 1500 ms and was followed by an inter-trial delay of 600 ms. It is important to note that in all conditions there was a partial offset of the central fixation stimulus in the second frame to ensure that the effects of manipulations (partial offset) of fixation (e.g., 'gap effect' Saslow, 1967) were equivalent across all conditions.

2.1.4. Procedure

A calibration routine was performed at the start of each block of trials. The calibration required participants to fixate nine points in succession around the computer screen. In order to validate the eye positions subjects again made saccades to the same nine points in succession. If landing position deviated by more than 0.5° then the procedure was completed again. Once the accuracy was within 0.5° a block of trials was completed.

A block of trials included single reflexive saccades, single voluntary saccades and two-step saccade trials (first reflexive saccade followed by a second voluntary saccade) interleaved. The single saccade conditions served as controls for saccades made in the two-step conditions. Reflexive saccades (control) were made to the peripheral saccade target which appeared simultaneously with the offset of two lines from the fixation stimulus (which formed an hour glass shape). Voluntary saccades (control) were made to the marker stimulus indicated by the arrow-cue formed by the offset of two lines from the fixation stimulus. In two-step conditions subjects first made a reflexive saccade to the peripheral target that appeared simultaneously with presentation of the arrow-cue, followed as quickly as possible by a second voluntary saccade in the direction indicated by the arrow-cue. The second saccade could, therefore, be made in either the same direction as the first step, or in the direction opposite to the first step. Subjects completed four blocks of 98 trials. Each block contained 28 single reflexive trials (14 upper and 14 lower field targets) and 14 single voluntary trials. In two-step conditions there were 28 same direction and 28 opposite direction trials (collapsed across up and down). This produced a total of: 56 single voluntary saccades; 112 single reflexive saccades; 112 reflexive saccades and 112 voluntary saccades in two-step trials (collapsed across hemifield and direction). The trial order was randomised within and between blocks.

2.2. Results

2.2.1. Discarded data

Saccades were classified as erroneous on the grounds of small amplitude (<2°, 8% of excluded trials), long latency (>500 ms, 1% of excluded trials) and incorrect direction (deviation greater than ±45° of target direction, 14% of excluded trials).
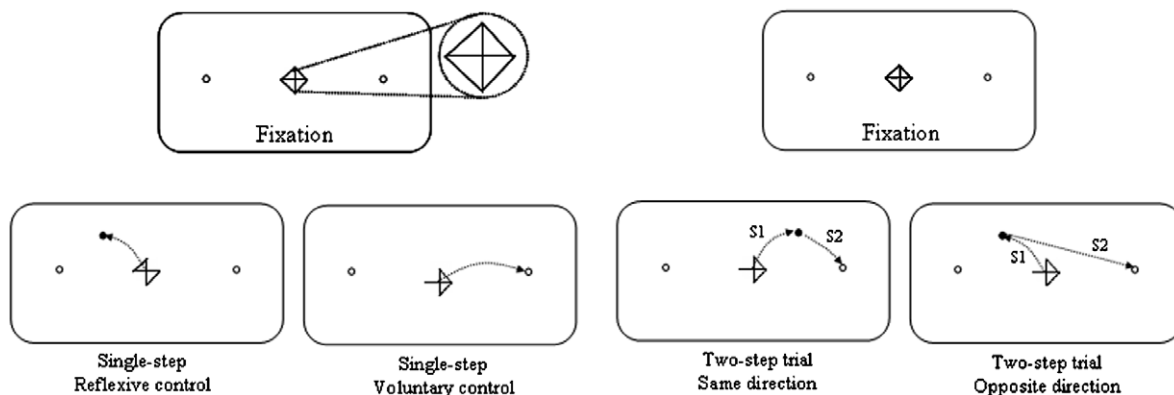

Fig. 1. Stimulus display sequence used. The dashed lines with small arrows show the desired response (one or two saccades) and were not part of the stimulus display.

2.2.2. Saccade latency

The main focus of interest is the difference in latency for voluntary saccades made in the two-step conditions compared to those in the single-step control condition. For this comparison saccade latency made in two-step conditions, to the left and right, and those made to (and from) upper and lower field targets were collapsed (paired *t* tests showed no difference between reflexive saccades made to upper and lower field targets in the control condition). The mean latency of saccades subtracted from their control conditions is displayed in Fig. 2. A positive value indicates a longer than control latency and a negative value a shorter than control latency. Actual mean latencies are shown in Table 1.

It can be seen from Fig. 2 that the mean latency of voluntary saccades in the two-step parallel programming conditions was significantly reduced when compared to the latency of voluntary saccades in the single-step control condition. The reduction in voluntary saccade latency was observed for voluntary saccades made in both the same and opposite direction to the first saccade. Paired *t* tests confirmed that the reduction in latency for voluntary saccades was significant compared to the control condition (same direction $t(6) = 4.2$ $p < 0.01$; opposite $t(6) = 3.4$ $p < 0.05$) but no difference between voluntary saccades made in the same and opposite directions ($t(6) = 0.2$, $p > 0.05$).
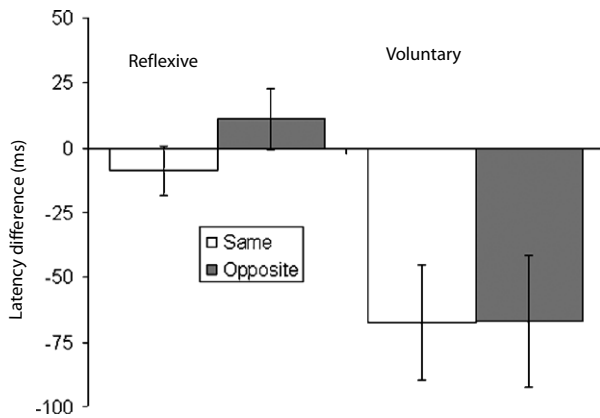

Fig. 2. Mean latency differences of reflexive (shown on the left) and voluntary (on the right) saccades made in two-step conditions relative to the single step control conditions (where the second saccade can be in either the same or opposite direction to the first step). A +ve value indicates that mean latency of second saccades was greater than in the control condition and a –ve value indicates that mean latency was less than in the control condition.

Table 1
The mean latencies (in ms) of voluntary and reflexive saccades made in the single-step (control) and two-step (reflexive–voluntary) conditions in Experiment 1

	Control		First step		Second step	
	Reflexive	Voluntary	Same	Different	Same	Different
Experiment 1	280 (R)	344 (V)	272 (R)	291 (R)	276 (V)	278 (V)

The two saccades could either be in the same, or opposite directions. Letters in brackets after the figures indicates the saccade type: R, reflexive; V, voluntary.

Paired *t* tests comparing the latency of reflexive saccades made in the two-step conditions to that in the control condition were performed. A small, but significant, reduction in mean latency was observed when the first and second saccades were in the same direction ($t(6) = 2.6$, $p < 0.05$) and a small, but significant, increase in mean latency was found when the second step was in the direction opposite to the first saccade ($t(6) = -3.2$, $p = 0.05$). Same and opposite direction 1st saccade latencies were also found to be significantly different from each other ($t(6) = -3.8$, $p < 0.05$).

Quartiles derived from the vincentising (Ratcliff, 1979) of the latency distributions for reflexive and voluntary saccades are shown in Fig. 3. These plots are generated by deriving the mean latency for each consecutive 25% of the latency distribution separately for each subject before averaging across them. Voluntary and reflexive control conditions are plotted on each graph as reference along with the first and second saccade when executed in the same direction (left plot) or in the opposite direction (right plot). For first and second saccades directed in the same and opposite direction it can be seen that the distributions for each condition are in the region of the reflexive baseline condition. First saccades can be seen to be consistently quicker or slower than the baseline for same and opposite conditions as reflected in the means discussed above. Second saccades can also be seen to be in the region of the reflexive baseline with a greater spread of latencies and a large shift away from the voluntary distribution. This confirms that there is little difference in the underlying latency distributions for reflexive and voluntary saccades in single and two-step conditions and indicates there were no dual-task interference effects on the generation of the first response. The latency distributions for voluntary saccades show a generalised reduction in latency for voluntary saccades made in the two-step condition resulting in an overall reduction in mean latency.

2.2.3. Saccade amplitude

Previous reports of parallel programming have shown that short ISIs between consecutive saccades are associated with hypometric first saccades. To examine this effect the amplitudes of all first saccades were examined in relation to the ISI (or latency) of the second saccade made in the two-step conditions. Table 3 shows mean amplitudes in terms of quartiles of mean voluntary saccade latency. It can be seen that the amplitude of first saccades does not vary in terms of second saccade latency. There is no suggestion of first saccade amplitude being reduced when the second saccade is of shorter latency.

2.3. Discussion

The results show clear evidence for the parallel programming of voluntary and reflexive saccades. Voluntary saccade latencies made in the two-step parallel programming condition were reduced by about 70 ms compared to mean latency observed in the single-step control condi-
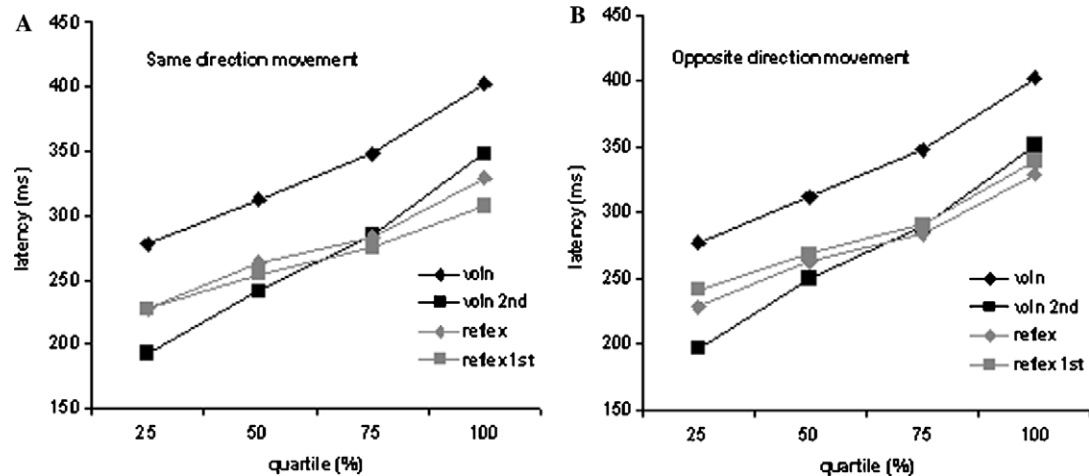
Fig. 3. Quartiles derived from the distributions of saccade latency for reflexive and voluntary saccades made in the single-step (control) and two-step same direction (A) and two-step opposite direction (B) conditions from Experiment 1. Control conditions plotted in each graph are comparable to the direction and amplitude of those elicited in the two-step conditions.

tions. This reduction in voluntary saccade latency in two-step conditions was observed for second saccades made in both the same and opposite directions to the first reflexive saccade. There was no evidence of dual-task interference effects on the latency of the first reflexive saccades made in the two-step conditions. However, the latency of the first reflexive saccades was subject to a small modulation depending on the direction of the second (endogenous) saccade. First saccade latency was reduced when a second step was to be made in the same direction and was increased when a second saccade was required in the opposite direction. This increase in first saccade latency may reflect competitive interactions operating between two saccade programmes similar to the remote distractor effect observed when distractors are presented along with a saccade target (Walker, Kentridge, & Findlay, 1995; Walker, Deubel, Schneider, & Findlay, 1997).

It should be noted that the voluntary saccades made in the three conditions (control, two-step same direction and two-step opposite direction) differ in terms of their amplitude and direction. It might be argued, therefore, that differences in latency between two-step and control, trials may result from differences in amplitude and direction. Evidence against this argument is provided in the mean latency of voluntary saccades observed in the same direction and opposite direction two-step conditions that were comparable (276 and 278 ms), even though they differed widely in their amplitudes (7.5° and 14°, respectively). It is known, however, that the latency of stimulus-elicited saccades is relatively stable across the amplitude range of 2°–15° (Kalesnykas & Hallett, 1994) but this has not been confirmed for endogenous saccades and there are also known influences of saccade direction on latency (Heywood & Churcher, 1980). So, to control for a possible influence of amplitude and direction on the results observed here a second experiment was carried out in which amplitudes of first and second saccades were the same. The second experiment also investigated the possi-

bility that a second reflexive saccade could be programmed in parallel with a first voluntary saccade.

3. Experiment 2

3.1. Introduction

Experiment 1 provided evidence showing that a voluntary saccade can be programmed, at least partially, in parallel with a first reflexive saccade. It was noted, however, that the saccades made in the two-step conditions differed in terms of amplitude and direction from those in the control conditions and that this may have contributed to the observed latency differences. This was addressed in a second experiment by ensuring that saccade amplitude and direction was carefully balanced across two-step and single-step control trials. Practical constraints imposed by equivalent stimulus locations means that it is not possible to include a condition in which second saccades were made in the opposite direction to the first saccades. Thus, in Experiment 2 the second saccades were always made in the same direction as the first saccade and these were compared to saccades made in control conditions that were matched for amplitude and direction.

Intuitively, it might be thought that the saccadic system would be more likely to have to deal with situations in which an erroneous 'reflexive' saccade has been made to a stimulus onset, that requires a subsequent corrective saccade that relies on endogenous control processes. Thus, the saccadic system may be biased towards parallel programming of a voluntary saccade in parallel with a first stimulus-elicited saccade. For this reason it is of interest to examine the situation in which a first voluntary saccade is followed by a second reflexive saccade to see if parallel programming can be demonstrated. To this end both types of saccades were examined in Experiment 2 in two separate conditions: reflexive saccade followed by a voluntary saccade (R–V); or a voluntary saccade followed by a reflexive saccade (V–R).

3.2. Method

3.2.1. Participants

Six observers, three female and three males, with an age range of 25–41 years and normal or corrected to normal vision, participated in the experiment.

3.2.2. Design and procedure

The apparatus was the same as Experiment 1. The spatial layout of the stimuli ensured that saccades were of equivalent amplitudes (5°) and directions (see Fig. 4). In the first condition (reflexive–voluntary or R–V) reflexive saccades are made first and voluntary saccades are made second. The reflexive saccades were made to positions **A** or **D** and voluntary saccades are made to **B** or **C**. In the control single-step conditions reflexive saccades were made to positions **A** or **D**; and voluntary saccades to positions **B** or **C**. The direction and amplitude of these single saccades corresponds to the direction and amplitude of saccades made in two-step conditions. In the second condition (voluntary–reflexive or V–R) voluntary saccades were made to positions **A** or **D** and reflexive saccades were made to **B** or **C**. In the control condition single voluntary saccades were made to positions **A** or **D** and reflexive saccades to positions **B** or **C**. In both conditions the specific control condition was matched, in terms of amplitude and direction, to the second saccades to examine the influence of parallel programming on second saccade latency.

At the start of each trial (see Fig. 4) participants view a central fixation stimulus consisting of a cross ('+') overlaid with a diamond and another cross ('×') overlaid with a square along with two circular markers that served as goals for the voluntary saccades. This particular fixation stimulus allows the same number of lines to be removed from fixation to reveal a directional arrow-cue, or a non-directional shape (an hourglass). (The important point about this is that the
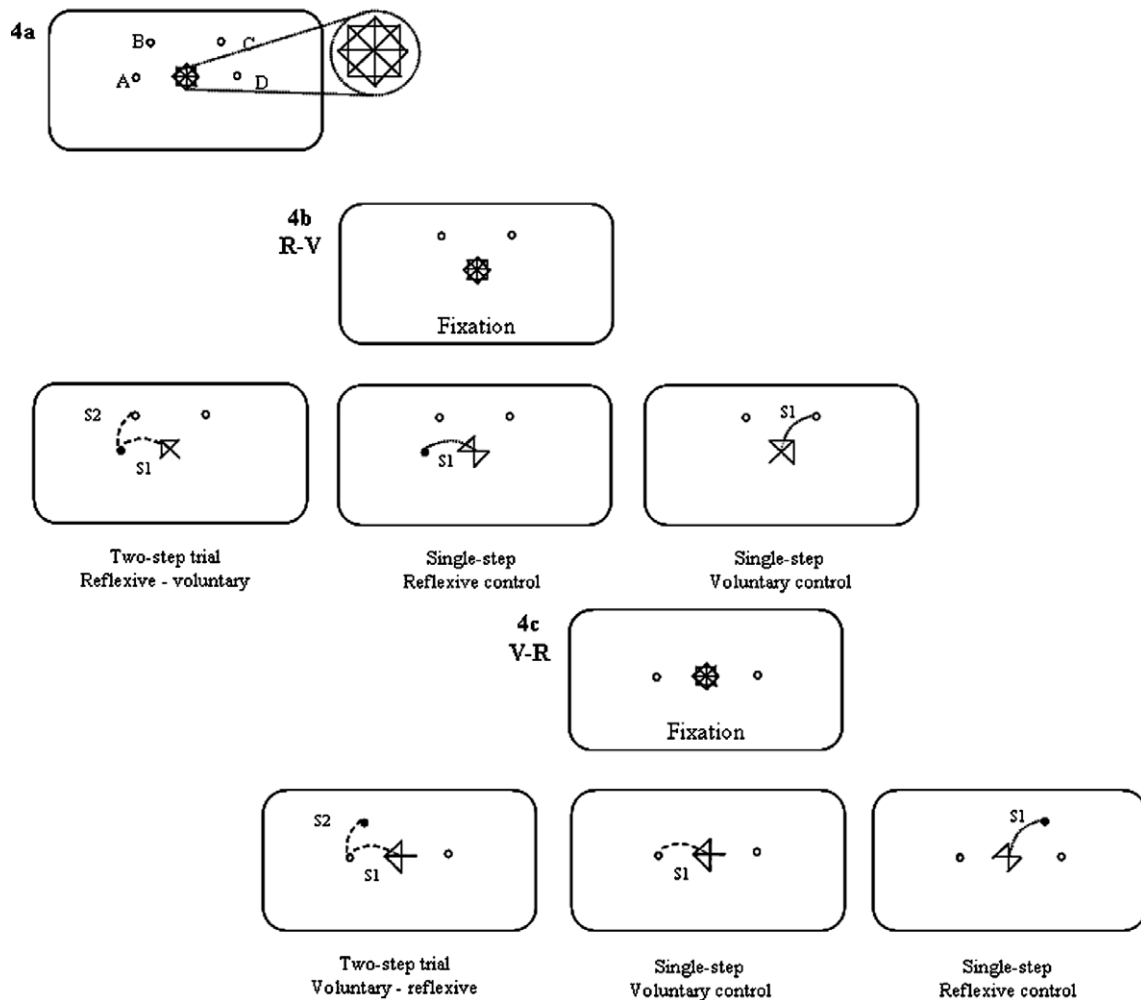

Fig. 4. Schematic diagram of stimulus display and trial sequences used in Experiment 2. (a) fixation stimulus and stimulus locations A–D (refer to text for details). (b) Reflexive–voluntary (R–V) condition. Upper frame shows the initial fixation stimulus that is presented along with two marker stimuli that serve as the goal for voluntary saccades. Lower frames (from left to right) show a R–V two-step trial (first saccade S1 made to abrupt stimulus onset; second saccade S2 made to location indicated by arrow-cue): single-step reflexive (control) trial and single-step voluntary (control) trial, made to equivalent stimulus positions. (c) Voluntary–reflexive (V–R) condition. Upper frame shows initial fixation and marker stimuli for voluntary saccades. Lower frames show a V–R two-step trial; a single-step voluntary (control) trial and a single-step reflexive (control) trial. N.b. in Experiment 2, the second saccade on two-step trials is always made in the same hemifield as the first step.

onset and offset of visual events at fixation are equivalent across all conditions.) After a random fixation foreperiod of 800–1300 ms the second frame was presented during which time a response (one or two saccades) was required. The reflexive target was a white spot 0.5° diameter with a hole in the centre of 0.25° diameter. Voluntary saccade targets were indicated by the central arrow-cue. If the partial offset of fixation formed an hourglass figure then a single reflexive saccade was required (as there is no cue for the second voluntary saccade). The second frame was presented for 1500 ms and was followed by an inter-trial interval of 600 ms.

The two conditions were run in succession with four counterbalanced blocks (two blocks of each condition followed by two blocks of the other condition) of 90 trials. There were 30 trials per trial sequence in each condition: single reflexive; single voluntary; two-step left and two-step right.

3.3. Results

3.3.1. Discarded data

Saccades were classified as erroneous on the grounds of small amplitudes (<2°, R–V = 2.4%; V–R = 2.2%), long latency (> mean plus 2.5. standard deviations separately for each subject, R–V = 0.6%; V–R = 0.1%) and direction (greater than ±30°—N.b. this was reduced from Experiment 1 as target locations were closer together, R–V = 11%; V–R = 28%).

3.3.2. Saccade latency

The mean latency of saccades made in each condition is shown in Table 2. It can be seen that the latencies of second saccades in the two-step conditions are much quicker than in the control single saccade trials by some 60–100 ms (voluntary and reflexive, respectively). The mean latency of second saccades made in the two-step conditions were subtracted from the mean latencies observed in the relevant control trials separately for each subject. The mean latency differences are shown in Fig. 5 (−ve values indicate second saccades quicker than control). Two separate one sample t tests were performed for each two-step condition. These show a significant quickening of the second saccade in both conditions (voluntary second: $t(5) = -4.19$, $p < 0.01$; reflexive second $t(5) = -3.13$, $p < 0.05$). The latency of the first saccades did not vary due to the demand of having to make a second saccade in the two-step conditions confirming an absence of a dual-task interference effect (reflexive first $t(5) < 1$; voluntary first $t(5) < 1$).

Table 2
The mean saccade latencies (in ms) for Experiment 2

	Control		Two-Step	
	Reflexive	Voluntary	First Step	Second step
Reflexive–voluntary	313	377	307 (R)	280 (V)
Voluntary–reflexive	352	330	331 (V)	293 (R)

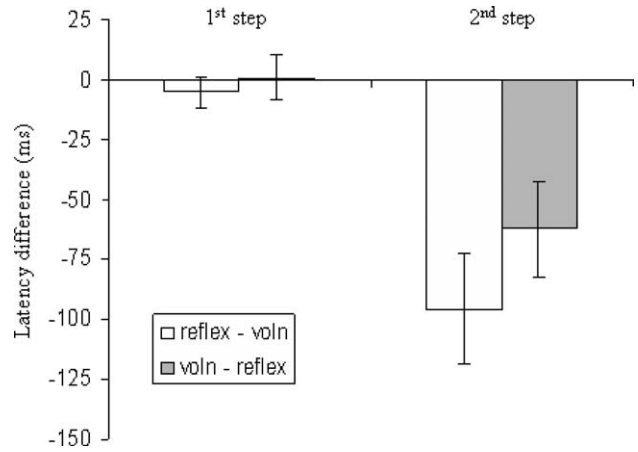Letter in brackets after the figures indicate saccade type: R, reflexive; V, voluntary.

Fig. 5. Mean latency differences of first saccades (shown on the left) and second saccades (shown on the right) saccades made in the two-step conditions relative to the single-step control conditions in Experiment 2. Open squares = reflexive–voluntary condition, filled squares = voluntary–reflexive condition.

Quartiles derived from the latency distributions for reflexive and voluntary saccades observed in the reflexive–voluntary (upper plot), and voluntary–reflexive (lower plot), conditions are shown in Fig. 6. The voluntary and reflexive baseline conditions are plotted as a reference. It can be seen that second saccade latencies are quicker than
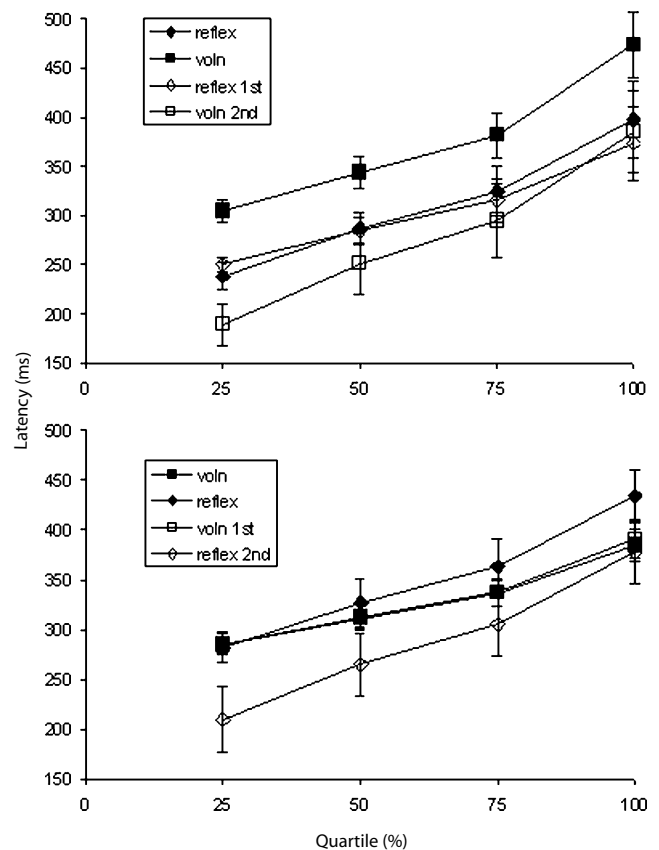

Fig. 6. Quartiles derived from the distributions of saccade latency for reflexive and voluntary saccades made in the single-step (control) and two-step reflexive–voluntary R–V (upper plot) and two-step voluntary–reflexive V–R (lower plot) conditions of Experiment 2.

the control latencies throughout all of the distribution. First saccades in both the R–V and V–R conditions are equivalent to their respective controls. In line with the means the control latencies observed in both conditions (corresponding to the 'type' of second saccade in two-step trials) are slower than all other saccades latencies. The increase in reflexive saccade latency in the single-step control trials in the V–R condition was not expected.

3.3.3. Saccade amplitude

As with Experiment 1 the amplitudes of the first saccades were examined for evidence of hypometria. The amplitudes of all first saccades were examined in relation to the ISI (viz. latency) of the second saccade made in the two-step conditions. Table 3 shows mean amplitudes in terms of quartiles of the second saccade latency. It can be seen that the amplitude of first saccades does not vary in terms of second saccade latency. Unlike previous reports of parallel programming, which have shown that short ISIs between consecutive saccades are associated with hypometric first saccades, there is no suggestion of first saccade amplitude being reduced when the second saccade is of shorter latency.

3.4. Discussion

Experiment 2 provided further evidence that voluntary and reflexive saccades can be programmed, at least partially, in parallel. The mean latency of voluntary saccades in the R–V two-step condition was reduced by some 100 ms compared to that in the single-step control conditions. A similar reduction in latency was observed in the V–R two-step condition when reflexive saccades were made after voluntary saccades, although the magnitude of the effect was smaller (62 ms). Despite this difference in the extent of the magnitude of the parallel programming facilitation effect the latency distributions were similar in both conditions. This experiment has confirmed that the observed latency reduction cannot be attributed to differences in saccade amplitude and direction between the two-step and single-step control conditions.

Table 3
Mean amplitude of first reflexive saccades, observed in two-step trials, in relation to the latency (quartiles) of the second saccades from Experiments 1 and 2

	1st quartile	2nd quartile	3rd quartile	4th quartile
Experiment 1				
Reflexive–voluntary				
Mean latency, ms	191	245	289	370
Mean amplitude, °	4.77	4.80	4.74	4.74
Experiment 2				
Reflexive–voluntary				
Mean latency, ms	189	251	295	385
Mean amplitude, °	5.33	5.47	5.30	5.31
Voluntary–Reflexive				
Mean latency, ms	210	265	306	378
Mean amplitude, °	5.51	5.53	5.26	5.50

An interesting effect observed across the two conditions (R–V and V–R) are the changes in the latencies of saccades made in the single-step control conditions (see Table 2). The latency of the reflexive saccades made in isolation in the voluntary–reflexive condition is very similar to the latency of voluntary saccades in the reflexive–voluntary control conditions. Indeed, the mean latency of reflexive saccades in the control condition is longer than the latency of voluntary saccades in the voluntary–reflexive control condition. Thus, there appears to be an effect of expectancy (e.g., expectation is to make a voluntary saccade) on the latency of the first reflexive saccades. It may be that when a subject is preparing an endogenous saccade that reflexive saccades are impaired (as indicated by the increase in reflexive latency in the V–R condition) due to the requirement of using endogenous control processes for saccade generation on the majority of trials. Similarly, the dependence on exogenous control processes in the R–V condition may result in an inflation of voluntary saccade latency. An alternative possibility is that the less likely stimulus locations (the upper field locations in the V–R condition) may be subject to a form of spatial inhibition. The frontal eye fields, for example, are able to inhibit regions of the collicular motor map that encode saccades to non-target locations (Schlag-Rey et al., 1992). In our two-step conditions some locations are less likely to be saccade goals and may be subject to such a form of inhibition.

4. General discussion

This study investigated the parallel programming of consecutive voluntary and reflexive saccades using a novel two-step saccade paradigm. In Experiment 1 a first stimulus-elicited ('reflexive') saccade was made to a peripheral onset that was followed by a second endogenous ('voluntary') saccade made to a location specified by a central symbolic arrow-cue. The latency of the second 'voluntary' saccades in the two-step trials was significantly faster than in the single-step control trials. This decrease in voluntary saccade latency was observed for second voluntary saccades made in either the same, or opposite direction, to the first reflexive saccade. This latency reduction supports the view that a voluntary saccade can be programmed, at least partially, during the time the first saccade was being generated. Importantly, there were no associated costs on first saccade latency in the two-step conditions relative to control single saccade latencies: thus the decrease in time required to make a second saccade was not related to an increase in the time required to make the first saccade (no 'dual-task' interference effects). A small increase in first saccade latency was observed, however, when a second voluntary saccade was required in the direction opposite to the first reflexive saccade. This may reflect a form of 'remote distractor interference effect' (Walker et al., 1995, 1997) that depends on competing saccade programmes, one a stimulus-elicited (reflexive) saccade and the other being purely endogenous. These findings add further support to the view that the saccadic system can programme two saccades

in parallel (Godijn & Theeuwes, 2002; McPeek et al., 2000; Theeuwes et al., 1998). A second experiment was performed which confirmed that the reduction in second saccade latency cannot be attributed to differences in amplitude and direction of saccades made in the control and two-step trials. Experiment 2 further showed that a second reflexive saccade can be programmed in parallel with a first voluntary saccade. A reduction in reflexive saccade latency was observed, in two-step trials, comparable to that observed for voluntary saccades although the effect was smaller in magnitude. Thus, voluntary (and reflexive) saccades can be programmed, in parallel during the time required to generate a first reflexive (or voluntary) saccade.

Recent reports of parallel programming of consecutive saccades have been based on an examination of the small number of trials on which a secondary corrective saccade was made after a short ISIs, following a first erroneous response in visual search paradigms (Godijn & Theeuwes, 2002; McPeek et al., 2000; Theeuwes et al., 1998). For example, Theeuwes et al. (1998) observed short ISIs for corrective saccades on trials in which participants incorrectly made a saccade to a distractor onset. They suggested that parallel programming may involve a secondary corrective saccade made under endogenous control being generated in parallel with a first reflexive response (Theeuwes et al., 1998). Godijn and Theeuwes (2002) further showed that the latency, trajectories and endpoints of saccades made to the search target were influenced by distractor onsets. Latency was increased when distractors were remote and saccade endpoint modulated when distractor were close to the target. This was interpreted in terms of a 'competitive integration model' in which exogenous and endogenous saccades are generated in a common motor map, in line with an earlier suggestion made by McPeek et al. (2000). Additional behavioural support, for competitive interactions operating between competing saccade programmes, comes from the observation that the amplitudes of the first reflexive (erroneous) saccades made in visual search are often hypometric (Findlay et al., 2001; Godijn & Theeuwes, 2002; McPeek et al., 2000). Hypometria has also been observed in the case of pro-saccade errors followed by short latency corrections in the anti-saccade task (Weber et al., 1998). The present study showed no relationship between the latency of the corrective saccades and primary saccade amplitude, but did reveal an influence of the second saccade on first saccade latency. The increase in first saccade latency observed here, when a second step was required in the opposite direction to the first step, may be taken as a form of remote distractor effect (Walker et al., 1997) operating between competing programmes one of which is entirely endogenous in nature. Our findings add further support to the view that parallel programming involves interactions between two competing saccade programmes in a common motor map (Godijn & Theeuwes, 2002; McPeek & Keller, 2002b). The modulation of first saccade latency depending on the direction of the second response observed in Experiment 1 of the present study is consistent with this interpretation.

An alternative account of parallel programming has been based on the view that the two saccades may be mediated by separate neural pathways. Specifically, it has been proposed that the reflexive saccade depends on the subcortical (collicular) pathway, while the second voluntary saccade may rely to a greater extent on the pathways and structures in the frontal lobe (e.g., FEF, SEF and DLPFC—Theeuwes et al., 1998). This suggestion was influenced by animal lesion studies showing that monkeys with collicular lesions are able to generate saccades. This ability to make a saccade after collicular ablation has been interpreted as evidence for a separate pathway from the frontal eye fields to the brainstem saccade generator (Schiller et al., 1980). This view has, however, been questioned on the basis of more recent studies which have shown that saccades are not elicited by electrical stimulation of the FEFs following reversible deactivation of the SC (Hanes & Wurtz, 2001). Furthermore, it has been noted that although a direct projection from the FEFs to brainstem omnipause neurons exists, there is no evidence of projections to the burst neurons that are required to generate a saccade of a particular direction (see Hanes & Wurtz, 2001 for a detailed discussion of these issues). This is consistent with the idea that parallel programming may involve preparatory processes (preparation of saccade timing) rather than the programming of saccade metrics (McPeek & Keller, 2002b). The cortical structures (IPS, FEFs and SEFs) involved in saccade generation appear to exert their influence, therefore, via the colliculus, that can be regarded as a "funnel" through which the cortex can influence the brainstem saccade generator (Wurtz, 2000). The cortical and subcortical maps involved in saccade generation may function as a whole network, with the final selection of a unique saccade goal being performed on a common motor map such as the SC (Godijn & Theeuwes, 2002; McPeek et al., 2000). It is plausible that the parallel programming of voluntary and reflexive saccades could involve differential activity in multiple maps (cortical and subcortical) involved in programming voluntary and reflexive saccades (Mort et al., 2003) that maintain separate representations of two saccades in a downstream common motor map.

The hypothesis that two saccades can be programmed on a common motor map (Godijn & Theeuwes, 2002; McPeek et al., 2000) is consistent with physiological observations made in the superior colliculus (McPeek & Keller, 2001, 2002b; McPeek et al., 2000). McPeek and Keller (2002b) recorded activity of collicular neurons at potential target locations in a visual search task and examined activity on trials in which a secondary corrective saccade was made. It was found that neural activity related to the actual saccade goal was maintained during the initiation of the first (incorrect) response. Critically, this maintained activity was observed only on trials where the second response was made within the cells response field and was restricted to trials on which a short ISI occurred between the end of the first saccade and the initiation of the second saccade. McPeek and Keller (2002b) highlight an important issue regarding activity encoding the second saccade goal, which

is that the vector of this second response has moved in relation to the initial retinotopic location. Thus, this second population of activity cannot encode the vector of the second response from the new fixation location. One possibility is that the locations of potential saccade goals are remapped into their new retinotopic location (Walker, Fitzgibbon, & Goldberg, 1995). McPeek et al. also suggested that such activity may reflect advance saccade target preparation (or preparatory set—Connolly et al., 2002) achieved by increasing the salience of the second saccade goal. Advance target selection, or preparation to make a response, was thought to be a likely mechanism for reducing the latency of second saccades. This view is consistent with models of saccade generation that have emphasised separate channels for the programming of saccade metrics ('where') processes and saccade triggering ('when') that controls saccade timing (Findlay & Walker, 1999). Thus, the partial programming of saccades, generated in parallel, may be related to the different underlying processes involved in their generation, specifically to advanced preparation of the 'when' (or trigger) signal.

We argue that the latency facilitation observed for second saccades in the two-step conditions can most plausibly be related to the partial programming of the second saccade go-signal during the time the first saccade is being prepared. An alternative possibility is that the reduction in second saccade latency may be attributed to the interpretation of the symbolic arrow-cue during the time the first saccade is being generated. We do not think this interpretation is likely for two main reasons. First, in Experiment 2 a reduction in saccade latency was observed for second reflexive saccades in the V–R condition, and this instance the second saccade does not require the interpretation of a symbolic cue. Second, neurophysiological studies have shown that the preparation to make a response (under endogenous control) involves neural activity associated with motor preparation (Gold & Shadlen, 2000). Gold and Shadlen (2000) trained monkeys to make a saccade the direction of which depended on the endogenous interpretation of a motion stimulus. Saccades were found to deviate in the direction of the monkey's judgement and the magnitude of the deviation was related to the strength of the motion signal. They argue that decision processes (where to make a saccade) and motor preparation appear to share a common level of neural organisation. These decision processes are most likely to involve neural activity in the superior colliculus, the lateral intraparietal area (LIP), or prefrontal cortex and each of these areas are also involved in generating eye movements. Thus, the decision processes involved in our two-step paradigm may not be dissociated from neural processes involved in saccade generation. This is consistent with the view upheld here that two responses may be generated in parallel and at some stage this may reflect activity associated with both responses being maintained in a common motor map.

It should be noted that the terms 'reflexive' and 'voluntary' are used throughout this paper as a convenient short-hand for 'stimulus-elicited' and endogenous saccades, respectively, consistent with the contemporary literature (e.g., Doyle and Walker, 2001; Fischer and Weber, 1998; Forbes and Klein, 1996; Henik, Rafal, and Rhodes, 1994; Mort et al., 2003; Reingold and Stampe, 2002; Sheliga, Brown, and Miles, 2002; Walker et al., 2000, 1998). In the strictest sense all saccades are in a sense voluntary in nature as an individuals can always stop him/herself from making a saccade (Carpenter, 1988) and we do not want to imply that the saccades made in the two-step paradigm are ever truly 'reflexive'. Even patients with frontal lobe damage, who are unable to prevent themselves from making pro-saccade errors in the anti-saccade task, are able to inhibit saccade generation to the same stimuli when asked to maintain fixation (Walker, Husain, Hodgson, and Kennard, 1998). Perhaps the closest a saccade can ever get to being truly reflexive, are the erroneous saccades that subjects appear to be unaware of having made in the anti-saccade task that are associated with short-latency secondary corrective saccades (Mokler and Fischer, 1999). The difference between stimulus-elicited (reflexive) and endogenous (voluntary) saccades should perhaps be considered as being on a continuum rather than a strict dichotomy, taking into account the different control processes involved in their generation (Amlôt and Walker, 2006). An abrupt stimulus-onset may have direct access to 'when' (trigger) processes leading to short-latency saccades. Anti-saccades are also generated following an abrupt stimulus onset, but in this case there is the requirement to inhibit one response and to generate a saccade (in the opposite direction) under endogenous control. Voluntary saccades made in the absence of a stimulus onset, such as symbolically cued saccades will rely entirely on endogenous signals for the generation of saccade metrics and for when decision processes and have the longest latency (Mort et al., 2003; Walker et al., 2000). Thus, the signals involved in the generation of when and when processes may be the most important factor in determining saccade latency.

In conclusion, the reduction in second saccade latency observed in the two-step paradigm in Experiments 1 and 2 here is suggestive of two saccades being programmed in parallel. Furthermore, in Experiment. 1 the latency of the first reflexive saccades was modulated in relation to the desired direction of the second voluntary response. First saccade latency was increased when the second step was to be made in a different direction relative to when the second step was to be made in the same direction. This interference effect supports the view that two saccades are being generated (at least in part) in a common motor map (Godijn and Theeuwes, 2002; McPeek et al., 2000). An advantage of the novel two-step paradigm used here is that it does not rely on an examination of a small proportion of erroneous trials and so it enables the behavioural characteristics of both the first and second saccades to be analysed quantitatively. This paradigm may also prove useful in functional imaging and transcranial magnetic stimulation (TMS) studies that could elucidate the underlying neural structures involved in parallel programming.

Acknowledgments

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