



Multimodal visual–somatosensory integration in saccade generation

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Abstract

Neurophysiological studies have demonstrated multisensory interaction effects in the neural structures involved in saccade generation when visual, auditory or somatosensory stimuli are presented bimodally. Visual–auditory interaction effects have been demonstrated in numerous behavioural studies of saccades but little is known about interaction effects involving somatosensory stimuli. The present study examined visual–somatosensory interaction effects on saccade generation using a multisensory paradigm, whereby task-irrelevant distractors appeared spatially-coincident with, or remote from the designated saccade target. Somatosensory distractors reduced the latency of saccades when presented before the visual target and the greatest facilitation effect was observed with spatially-coincident stimuli. Visual distractors spatially-coincident with a somatosensory target reduced latency (and increased peak velocity) when presented before and after the target. Visual distractors contralateral to somatosensory targets increased saccade latency and produced high error rates of saccades made to the distractor. The high error rates and latency modulation with visual distractors is consistent with a bias for visual stimuli in the saccadic system. In the visual target condition, saccade latency was modulated by a somatosensory distractor that was entirely task-irrelevant and this effect was always greatest with spatially-coincident distractors. The multisensory distractor effects are discussed in terms of saccades being programmed to the non-target modality, the early triggering of a non-spatial saccade ‘when’ signal, and multisensory neuronal enhancement effects.

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1. Introduction

Saccades are fast voluntary movements of the eyes made to align the high acuity fovea with objects and events of interest. Although typically regarded as involving the visual modality, saccades can also be directed to the location of sounds or tactile stimulation on the body’s surface. Studies of saccade generation have typically focused upon visual and auditory stimuli and their interaction, while studies involving somatosensory are rare and almost nothing is known about visual–somatosensory interaction effects. Groh and Sparks [10] were the first to examine the characteristics of somatosensory saccades (in man and monkey) and found that they had longer latency, lower peak velocity and were less accurate than saccades to visual stimuli (see also [1,22]). Multimodal interaction effects were examined behaviourally (in monkey only) by presenting visual and somatosen-

sory stimuli simultaneously at the same spatial location. Although there was a tendency for saccade latency to be reduced in the multimodal condition this did not always reach significance.

The absence of consistent visual–somatosensory interaction effects in Groh and Sparks’ study [10] contrasts with numerous demonstrations of multimodal interaction effects between the visual and auditory modalities [8,9,14,16,19], and with neurophysiological evidence of multimodal facilitation in neurons in the deep layers of the superior colliculus [17,30]. The deep layers of the superior colliculus (DLSC), a midbrain area involved in saccade generation [28], contains maps of visual, auditory and somatosensory space and provides a site where stimuli from different modalities can interact in the control of saccade generation [30]. Meredith and Stein [17] have shown that the firing rates of collicular neurons are enhanced when multimodal stimuli are presented coincidentally at the same spatial location and that this neuronal enhancement effect decreases as the spatial separation between stimuli increases. A number of behavioural

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studies have demonstrated visual–auditory interaction effects in saccade generation that appear to be consistent with the neurophysiological evidence of neuronal interactions observed in the DLSC. Behavioural studies of saccades have shown visual–auditory interaction effects when a saccade target is presented along with a task-irrelevant distractor from a different modality [8,9,14,16,19]. A consistent finding is a reduction in saccade latency when the visual and auditory stimuli are spatially-coincident, but latency increases as the spatial separation between the target and distractor increases [8,9,14,16,19]. These behavioural effects appear consistent with the neuronal enhancement observed in collicular neurons when multimodal stimuli are spatially-coincident, and neuronal depression observed when one stimulus falls outside the receptive field of the other [30].

The spatial and temporal relationship between target and distractor stimuli has been found to be critical in studies of visually guided saccades when competing visual distractors are presented. For example, a visual distractor presented remote from a visual target increases saccade latency ('the remote distractor effect') while visual distractors close to the target have little or no effect on latency but can modulate amplitude (see [5] for a recent review). The remote distractor effect is greatest with near simultaneous target–distractor onsets (± 50 ms), but if distractors appear at longer intervals before the target, latency is facilitated [34]. The facilitation effect observed when a remote distractor appears before the saccade target is thought to reflect a temporal warning signal effect [26,27] enabling early saccade triggering. In a similar fashion, a generalised warning signal effect might also account for the reduction in latency observed when auditory distractors are presented along with visual saccade targets [9,14]. By contrast, the increase in saccade latency observed with a remote visual distractor has been attributed to processes of competitive inhibition operating between separate populations of neurons within a 'saliency map' as is observed within the deep layers of the superior colliculus [38]. Models of saccade generation have been able to relate behavioural characteristics of saccades, such as the remote distractor effect, to competitive interactions within the superior colliculus [5,32].

Models of visual–auditory multimodal interaction effects [2,9,14] have related the effects of a crossmodal distractor on saccade latency to neuronal interactions within the intermediate and deep layers of the superior colliculus. The neurophysiological studies of Stein and Meredith [30] have shown that neurons in the superior colliculus respond to stimuli from the visual, auditory and somatosensory modalities and that the rate of activity of multimodal neurons is modulated when stimuli from more than one modality are presented together. Furthermore, this modulation depends critically on the spatial and temporal relationship between the multimodal stimuli [30], mirroring the effects that have been observed with visual stimuli [20,23]. To date few studies have examined the behavioural charac-

teristics of somatosensory saccades and almost nothing is known about visual–somatosensory interactions in saccade generation. Although visual–auditory multimodal interaction effects have been demonstrated it might be argued that this represents a special case, as a primary function of both the visual and auditory systems is to direct the eyes [15]. It is possible that crossmodal interaction effects may not be observed with visual–somatosensory stimuli in overt orienting behaviour such as saccade generation. Some indirect support for this view comes from studies of so-called inhibition-of-return (IOR) in covert orienting that have found only weak crossmodal IOR between vision and touch [31].

The present study was motivated, therefore, by the neurophysiological evidence of convergence and integration of multimodal (visual, auditory, and somatosensory) inputs in structures, such as the superior colliculus involved in the generation of saccadic eye movements [11,12,30]. Groh and Sparks [11] found that individual neurons in the SC responded to visual and somatosensory stimuli and most importantly that the same populations of neurons represented saccades to visual and somatosensory targets. Our aim was to investigate multimodal interactions between the visual and somatosensory modalities in human saccade generation. The following predictions were made (i) saccade latency will be facilitated when a saccade target is presented along with a spatially-coincident distractor from the other modality; (ii) saccade latency will increase when a saccade target is presented with a remote distractor from the other modality; and (iii) saccades to visual targets will have shorter latency, higher peak velocity, and be more accurate than those to somatosensory targets.

Multimodal visual–somatosensory interaction effects were examined in two experiments using a simple distractor paradigm that has been used in the visual modality to examine competitive interactions in saccade target selection [33,34]. In the first experiment, saccades were made to either visual or somatosensory targets while task-irrelevant distractors were presented at the same (coincident) or opposite location to the target. As there are known differences between the conduction rates of visual and somatosensory signals (collicular responses to somatosensory signals lag those to visual stimuli by some 30–40 ms [12]) a range of stimulus onset asynchronies (SOAs) between the onset of the target and distractor stimuli were used. The experiment was performed both with and without an additional auditory warning signal located in the fixation direction with the additional aim of elucidating the contribution of generalised spatially uninformative warning signals to multimodal interaction effects. In a second experiment, multiple somatosensory stimulus locations were used to examine the spatial nature of visual–somatosensory interaction effects. The findings of both experiments revealed evidence of visual–somatosensory interaction effects that were modulated by the temporal and spatial relationship between the visual and somatosensory stimuli.

2. Experiment 1

2.1. Method

2.1.1. Subjects

Six volunteers (three male, and three female) participated in the experiment. The age ranged from 19 to 35 years and all had normal or corrected to normal vision. Three were naive to the purposes of the experiment and were paid £10 for their participation.

2.1.2. Apparatus

Stimulus generators were mounted on an upright metal frame positioned at a distance of 40 cm from the observer (see Fig. 1A). A chin rest was used to maintain a constant viewing distance and reduce head movements. Visual stimuli were produced by small (3 mm) light emitting diodes

(LEDs) positioned 16.7° to the left and right of central fixation. A third LED positioned centrally served as a fixation stimulus. A piezoelectric speaker was mounted behind the central LED and provided an auditory ‘warning’ signal (high frequency white noise burst). Tactile stimuli were generated using linear actuators (TransDimension International Corporation, TDITAC) which were positioned directly behind each of the peripheral LEDs. Tactile stimuli were administered to the index finger of the subject’s outstretched hand. The linear actuators were driven throughout the stimulus onset period at a rate of 31.25 Hz and provided a silent but strong vibration to the subject’s fingertip.

Eye movements were recorded using a binocular video based eye-tracker (‘Eyelink’ SensoMotoric Instruments, GmbH). The eye-tracker was controlled by a Pentium PC that sampled the eye position signal at a rate of 250 Hz. A second PC connected by a remote Ethernet link was used to control the stimulus presentation sequence and to trigger the eye-tracker on each trial. Saccades were detected on a trial by trial basis using velocity ($22^\circ/\text{s}$) and acceleration ($8000^\circ/\text{s}^2$) criteria and written to disk for later analysis. An automated calibration routine, which involved tracking a small stimulus from the centre of the screen to positions left and right of centre, was performed at the start of each block of trials.

2.1.3. Procedure

Subjects were tested in the dark and were unable to see the position of their outstretched hands or the metal framework. They completed two experimental sessions defined by target modality (visual or somatosensory). Each session lasted approximately 1 hour and consisted of four blocks of trials (96 trials in each), two with an auditory warning signal and two without, which were interleaved within a session (ABAB design counterbalanced across subjects).

The stimulus timing sequence was as follows (see Fig. 1B). Each trial started with the onset of the central LED, which remained on for a random period chosen in 1 ms steps between 1000 and 1500 ms. The target onset was simultaneous with the offset of fixation (zero gap). On warning signal trials, a broad band noise burst was presented from the central speaker, 200 ms before target onset, for a duration of 90 ms. Targets and distractors were presented from the peripheral stimulus generators for a duration of 400 ms. The interval between target and distractor onset varied: distractors could appear simultaneously with the target (0 ms) or at intervals of 50 or 150 ms before or after the target onset. Each block contained 16 trials for each of the five SOA intervals and 16 single target trials producing 96 trials per block. These trial types were randomly assigned within a block and there were equal numbers of left and right-sided targets. Distractors could appear either coincident, or opposite, to the target with equal probability (50:50) and were therefore entirely non-predictive of target direction.

Subjects were instructed to fixate the central LED at the start of each trial and to make a saccade to the visual (or

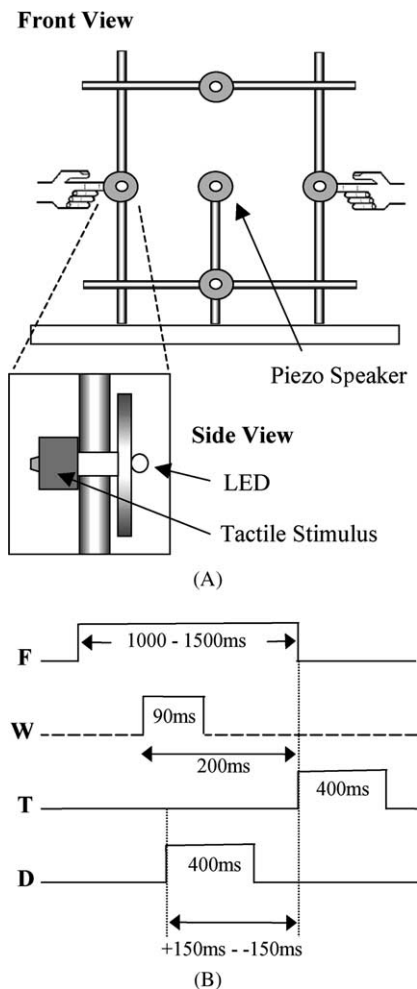


Fig. 1. (A) Framework for presenting visual (LED's) and somatosensory (linear actuators) stimuli. Subjects made eye movements to visual or somatosensory targets presented to the left or right of central fixation. A Piezoelectric speaker at fixation produced a broad band noise burst on warning signal trials only. (B) Schematic representation of trial events. F: fixation; W: warning signal; T: target; D: distractor.

tactile) target as quickly and as accurately as possible. They were also told that on some trials, distractors from the other modality would be presented at either the same or opposite location to the target but that distractors were task-irrelevant and they should try to ignore them.

2.2. Results

Any trial contaminated by a blink or where deviation of initial fixation was greater than 1 degree were excluded. Saccades with a latency less than 80 ms were regarded as anticipations [37] and those with a latency greater than the mean plus 2.5 times the standard deviation regarded as not being stimulus driven. Saccades were also excluded if the amplitude was less than 10° or greater than the mean amplitude plus 2.5 times the standard deviation. In the visual target conditions, 6.82% (S.D. = 10.70) of trials were excluded according to these criteria. In the tactile target conditions this figure increased to 12.71% (S.D. = 5.85) and the majority of these exclusions were due to saccades falling outside of the amplitude criteria. In the visual target condition 36.98% (S.D. = 20.72) of saccades were excluded as anticipatory when accompanied by a coincident tactile distractor presented 150 ms before the target. This figure was reduced to <2% with a 50 ms SOA and <4% for all remaining SOA intervals. Saccades were also excluded if they were made in the wrong direction (to the distractor on ‘opposite’ trials—see Table 1). Trials for left and right saccades and from the two separate blocks were collapsed together producing 32 single target trials and 16 trials in distractor conditions for each SOA. The mean latency of ‘correct’ saccades for all six subjects is plotted in Fig. 2.

2.2.1. Visual targets—somatosensory distractors

The mean percentage of erroneous saccades made to the distractor (direction errors) is shown in Table 1. Subjects rarely made directional errors to opposite-side somatosen-

sory distractors except when they appeared 150 ms before the onset of the saccade target. In the 150 ms SOA condition directional errors were high and occurred on some 34–38% of trials, error rates at all other SOAs were low (in the region of <2%).

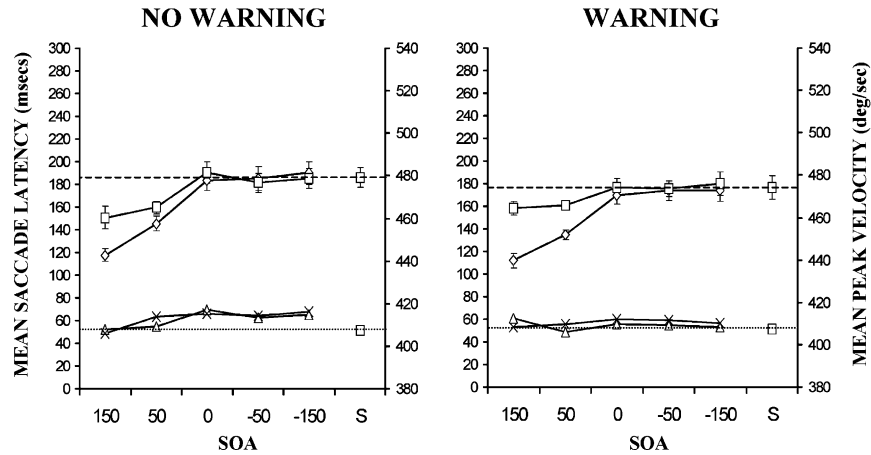
The mean latency for saccades made to unimodal visual targets was 186 ms in the no warning signal condition and was reduced to 177 ms in the auditory warning signal condition, however, this difference was not significant ($t(5) = 2.14$, $P = 0.086$). Somatosensory distractors modulated saccade latency but only when they appeared before the onset of the visual target in which case latency was reduced compared to the unimodal target condition. The greatest facilitation effect was observed with spatially-coincident distractors. A three-way ANOVA (warning signal (2), distractor location (2) and SOA (5)) revealed significant main effects of distractor location ($F(1, 5) = 51.43$, $P < 0.01$) and SOA ($F(1.07, 5.37) = 20.45$, $P < 0.01$) and a significant two-way interaction effect between distractor location and SOA ($F(4, 20) = 12.385$, $P < 0.001$). Mean saccade latency was significantly faster to targets with spatially-coincident distractors versus opposite side distractors, and a latency reduction was observed when distractors appeared before the saccade target. There were no other significant main effects or interactions. Paired t -tests were used to perform planned comparisons of saccade latency in distractor conditions and the unimodal (single target) condition. Spatially-coincident somatosensory distractors presented 50 and 150 ms before the visual target produced a reliable latency facilitation effect in both warning ($t(5) = 4.80$, $P < 0.01$ and $t(5) = 4.35$, $P < 0.01$, respectively) and no warning signal conditions ($t(5) = 9.74$, $P < 0.001$ and $t(5) = 9.39$, $P < 0.001$). By contrast, somatosensory distractors opposite to the target significantly reduced latency when presented 50 ms before the target in the no warning signal condition only ($t(5) = 3.80$, $P < 0.05$).

Table 1
Mean percentage of saccades made to opposite-side distractors in Experiment 1^a

Target	Stimulus onset asynchrony (SOA)				
	150 ms	50 ms	0 ms	-50 ms	-150 ms
Visual (errors %)	37.5 (20.9)	1.0 (2.6)	1.0 (2.6)	0.0 (0.0)	0.0 (0.0)
No warning (latency ms)	68.4 (28.5)	–	–	–	–
<i>n</i>	36	1	1	–	–
Visual (errors %)	34.4 (20.1)	2.1 (3.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Warning (latency ms)	57.3 (43.4)	–	–	–	–
<i>n</i>	36	2	–	–	–
Somatosensory (errors %)	39.6 (15.1)	25.0 (13.7)	18.8 (25.3)	19.8 (18.3)	8.3 (12.3)
No warning (latency ms)	98.8 (61.3)	156.7 (54.7)	213.4 (52.2)	224.6 (46.3)	363.4 (78.0)
<i>n</i>	38	24	18	15	8
Somatosensory (errors %)	40.6 (9.5)	36.5 (16.5)	17.7 (11.5)	15.6 (20.4)	9.4 (14.1)
Warning (latency ms)	56.9 (42.6)	143.5 (35.1)	180.9 (46.2)	231.5 (37.3)	289.2 (129.6)
<i>n</i>	39	35	17	15	9

^a The mean latency of these direction errors is shown (S.D. in parenthesis).

A. Visual Targets



B. Somatosensory Targets

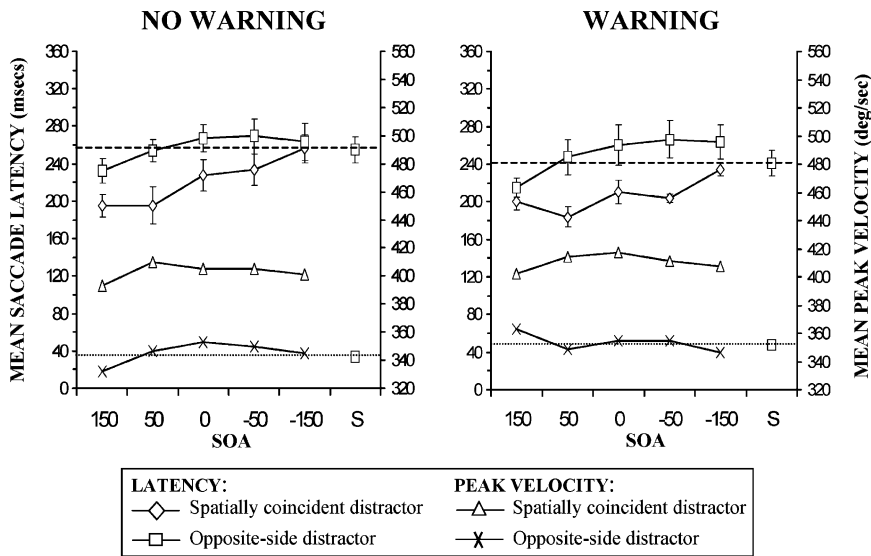


Fig. 2. Mean latency and peak velocity of saccades made in the visual (A) and somatosensory (B) target conditions as a function of SOA (bars = 1 S.E.M). Unimodal single (S) target latency (dashed lines) and peak velocity (dotted lines) are indicated across the figures. No auditory warning signal conditions are presented on the left, warning signal conditions on the right.

Fig. 3A and B show latency distributions for saccades to visual targets when accompanied by a 150 and 50 ms coincident somatosensory distractor in the warning signal conditions. In the 150 ms condition, the distribution of accurate responses are unimodal and fast ($M = 114$ ms). Taken from the onset of the distractor, a proportion of saccades are at approximately the equivalent latency for somatosensory saccades (240–250 ms). It is likely, therefore, that many of these saccades were triggered by the somatosensory distractor, and this observation is supported by the high number of directional and anticipation errors in this condition. In the 50 ms condition, however, few directional errors were made and the absence of any bimodality in the latency distribution suggests that subjects were not employing a separate strategy of responding to the somatosensory distractor. In the somatosensory distractor conditions (Fig. 3C and D),

the distribution of saccade latencies are broad and the directional error rates were high. It is likely, therefore, that saccades were triggered by both the somatosensory targets and visual distractors in these conditions.

2.2.2. Somatosensory targets—visual distractors

Directional error rates were high in the somatosensory target condition and subjects frequently made saccades to visual distractors presented opposite to the target across all SOAs (see Table 1). Error rates were highest (approximately 40% of trials) when distractors appeared 150 ms before the saccade target (no warning signal conditions: $\chi^2(5, n = 103) = 24.82, P < 0.01$; warning signal conditions: $\chi^2(5, n = 115) = 30.26, P < 0.01$). Subjects continued to make errors on approximately 8–20% of trials even when distractors appeared simultaneously and after the saccade target.

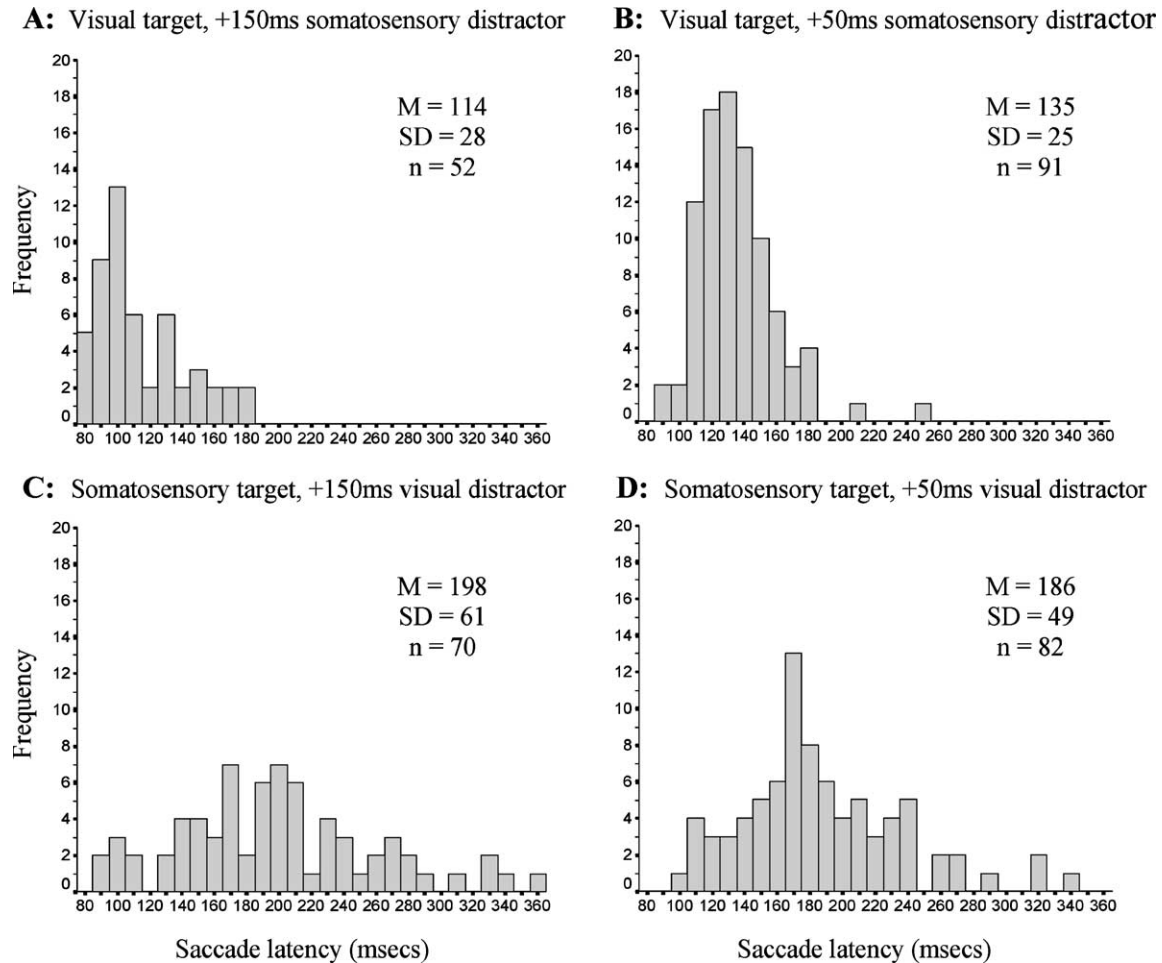


Fig. 3. Distributions of saccade latency for all subjects ($n = 6$), upper panels (A and B) are saccades to visual targets, lower panels (C and D) saccades to somatosensory targets in the coincident distractor conditions at SOA's of 150 ms (left panels) and 50 ms (right panels).

The mean latency of saccades made to visual distractors are shown in Table 1. The latency of these visually-guided saccades is somewhat greater than that observed to a single visual target (approx. 180 ms). For example, when the distractor preceded the target by 150 ms the mean latency is 57 and 99 ms in the warning and no warning conditions, respectively, which shows that the saccade were initiated some 207 and 249 ms after the onset of the visual distractor. Visual distractors presented 50 and 150 ms after the somatosensory target produced errors on 8–20% of trials, with a mean latency from distractor onset ranging from 175–213 ms. This is comparable to the latency of visually-guided saccades and indicates the dominance of the saccadic system for visual stimuli—any pre-programming of a somatosensory saccade is vetoed and a new saccade program started from the time of distractor onset with little additional cost.

The latency of unimodal somatosensory saccades was approximately 255 ms in the no warning signal condition and 241 ms in the warning signal condition ($t(5) = 1.64$, $P > 0.05$), some 70 ms greater than for visually-guided saccades. Somatosensory saccade latency was modulated by

visual distractors and a reduction in latency (compared to the unimodal condition) was observed with spatially-coincident distractors at all SOAs. Saccade latency was increased in all opposite-side distractor conditions except when the distractor appeared 150 and 50 ms before the somatosensory target in the no warning signal conditions, and 150 ms in the warning signal conditions. A three-way within-subjects ANOVA revealed significant main effects of distractor location ($F(1, 5) = 11.14$, $P < 0.05$) and SOA ($F(4, 20) = 23.35$, $P < 0.01$) but the two-way interaction effect between distractor location and SOA was not significant ($F(4, 20) = 2.62$, $P = 0.066$). Overall, mean saccade latency was significantly faster to targets with spatially-coincident distractors versus opposite side distractors, and a latency reduction was observed when distractors appeared before the saccade target. Paired t -tests were used to perform planned comparisons of saccade latency in distractor conditions and the single target condition. The latency reduction associated with coincident visual distractors was significant in the no warning conditions with SOA's of 150 ms ($t(5) = 10.42$, $P < 0.001$), 50 ms ($t(5) = 3.35$, $P < 0.05$), 0 ms ($t(5) = 2.77$,

$P < 0.01$). In the warning signal condition, the latency reduction was significant at SOA's of 150 ms ($t(5) = 3.45$, $P < 0.05$), 50 ms ($t(5) = 3.50$, $P < 0.05$), -50 ms ($t(5) = 3.44$, $P < 0.05$) but not with simultaneous (0 ms) target–distractor onsets ($t(5) = 1.76$, $P = 0.14$) or -150 ms ($t < 1$). Opposite-side visual distractors produced a significant latency facilitation effect when presented 150 ms before the somatosensory target in the warning signal condition only ($t(5) = 3.16$, $P < 0.05$). A significant increase in latency was observed when opposite-side visual distractors appeared at intervals of -50 ms ($t(5) = 3.88$, $P < 0.05$) and -150 ms ($t(5) = 2.77$, $P < 0.05$) after the target in the warning signal condition only.

2.2.3. Saccade peak velocity

The peak velocity (see Fig. 2) of saccades to unimodal visual targets ($407^\circ/\text{s}$) was greater than that observed under somatosensory target conditions ($347^\circ/\text{s}$). A three-way within-subjects ANOVA (warning signal (2), distractor location (2) and SOA (5)) was conducted for each target modality (the no distractor condition was not included). For visual saccades there were no significant main effects nor interactions, therefore, somatosensory distractors had no influence on the peak velocity of saccades made to visual targets. By contrast, a significant main effect for distractor condition ($F(1, 5) = 18.66$, $P < 0.01$) indicated that peak velocity was greater for somatosensory saccades when visual distractors appeared at the target location (mean $407^\circ/\text{s}$) than when they were on the opposite side (mean $350^\circ/\text{s}$). The increase in peak velocity was observed across all SOA's and is comparable to that of saccades to visual targets. No other main effects or interactions were significant. The observed increase in peak velocity for saccades to somatosensory targets with coincident visual distractors could be attributed to a modulation of saccade amplitude (as saccades to visual targets will be more accurate). To investigate this possibility, an identical three-way within-subjects ANOVA was performed to compare the amplitude of somatosensory saccades made with coincident and contralateral visual distractors. No main effects nor interactions were significant ($F < 1$), therefore, the increase in saccade peak velocity in the coincident distractor condition is not readily attributable to a modulation of saccade amplitude but could be due to saccades being initiated to the visual stimulus.

2.3. Discussion experiment 1

Experiment 1 has demonstrated multimodal interaction effects between the visual and somatosensory modalities on human saccade latency. Spatially-coincident task-irrelevant somatosensory distractors reduced the latency of saccades to visual targets, but only when the distractor preceded the target. Opposite-side somatosensory distractors reduced saccade latency but only in the no warning signal condition at 50 ms SOA which may be attributed to a warning signal effect for somatosensory stimuli. Spatially-coincident visual

distractors reduced the latency of somatosensory saccades, when presented before and after, the target. Opposite side visual distractors produced a small latency reduction when presented before the visual target, but increased latency when presented simultaneously and after the visual target (warning signal condition only). High error rates were observed with contralateral visual distractors even when they were presented -150 ms after the somatosensory target, a finding that demonstrates a strong bias in the saccadic system for visual stimuli.

The bias of the saccadic system for visual stimuli indicates that saccades may have been directed towards visual distractors in the somatosensory target condition, even though the distractors were entirely task-irrelevant, non-predictive of target location and the target modality was kept constant throughout each block. This might be expected when the distractor appeared before the target and could also occur with near simultaneous target–distractor onsets due to the faster neural conduction rate of visual stimuli [12]. Thus, the difference in latency between the coincident and contralateral distractor conditions might be because ipsilateral saccade latency contains a proportion of saccades made to the visual distractor and not the somatosensory saccade target. By contrast, correct saccades made in the contralateral visual distractor conditions must have been directed to the somatosensory target alone. This possibility was examined post-hoc as follows: The erroneous visually-guided saccades directed to contralateral visual distractors were included in the calculation of mean latency for the contralateral distractor condition (thereby reducing mean latency for this condition only). For the no warning condition (0 ms SOA) the difference in mean latency for coincident and contralateral distractors when the erroneous saccades were included was 24 ms ($t(5) = 1.66$, $P = 0.16$). In the warning signal condition (0 ms SOA) the mean difference was 31 ms ($t(5) = 1.75$, $P = 0.14$). So, when the erroneous visually-guided saccades are included in the analysis saccade latency remained faster in the coincident distractor condition, but there is no significant difference between the two conditions. This supports the idea that the latency difference may be due to the exclusion of visually-guided saccades in the opposite-side distractor condition only.

A further observation from Experiment 1 was that there was no observable influence of the auditory 'warning signal' on saccade latency. The absence of a warning signal effect is in contrast with the generalised latency reduction observed in other studies. One possibility is that in the present study the use of an auditory warning signal requires the processing of a third modality and subjects may have found it difficult to make use of this information, while simultaneously trying to ignore task-irrelevant distractors that were from a different modality to the target.

The most convincing demonstration of visual–somatosensory interaction effects from Experiment 1 is the reduction in saccade latency observed with coincident somatosensory distractors when presented 50 ms before the

visual saccade target. At this interval, the somatosensory and visual signals would be expected to arrive near simultaneously on multimodal neurons in the superior colliculus and it is unlikely that a saccade would be programmed to the distractor modality in advance of the target onset. However, the use of only two somatosensory stimulus locations leads to the possible criticism that the observed reduction in latency with coincident stimuli reflects either pre-cueing of saccade direction or a generalised hemispheric arousal effect. A restricted number of spatial locations were used due to the practical limitations imposed when presenting somatosensory stimuli. Subjects have only two hands on which to present tactile stimuli and these tend to be poorly localised in the dark [3]. Despite these practical constraints we extend the range of somatosensory stimuli by presenting visual saccade targets and somatosensory distractors at four different locations in a second experiment designed to further examine visual–somatosensory interaction effects.

3. Experiment 2

Experiment 2 was performed with the aim of examining the spatial nature of multimodal visual–somatosensory interaction effects. The number of possible target and distractor locations was increased as far as possible (given the practical constraints imposed by somatosensory stimulation) and saccades were made to four visual targets located in the upper and lower quadrants of each visual field (see Fig. 4). Task-irrelevant somatosensory distractors were presented to the index and little finger of either hand located directly behind the visual saccade target. A blocked design was used in which subjects made saccades in the visual

modality while ignoring the tactile distractors, an auditory warning signal was again used on every trial. Four SOA intervals were used (150, 50, 0 and –50 ms) so distractors appeared before, simultaneously with and after the visual target. The predictions were (i) somatosensory distractors will reduce saccade latency when presented before the visual target; (ii) the latency facilitation effect will be greatest with coincident distractors; (iii) distractors in the opposite visual field will increase saccade latency.

3.1. Method

3.1.1. Subjects

Six volunteers (four male and two female) participated in the experiment. The age ranged from 24 to 35 years and all had normal or corrected to normal vision. Four were naive to the purposes of the experiment and were paid £5 for their participation.

3.1.2. Procedure

The apparatus and general method were as described for Experiment 1. Subjects completed one experimental session lasting approximately 1 hour, consisting of six blocks of trials. The stimulus generators were positioned 35° above and below the horizontal meridian on a circle with a radius of 12° centred on the fixation stimulus (see Fig. 4). A fifth LED positioned centrally served as a fixation stimulus.

Somatosensory (distractor) stimuli were applied to the fingertips of the index and little fingers of each hand at a distance of 40 cm. Distractors could appear in one of four possible locations—coincident with the target, horizontally-aligned but vertically opposite (e.g. target on index finger, distractor on little finger of the same hand),

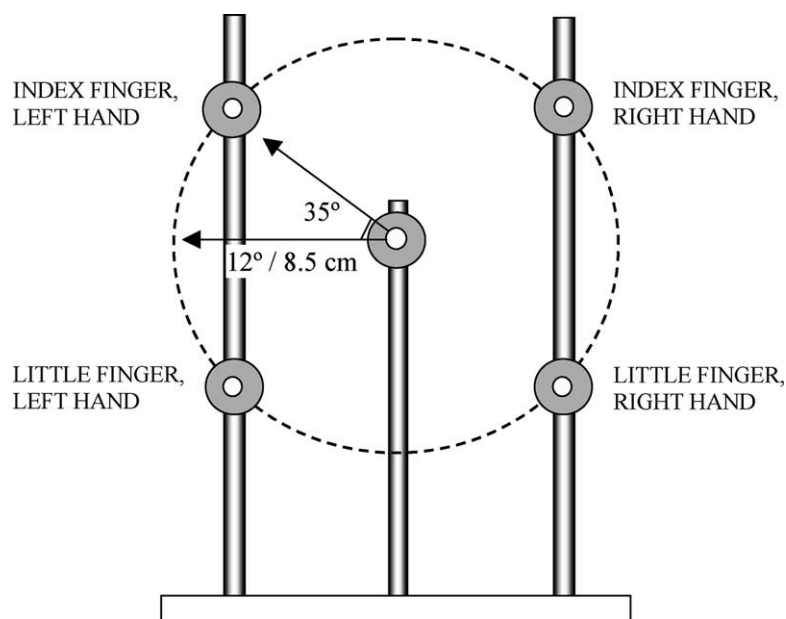


Fig. 4. Stimulus display used in Experiment 2. Visual and somatosensory stimuli were delivered as described in Experiment 1.

vertically-aligned but horizontally opposite (e.g. target on left index finger, distractor on right index finger), or positioned diagonally opposite to the target (e.g. target on right index finger, distractor on left little finger). Target and distractor locations were randomly assigned within a block, ensuring that distractors were entirely non-predictive of target location.

Each trial started with the onset of the central LED, which remained on for a random period chosen in 1 ms steps between 1000 and 1500 ms. The target onset was simultaneous with the offset of fixation (zero gap). An additional auditory warning signal was used in all trials (as in Experiment 1). Targets and distractors were presented for a duration of 400 ms. The interval between target and distractor onset (SOA) varied: distractors could appear simultaneously with the target (0 ms), or at intervals of 50 and 150 ms before the target onset or 50 ms afterwards. Each distractor block contained 16 trials for each of the four SOA intervals and 16 single target trials producing 80 trials per block. These trial types were randomly assigned within a block and there were equal number of trials for each target position.

The experimental session began with two localisation blocks of 40 trials each (preliminary analysis showed that subjects had difficulties localising the somatosensory stimuli in the dark and so dim background illumination was used). In the first block, the subjects made eye movements to single somatosensory stimuli presented randomly at each stimulus location and then single visual targets in the second block. The stimulus timing was identical to the distractor blocks, however, no warning signal or distractors were presented. Subjects were instructed to fixate the central LED at the start of each trial and to make a saccade to the visual target as quickly and as accurately as possible. They were also told that on some trials tactile stimuli would be presented at one of the four distractor locations but that distractors were task-irrelevant and they should try to ignore them.

3.2. Results

Any trial contaminated by a blink was excluded. Saccades with a latency less than 80 ms were again regarded as anticipations and those with a latency greater than the mean plus 2.5 times the standard deviation regarded as not being stimulus driven. Saccades were also excluded if the amplitude was less than 9° or greater than 15°. The mean percentage of trials in all conditions excluded according to these criteria was 4.81% (S.D. = 3.94). Saccades were also excluded if they

were made in the wrong direction. Subjects only made directional errors when the tactile distractor was presented 150 ms before the visual target. In this situation, directional errors were highest in the horizontally-aligned distractor condition (22.92%; S.D. = 9.41), followed by the vertically-aligned (15.63%; S.D. = 11.00) and diagonally opposite (15.63%; S.D. = 8.62) distractor conditions. Fewer directional errors were made in the coincident distractor (6.25%; S.D. = 6.85) and single target (4.17%; S.D. = 3.23) conditions. Subjects were able to accurately localise both visual and somatosensory stimuli. Fig. 5 shows the trajectories of saccades made by two subjects to visual and somatosensory stimuli under conditions identical to those used in Experiment 2. Visual and somatosensory mean saccade latency, deviation of amplitude, deviation of saccade end-point and peak velocity are shown in Table 2. It can be seen that somatosensory saccades were less accurate and showed greater variability of end-point than saccades made to visual targets.

An examination of the saccades made by the six subjects in the localisation blocks showed that saccades to somatosensory targets have longer mean latency (274 ms) than saccades to visual targets (186 ms), slower peak velocity (somatosensory: 377°/s; visual 452°/s) than their visual counterparts. A series of two-way ANOVAs were performed with two within-subjects factors—target modality (2) and target location (4)—for each of these measures. There were no significant main effects, nor interactions for mean amplitude and endpoint deviation. This suggests that despite a small decrease in accuracy for somatosensory saccades, there was no significant difference in localisation accuracy between the two modalities nor the four target locations under the current conditions (dim lighting, hands visible). Significant main effects of target modality for saccade latency ($F(1, 5) = 92.10$, $P < 0.001$), and peak velocity ($F(1, 5) = 8.56$, $P < 0.05$), suggest that visual saccades have a significantly faster latency and peak velocity compared to somatosensory saccades. These support the findings for saccades to single somatosensory and visual targets observed in Experiment 1.

Trials for all four target positions from each of the four separate blocks were collapsed together producing 64 single target trials and 16 trials in distractor conditions for each SOA. The mean latency of ‘correct’ saccades for all six subjects is plotted in Fig. 6. The mean latency for saccades made to unimodal visual targets was 171 ms. Somatosensory distractors modulated saccade latency when presented both before and after the visual targets. When presented at 150 and 50 ms before the target, somatosensory distractors

Table 2
Characteristics of saccades made to visual and somatosensory stimuli in localisation blocks^a

Target modality	Mean saccade latency (ms)	Deviation of amplitude (°)	Deviation of endpoint (°)	Peak velocity (°/s)
Visual	185.7 (19.4)	0.96 (0.17)	2.6 (0.4)	451.8 (45.33)
Somatosensory	273.6 (33.9)	1.65 (0.65)	3.4 (0.8)	376.9 (56.3)

^a Measures include mean latency, mean deviation of amplitude from target amplitude (12°), mean deviation of saccade endpoint, and mean peak velocity (S.D. in parenthesis).

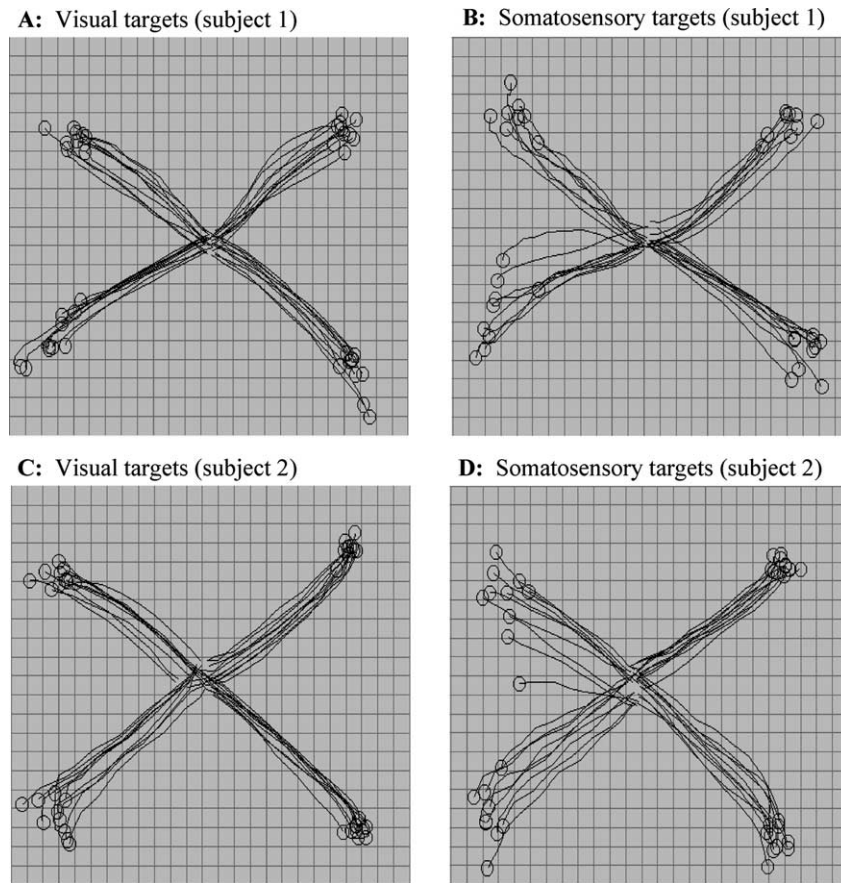


Fig. 5. Trajectory plots of saccades made by two subjects in the localisation trials to visual (A and C) and somatosensory (B and D) stimuli with dim background illumination. Open circles show saccade endpoints. Stimulus locations were as used in Experiment 2.

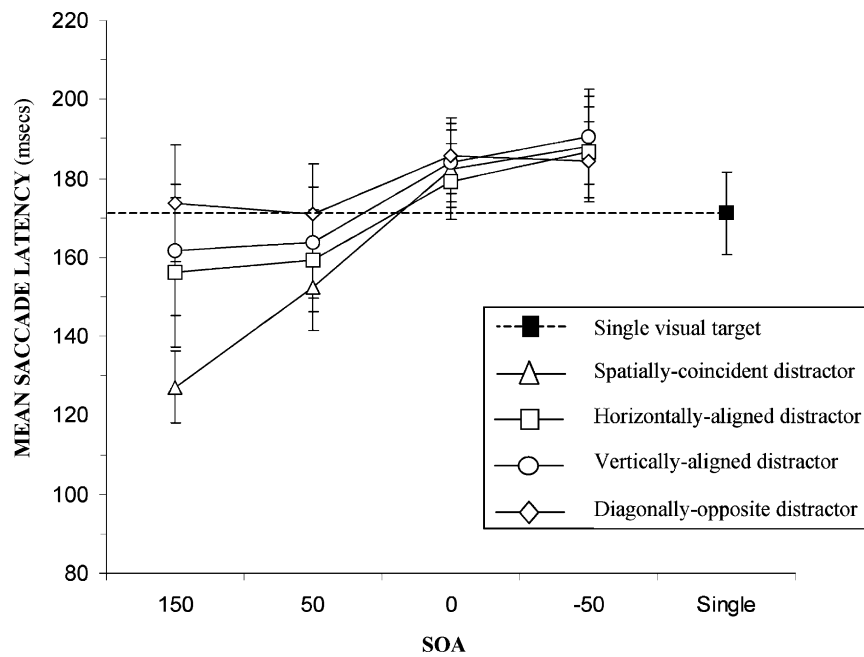


Fig. 6. Mean latency (bars = 1 S.E.M) of saccades made to visual targets as a function of SOA in Experiment 2. The mean latency of saccades made to unimodal (single) targets is also shown (dashed line).

reduced latency in all but the diagonally-opposite distractor condition. The greatest facilitation effect was observed with spatially-coincident distractors at both SOA's.

These results were examined in a two-way ANOVA (distractor condition X SOA) which revealed significant main effects of distractor condition ($F(3, 15) = 15.24$, $P < 0.001$) and SOA ($F(3, 15) = 26.87$, $P < 0.001$). Mean saccade latency was significantly faster to targets with spatially-coincident distractors versus vertically aligned and diagonally opposite distractors, and a significant latency reduction was observed when distractors appeared 150 ms before the saccade target, compared to distractors appearing simultaneously with or 50 ms after the target. A significant interaction between distractor condition and SOA ($F(9, 45) = 6.70$, $P < 0.001$) confirmed the observed differences between coincident and spatially disparate distractor conditions at early SOA's. A series of planned comparisons were performed to investigate each distractor condition versus the unimodal visual target condition. Repeated measures *t*-tests revealed a significant reduction in saccade latency for coincident somatosensory distractors occurring at 150 ms ($t(5) = 14.8$, $P < 0.001$) and 50 ms ($t(5) = 5.21$, $P < 0.01$) before the visual target. Both horizontally- and vertically-aligned distractors reduced saccade latency when presented before the visual target, however, this was only close to significance for the horizontally-aligned distractors at 50 ms ($t(5) = 2.42$, $P = 0.06$) and non-significant for all other distractor and SOA combinations ($t < 1.3$). When presented simultaneously with or after the visual target, somatosensory distractors increased saccade latency compared to unimodal visual targets, and this difference was significant for all distractor conditions (coincident 0 ms, $P < 0.05$; -50 ms, $P < 0.01$; horizontally-aligned 0 ms, $P < 0.05$; -50 ms, $P < 0.01$; vertically-aligned 0 ms, $P < 0.01$; -50 ms, $P < 0.01$; diagonally opposite 0 ms, $P < 0.01$; -50 ms, $P < 0.05$).

3.3. Discussion experiment 2

Experiment 2 was performed to examine visual–somatosensory interaction effects with multiple somatosensory distractor locations. Subjects made saccades to visual targets and on some trials somatosensory distractors were applied to the subjects' fingertips located directly behind each of the four visual targets. The distractors were entirely task-irrelevant and were presented at a range of SOA's. Saccade latency was significantly reduced when somatosensory distractors were presented 50 or 150 ms before the saccade target, but only when applied to the ipsilateral hand, with the largest facilitation effect being observed with spatially-coincident distractors. Distractors presented on the contralateral hand, prior to the onset of the saccade target, did not reduce saccade latency. An increase in latency was observed when distractors were presented simultaneously or 50 ms after the onset of the visual target. This latency increase was observed when distractors were presented to

either the ipsilateral or contralateral hand. This non-spatial interference effect may be due to a shift of attention to the non-target modality that interferes with the ongoing saccade programme initiated by the onset of the visual target. A similar argument has been made for costs associated with exogenous shifts of attention to distractors that produce a cost on manual response times when the target is from a different modality [29].

The large reduction in saccade latency observed with spatially-coincident distractors when they appear 150 ms before the saccade target might arise as at least some saccades may be initiated to the task-irrelevant distractor. A crude estimate of saccade latency based on this assumption can be made using the mean latency for somatosensory saccades from Experiment 1 (240 ms). Saccades triggered by a somatosensory stimulus presented 150 ms before the target onset would therefore have a mean latency around 90–100 ms which is within the range of observed mean latency in this condition (125 ms). The large reduction in latency observed in the 150 ms SOA condition could therefore be due to a number of saccade being made to a task-irrelevant distractor, a view supported by the high directional error rates (15–22%) observed in the 150 ms condition only. A further possibility for the reduction in latency when distractors preceded the target is that the distractor may have a generalised warning signal effect (despite the use of an auditory warning signal) that enables some pre-programming of the saccade trigger signal. This could account for the small reduction in latency observed with both horizontally- and vertically-aligned distractors, although if this was the case it is not clear why it was not found with diagonally opposite distractors also.

The most compelling evidence of a multimodal facilitation effect, that could be attributed to multimodal neural summation effects, is the reduction in latency observed when somatosensory distractors appeared 50 ms before the visual target. In this condition (50 ms SOA) differences in neural conduction rates for the stimulus modalities should result in both signals activating collicular neurons at approximately the same time. This assumption is based on the neural response rates reported by [12] who found that bimodal SC neurons responded some 40 ms (S.D. 15 ms) faster for visual than somatosensory stimuli.¹ If the visual and somatosensory signals reach the SC approximately simultaneously then there is no reason why a saccade should be pre-programmed to the somatosensory distractor. A significant latency reduction was observed in the 50 ms condition and this was greater for spatially-coincident distractors than when the distractor was presented horizontally-aligned (ipsilateral hand). Although a reduction in latency was

¹ Shorter neural conduction rates for somatosensory stimuli have been reported but these were based on the stimulation of hair follicles and whiskers in the cat [30]. The estimates provided by Groh and Sparks [12] were based on pulsating vibratory tactile stimuli presented to the monkeys paws which more closely matches the conditions used in the present study.

observed with horizontally-aligned distractors this effect was smaller than that observed with spatially-coincident distractors. The coincident distractor effect could be attributed to crossmodal neural summation effects rather than saccades being triggered to the distractor. This view is supported by the absence of directional errors when the distractor was at non-target locations.

4. General discussion

The present study was performed to examine visual–somatosensory interaction effects in human saccade generation. Behavioural evidence of multisensory interaction effects was revealed in Experiment 1 by a reduction in saccade latency with spatially-coincident distractors in the other modality. The latency facilitation effect with spatially-coincident distractors was observed for both target modalities, in both warning and no warning signal conditions, and was greatest when distractors preceded the target. A smaller facilitation effect was also observed when opposite-side (contralateral) somatosensory distractors appeared before a visual target. Multisensory interactions were also revealed by an increase in latency with contralateral visual distractors when presented simultaneously, or after, the somatosensory target. In Experiment 2 multiple somatosensory distractor locations were used to exclude the possibility that the crossmodal facilitation effect may have been due to either a directional (left or right) cueing effect or a generalised hemispheric arousal process. A spatially-coincident distractor facilitation effect was observed when distractors preceded the target and the effect was greater than that observed with distractors presented to either the ipsilateral or contralateral hand. The observed multisensory distractor effects on saccadic performance may involve a number of different mechanisms, which should not be regarded as mutually exclusive.

At least part of the observed crossmodal latency facilitation effects might involve the distractor providing a ‘warning signal’, which gives temporal information about the forthcoming target onset [9,14]. Warning signal explanations have been invoked to account for a portion of the reduction in saccade latency (‘gap effect’) observed when a central visual fixation stimulus is removed simultaneously or before the onset of the saccade target [24,26]—the release of activity of fixation neurons [20,21] accounts for the remaining reduction. The parallel programming of spatial (‘where’) and non-spatial (‘when’) channels has been emphasised in a recent model of saccade generation [5]. The spatial program controls saccade metrics while the temporal pathway controls saccade initiation. In the present study distractors were not predictive of target direction but may have initiated the non-spatial ‘when’ program prior to target onset. This early triggering could account for the non-spatial warning signal effects, but cannot explain why our distractor effects were greatest with spatially-coincident distractors. Furthermore, spatially-coincident distractor facilitation effects were ob-

served in Experiments 1 and 2 on trials that incorporated an additional auditory warning signal, indicating that not all of the latency reduction can be attributed to temporal warning-signal effects.

One plausible explanation of the spatially-coincident distractor facilitation effect is that saccades may have been programmed to the distractor and were not restricted to the target modality. It is important to note in this context that the distractors were entirely non-predictive of target direction and that subjects had prior instructions of target modality, which remained constant throughout a block. Hence, any such effect would still reveal a major limit in control over saccades to task-relevant versus irrelevant modalities. In some conditions, however, a saccade program may have been automatically generated following distractor onset prior to generation of the target saccade. This might be expected when distractors led the targets (positive SOAs) or when the distractor was processed faster than the target. The speed of processing may be of particular relevance with somatosensory targets and visual distractors, as saccades to visual stimuli typically have shorter latency than somatosensory saccades [10], and because visual signals may reach the superior colliculus before somatosensory signals, (visual = 61 ms, somatosensory = 97 ms under conditions similar to those in the present study [12], but see also [30] who reported shorter somatosensory transmission rates with hair/whisker stimulation in the cat). The reduction in somatosensory saccade latency with spatially-coincident visual distractors observed in Experiment 1 could therefore be attributed to saccades being triggered by the visual distractor. This interpretation is supported by high number of directional errors observed with opposite-side visual distractors and the increase in the peak velocity of somatosensory saccades with spatially-coincident visual distractors which is comparable to that of visually-guided saccades. It should be noted that the result of faster saccades to somatosensory targets with spatially-coincident rather than opposite visual distractors holds up even when directional errors (visually-guided) for the opposite distractor condition are included in the latency analysis, however, this difference is no longer significant (see Section 2.3).

In Experiment 1, the latency of saccades to visual targets was reduced by both spatially-coincident and opposite-side somatosensory distractors when they preceded the saccade target, but the reduction was greatest with spatially-coincident distractors. Moreover, the smaller facilitation effect produced by opposite-side somatosensory distractors was significant only in the no warning signal condition which indicates a non-spatial warning signal effect may contribute to the reduction in saccade latency. Spatially-coincident somatosensory distractors did not modulate saccade peak velocity and directional errors were infrequent in this condition. The pre-programming of a saccade to the distractor thus seems unlikely to provide the whole explanation of the latency reduction observed with somatosensory distractors. If a saccade was pre-programmed

to an opposite-side distractor then an increase in latency might be predicted when the target then appears in the opposite direction due to the additional cost of cancelling one saccade program and initiating another to the saccade target (see [25]), but no such delay was found in Experiment 1. Moreover, the differential effects observed on latency with coincident and opposite-side distractors indicates that more than one underlying process may be involved (e.g. both non-spatial temporal alerting, and also spatially-specific effects). In Experiment 2, a greater range of somatosensory distractor locations was used and saccades were made to visual targets. A multimodal distractor facilitation effect was again observed with spatially-coincident somatosensory distractors and this effect was greater than that observed when a distractor was presented at the non-target location of the ipsilateral hand. Critically, the coincident distractor effect was observed when the distractor preceded the target by 50 ms making it unlikely that the latency reduction was due to the pre-programming of a saccade to the distractor. The reduction in saccade latency observed with spatially-coincident distractors might be attributed, in part, to a neural summation effect [30].

Neurophysiological studies have demonstrated multimodal neuronal enhancement effects, in structures involved in saccade generation, with spatially-coincident visual, auditory and somatosensory stimuli. Meredith and Stein [30] showed that the firing rate of approximately half of the neurons in the colliculus are enhanced when multimodal stimuli are presented coincidentally, and that this enhancement effect decreases as the spatial separation increases. Behavioural studies of audio–visual interaction effects (in cat [30] and human [9]) have revealed effects that mirror those observed at neural level. The spatially-coincident distractor facilitation effects could involve both temporal warning signals and spatially-specific neural effects [9]. Frens et al. [9] found that coincident auditory distractors facilitated the latency of visually-guided saccades and that the effect was reduced as the distractor to target spatial separation increased. They proposed a detailed model with two components that were related to the neurophysiology of the saccadic system. Visual and auditory stimuli project to the deep layers of the colliculus and when in close spatial proximity can facilitate pre-saccadic activity, but when spatially separate activity may be reduced due to lateral inhibition (as in the remote distractor effect [33]). The auditory distractor is also thought to provide a temporal warning signal that exerts a non-specific inhibitory effect on brainstem omnipause neurons releasing the inhibitory effect on the brainstem burst generator. A similar model could be invoked to account for the visual–somatosensory interaction effects observed in the present study. Coincident and opposite side distractors may reduce latency due to a warning signal effect enabling the temporal preparation of a saccade in advance of the target, while spatially-coincident distractors may produce an additional enhancement due to neural summation (see [2] for a similar two-stage model of

visual–auditory facilitation effects). The caveat suggested by the present results is that visual stimuli are dominant in the saccadic system as revealed by the high numbers of directional errors with opposite side visual distractors and the increase in peak velocity with spatially-coincident distractors. It is plausible that somatosensory stimuli are less salient for the saccadic system than visual (or auditory) stimuli as they activate fewer collicular neurons and smaller populations are sensitive to visual–somatosensory multimodal enhancement effects (estimated at 14–22% [30]). The absence of a remote distractor increase in saccade latency with opposite-side somatosensory distractors in Experiment 1 (versus its presence for visual distractors) could also reflect the bias for visual stimuli in neuronal responses.

The use of somatosensory stimuli as targets for goal-directed eye-movements leads to another important question regarding the mode of generation of this form of saccades. Saccades made to a peripheral visual onset are typically regarded as being ‘reflexive’ in nature as they are directed towards an exogenous stimulus, while anti-saccades are regarded as a form of voluntary saccade as they require the interpretation of an endogenous instruction [4,13]. When somatosensory stimuli are used, it is possible that the saccades are not truly reflexive but are a form of voluntary saccades similar to those saccades made on the basis of a symbolic cue or verbal instruction [35]. In a separate (unpublished) study we examined this possibility by comparing the latency of pro-saccades made to a peripheral somatosensory stimulus to that of anti-saccades made away from the same stimuli. We reasoned that if somatosensory saccades are a form of voluntary saccade then there should be little effect on latency of changing the instruction from ‘saccade towards’ to ‘saccade away from’ the target. The mean latency (six subjects) of somatosensory anti-saccades was some 100 ms greater than for somatosensory pro-saccades. This supports the view of Groh and Sparks that pro-saccades made to somatosensory stimuli are a form of exogenous saccade generated using the same neural structures as saccades made to a peripheral visual stimulus [10,11].

A further consideration regarding the mode of saccade generation arises in the contralateral distractor condition as saccades could be regarded as a form of crossmodal anti-saccades. A saccade made to the target will be directed away from the distractor and erroneous saccades made to the distractor will be directed away from the target. Fischer and colleagues have examined anti-saccades made in the visual modality when visual cues are presented contralateral to a visual anti-saccade target [6,7,36]. They found that valid contralateral pre-cues increased anti-saccade latency and error rates at short cue-lead times (around 100 ms), and that reaction time and error rates returned to normal levels as the cue lead time was increased (200–500 ms) [36]. Furthermore, subjects were often unaware of their pro-saccade errors although these were frequently followed by a secondary corrective saccade that had short latency (see also [18]).

These results have been attributed to different orienting mechanisms involved in pro- and anti-saccade generation that involve a fast acting automatic control process involved in generating pro-saccades to an abrupt visual onset and a slower voluntary mechanism for the control of anti-saccades [36]. The paradigm used in the present study could be regarded as a crossmodal analogue of the anti-saccade pre-cueing paradigm. In Experiment 1 an increase in latency and error rates was observed with contralateral visual distractors, although in contrast to the finding with anti-saccades described above, saccade latency was not increased when distractors preceded the saccade target. Furthermore, contralateral somatosensory distractors did not increase visual saccade latency and this could reflect the stronger modulation produced by visual stimuli on saccade generation. In this context it should be noted that smaller somatosensory distractor effects have also been found in crossmodal studies of curved saccade trajectories and it has been suggested that this could reflect the smaller numbers of neurons involved in encoding somatosensory stimuli for saccade generation (see [3]).

In conclusion, the present study has provided the first demonstration of visual–somatosensory interactions on the latency of saccadic eye movements. Multisensory interaction effects were most clearly demonstrated in the visual target condition. A latency facilitation effect was observed when somatosensory distractors appeared before the visual saccade target (in Experiment 1 and 2) and this effect was greatest with spatially-coincident stimuli. This multimodal facilitation effect may reflect both the early triggering of a non-spatial ‘when’ signal and a spatially-specific multimodal neuronal enhancement effects. A reduction in saccade latency was observed in the somatosensory target modality also, but only with spatially-coincident visual distractors. In this case, the peak velocity of saccades was increased, indicating that saccades may have been triggered to the visual distractor, against intentions. This demonstrates a strong bias of the saccadic system for visual stimuli despite the subjects intention to make a saccade in another modality. Visual distractors presented opposite to somatosensory targets increased saccade latency and this may reflect a multimodal remote distractor effect [33].

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