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Audio-visual integration and saccadic inhibition

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Abstract

Saccades operate a continuous selection between competing targets at different locations. This competition has been mostly investigated in the visual context, and it is well known that a visual distractor can interfere with a saccade toward a visual target. Here, we investigated whether multimodal, audio-visual targets confer stronger resilience against visual distraction. Saccades to audio-visual targets had shorter latencies than saccades to unisensory stimuli. This facilitation exceeded the level that could be explained by simple probability summation, indicating that multisensory integration had occurred. The magnitude of inhibition induced by a visual distractor was comparable for saccades to unisensory and multisensory targets, but the duration of the inhibition was shorter for multimodal targets. We conclude that multisensory integration can allow a saccade plan to be re-established more rapidly following saccadic inhibition.

Keywords: Saccadic inhibition, multisensory integration, visual distractors, race model analysis.

Introduction

Eye movements are usually studied in response to visual targets, but saccades can also be directed to auditory, tactile and multimodal stimuli (Corneil, Van Wanrooij, Munoz, & Van Opstal, 2002). When saccades are triggered by multimodal targets, a Multisensory Response Enhancement (MRE) is often observed, which can be expressed as a decrease in saccadic reaction time (SRT) and/or an increase in response force (Giray & Ulrich, 1993), suggesting that it might be partially due to co-activation within the motor system (Schmidt, Gielen, & Van den Heuvel, 1984). When considering the effect on SRTs, a certain amount of MRE could be explained by statistical facilitation, reflecting the increased probability that one or the other unisensory component of a bimodal stimulus will trigger a saccade. The upper boundary of MRE can be calculated from a 'race model', which holds that, if unisensory events are processed in separate channels, the cumulative probability of a response to a multisensory event can never exceed the sum of the cumulative probabilities of responses to the unisensory components (Miller, 1982; Raab, 1962). If the degree of MRE can be shown to violate this race model, by exceeding its upper boundary, it cannot be due solely to statistical facilitation, and this is diagnostic of multisensory integration (MI) of the unisensory inputs (i.e. neural co-activation) (Hughes, Reuter-Lorenz, Nozawa, & Fendrich 1994; Nozawa, Reuter-Lorenz, & Hughes, 1994).

An important neural structure in which MI has been shown physiologically, is the superior colliculus (SC). The SC is a multisensory structure located in the midbrain, and is the major subcortical centre for the planning of eye movements. In the intermediate and deep layers of the SC, visual information converges with auditory and tactile input (Meredith & Stein 1983; Stein & Stanford, 2008). When a

target is presented, build-up neurons for the target location increase their discharge rate up to a threshold level that triggers the brief discharge of burst-neurons prior to saccade execution (McPeck & Keller, 2002). When the target is accompanied by a stimulus from a different modality, the discharge of burst-neurons can be increased in a superadditive manner, indicative of MI (Meredith & Stein 1983; Perrault, Vaughan, Stein, & Wallace, 2003). The effects of MI are most powerfully observed when the unisensory stimuli are individually relatively weak, although MI occurs also with supra-threshold component stimuli (Meredith & Stein, 1983). MI is most likely when the sources of the signals are aligned in space and time, so that they stimulate a common portion of the SC spatial map within a critical time window (Meredith & Stein, 1983). Under these conditions, the physiological salience of multisensory stimuli (Meredith & Stein 1983; Rowland & Stein, 2007) and the neural response elicited differ significantly from those of the unisensory stimuli individually (Stein & Stanford, 2008), suggesting that multisensory stimuli are more strongly represented than unisensory stimuli in the target selection process.

One strategy, used often in the study of eye movements, to probe the strength of target representation, is to observe how the system responds to competing stimulation. A stronger target representation should be relatively more resistant to distraction from competing stimulation. Neurophysiological recordings from visual-auditory neurons in the cat SC suggest exactly this pattern, with multisensory responses less perturbed by competing stimuli than are unisensory responses (Pluta, Rowland, Stanford, & Stein, 2011). Pluta and colleagues did not investigate overt behavioural responses, but the behavioural prediction from their data is clear. Specifically, given the close association of the SC with eye-movements, we would

predict that saccades to multisensory targets should be less prone to distraction than saccades to unisensory targets.

The effects of distracting stimuli on saccades in humans are quite well understood, and very stereotyped, providing a firm basis for testing the above prediction. *Saccadic Inhibition* (SI) is a behavioural phenomenon first described by Reingold & Stampe (1999), that is revealed by means of a distributional analysis comparing the SRT distribution following a task-irrelevant visual transient (*i.e.* an abrupt onset of a visual stimulus) against that obtained under identical target conditions without the visual transient. The raw SI profile emerges from the histogram of differences between the SRT distribution in the distractor and the baseline conditions. It is now common to scale these raw differences by the baseline value at each time point to give a proportional difference (Bompas & Sumner, 2011). This step renders the recovered SI profile immune to variations in the underlying baseline distribution. The SI profile typically reveals that saccades are inhibited during a temporal window spanning between ~65-125 ms after the onset of the distractor, with maximum inhibition at around 90 ms. This pattern is obtained consistently across a range of exploratory and reactive eye movement tasks, including simple target-directed saccadic tasks (Buonocore & McIntosh, 2008, 2012; 2013; Reingold & Stampe, 2000; 2002; 2003; 2004).

The distributional analysis that is used to reveal SI affords a detailed description of the time-course of distraction and recovery-from-distraction, characterised usually in terms of three measures: *magnitude* (maximum amount of inhibition), *latency* (time to the maximum inhibition) and *duration* (duration of the period in which inhibition remains above 50% of its greatest strength). To some extent, these measures can vary independently, suggesting that they may be sensitive

to different aspects of the inhibitory process. For example, the physical properties of the distractor influences the SI profile, whereby changes in distractor luminance modulate both the magnitude and latency of inhibition (Bompas & Sumner, 2011), and changes in distractor size affect magnitude (and, more weakly, duration) but not latency (Buonocore & McIntosh, 2012).

Accordingly, if multisensory targets do indeed create a stronger target representation, less vulnerable to distraction, then possible differences in the SI profile might include any or all of a reduced magnitude of inhibition (reflecting a lower probability that saccades will be inhibited), an increased latency of maximum inhibition (reflecting an increased time necessary for the distractor to have maximum effect), or a reduced duration (reflecting a faster re-establishment of a saccade plan following inhibition). In order to test this prediction, however, expected differences in the time course of saccades to unisensory and multisensory targets should be taken into account. The hallmark of MI is that the response to the multisensory event is faster than that to either unisensory event in isolation so, assuming MI is obtained, we will see the SRT distribution for multisensory targets shift earlier in time relative to that for unisensory targets. On the other hand, the hallmark of SI, is that it is temporally specific, depressing saccadic behaviour within a tightly specified time-window (~65-125 ms) following distractor onset. Thus, if the distractor were simply presented at a constant time following target onset in unisensory and multisensory trials alike, it would impact upon a relatively later portion of the SRT distribution in the multisensory case. This is not problematic, in itself, if the SI profile is expressed as a *proportional* change of SRT frequency, to normalise across differences in the baseline level. However, the estimate of SI parameters will be most reliable if the distractor is timed so that SI impacts around the peak of the baseline distribution,

where baseline SI frequency is high; this will also maximise the chances that the full time-course will be captured, as a change from baseline can be measured only for active (i.e. non-zero) portions of the baseline distribution. Given these considerations, it is desirable to stagger distractor onset across conditions to offset baseline SRT differences and consistently target SI toward the peak of the baseline distribution, as well as using a proportional method to recover the SI profile. This should allow us to test for differences in vulnerability to distraction that probe the strength of the target representation, independent of the earlier timeframe of multisensory responses.

SI is an intriguing behavioural effect, the consistency of which makes it a powerful vehicle for studying the dynamic time-course of distraction in the saccadic system. The functional basis of SI is still debated, and may not be unitary (McIntosh & Buonocore, 2014; Walker & Benson, 2013; Casteau & Vitu, 2012). Nonetheless, it is highly likely that SI involves competitive interactions between subpopulations of build-up neurons in the intermediate layers of the SC (Reingold & Stampe, 2002; Buonocore & McIntosh, 2008) coding for spatially incompatible motor programs (Li & Basso, 2005; Munoz & Istvan, 1998; Olivier, Dorris, & Munoz, 1999). Given that these neural substrates overlap with those in which MI has been demonstrated neurophysiologically, (e.g. Frens & Van Opstal, 1998; Meredith & Stein, 1983; Pluta et al, 2011), SI seems an ideal behavioural phenomenon via which to probe for differences in the competitive strength of multisensory and unisensory saccade targets, predicted from the neurophysiological data.

Method

Participants

Nine participants (mean age= 24.24, SD = 2.33) took part to the experiment. All had normal or corrected-to-normal vision and gave informed consent prior to the experiment. This experiment was conducted in accordance with the 1964 Declaration of Helsinki and with the approval of the Psychology Research Ethics Committee at the University of Edinburgh

Method and general procedure

Visual stimuli were displayed on a mid-level grey background on a 19 inch CRT monitor (1024 x 768 pixels resolution) at 100 Hz. Participants were seated with their head in a chin rest and their eyes horizontally and vertically aligned with the centre of the screen at a distance of 80 cm. Eye movements were recorded with the EyeLink 1000 system (detection algorithm: pupil and corneal reflex, 1000-Hz sampling). A five point-calibration on the horizontal and vertical axis was run at the beginning of each session and after three consecutive blocks. Each trial began with a drift-correction followed by the fixation cross (0.5°) presented at the centre of the screen together with two outline squares ($1.65^\circ \times 1.65^\circ$) at 5° eccentricity on either side, acting as placeholders for audio targets. After a random period (500-1000 ms), the target was presented on the left or right side of fixation.

The target was either a black square ($0.3^\circ \times 0.3^\circ$: V) filling a placeholder box, an auditory tone (150 ms, 60 dB white noise burst: A) or a multisensory audio-visual target (simultaneous V and A: M). Auditory stimuli were presented through hidden loudspeakers at the vertical centre of the two screen edges, 5° more eccentric than the visual placeholder on the same side. The experimental set-up in the present study did

not allow for a complete spatial overlap between the V target and the A source due to the computer frame width ($\sim 2.5^\circ$) and the distance between the loudspeaker margins and the centre of the loudspeakers ($\sim 2.5^\circ$). The target-to-speaker distance sum up to $\sim 10^\circ$ that despite being a large difference we assumed to be acceptable based on previous result reporting strong MI between A and V stimuli appearing simultaneously with a comparable spatial misallocation (Hughes, Nelson, & Aronchick 1998), an assumption borne out by our data (which showed evidence of MI; see Results).

As illustrated in Figure 1, participants were required to fixate the fixation cross in the centre of the screen and to generate a single saccade toward any target (V, A or M) as soon as it appeared on the left or right side. In half of all trials, randomly shuffled, a white distractor flashed ($25.6^\circ \times 4.2^\circ$, D) for 33 ms, filling the top and bottom thirds of the screen. The distractor timing was adjusted individually per participant and target type, according to their baseline SRTs (see below). The auditory target lasted for 150 ms only (to avoid a protracted, aversive, white noise burst), whereas the visual target remained on-screen until the end of the trial.

For each participant and target type, baseline SRTs were assessed through a preliminary block of target-only trials, which randomly intermingled 50 visual, 50 auditory and 50 multisensory target trials (for each modality, half the targets were to the left, and half to the right of fixation). This allowed us to take account of baseline SRT differences, between individuals and between stimulus conditions, by standardising the onset of the distractor to impact upon an equivalent portion of the SRT distribution. For each participant separately and for each target type, distractor onset was determined by the formula: $D_{\text{onset}} = \text{median SRT} - 90 \text{ ms}$ (Buonocore & McIntosh, 2012, 2013, for similar procedures). Note that this timing implies that the

peak of SI (around 90 ms after distractor onset) should coincide approximately with the peak of baseline saccadic behaviour for that target type, so that the estimate of the SI profile should be reliable.

Following the preliminary block, 1080 trials were run (divided into four sessions of nine blocks of 30 trials each, lasting 120 min in total).

Results

Data screening

Saccades made in the wrong direction (3.53%), saccades of less than 1° amplitude (2.34%) and saccades with a latency of less than 70 ms (3.12 %) or more than 500 ms (2.11 %), were excluded. All analyses were collapsed across target side.

SRT analysis

Across participants, the average SRTs in the preliminary block of target only trials were: 232.11 ms (SD = 59.64) for visual, 242.78 (SD = 45.08) for auditory and 186.55 ms (SD = 37.47) for multimodal targets (see Table 1). These average SRTs were used solely to adjust the onset of the distractor, per participant and target type, according to the formula $D_{\text{onset}} = \text{median SRT} - 90 \text{ ms}$. Consequently, the average timings of the distractor were: 142.11 ms (range 74.21 – 245.34 ms; SD = 59.62) for visual, 152.78 ms (range 69.12 – 217.41 ms; SD = 45.11) for auditory and 96.57 ms (range 52.12 – 161.23 ms; SD = 37.47) for multimodal targets (see Table 1). As emphasised already, this procedure was adopted to compensate for the shorter latency of baseline saccades to multisensory targets, so that the temporal relationship between the distractor and the expected saccade was held constant.

Table 1 about here

For the subsequent experimental blocks, group mean saccadic amplitudes and SRTs are reported in Table 1. Separate three by two repeated measures ANOVAs were conducted for these variables, with target modality (visual, auditory, multisensory) and distractor (absent, present) as factors.

For amplitude, saccades were generally accurate (mean = 4.69°, SD = .25°), but amplitude was affected by target modality ($F(2,16) = 3.79$, MSE = .08, $p < .05$, $\eta_p^2 = .46$), with larger saccadic amplitudes towards auditory (4.85, SD = .29) in comparison to visual targets (4.59, SD = .09), presumably because the hidden loudspeakers were positioned more eccentrically than the visual placeholders (~12.5° vs. 5°). For amplitude, we did not record a significant effect of distractor ($F(1,8) < 1$, MSE = .01, $p = .99$, $\eta_p^2 = .00$) nor interaction ($F(2,16) < 1$, MSE = .03, $p = .52$, $\eta_p^2 = .08$). Notably, the amplitudes of saccades to M targets were not larger than saccades in the visual only condition. This result could be considered contrary to the well-known *global effect*, which describes the tendency for saccades to land at an intermediate position between two targets presented adjacent to one another (Pitts & McCulloch, 1947; van der Stigchel & Nijboer, 2013). In the present case, we suggest that the placeholder surrounding the visual target was sufficiently salient to ensure dominance of the visual signal in determining saccade amplitude.

SRTs were strongly affected by target modality ($F(2,16) = 20.91$, MSE = 951.55, $p < .001$, $\eta_p^2 = .72$) with saccades to M targets (197.54 ms, SD = 35.14) 53 ms faster on average than saccades toward V (250.62 ms, SD = 52.81, $t(8) = 7.3$, $p < .001$) or A targets (258.83 ms, SD = 47.18; $t(8) = 6.4$, $p < .001$), which did not differ

($t(8) = .62, p = .55$). SRTs were elevated significantly by the presence of a distractor (pooled data in distractor condition = 242.54 ms, SD = 40.40 vs. pooled data in non distractor condition = 228.79 ms, SD = 43.91; $F(1,8) = 30.6$, MSE = 951.55, $p < .01$, $\eta_p^2 = .72$), but this effect did not interact with target modality ($F(2,16) = 1.56$, MSE = 36.99, $p = .24$, $\eta_p^2 = .16$) (Figure 2a). Therefore, simply in terms of average SRTs, saccades to multisensory and unisensory targets were equally vulnerable to distraction. Note, however, that this initial outcome for average SRT will be reconsidered in light of the subsequent distributional analysis of SI profiles (Figure 2b).

Race model analysis

The analysis of average SRTs confirmed that participants responded to multisensory targets faster than to unimodal ones. To test whether this MRE exceeded the level that could be explained by simple statistical facilitation from multiple unimodal signals, we followed the general ‘race model’ method of Miller (1982). For each target condition (A, V, M and A+D, V+D and M+D), for the no distractor (Figure 3a) and distractor conditions (Figure 3b), cumulative probability distributions were calculated with a 4-ms bin resolution, and the values for conditions A and V (D and target-only condition) were summed in order to obtain the upper limit of the distribution predicted by the race model at each point in time (RM and RM+D, respectively). As can be seen in Figures 3a and 3b, this upper boundary was exceeded, regardless of the presence of a distractor.

The statistical significance of these RM violations was tested following an established procedure (Laurienti, Burdette, Maldjian, & Wallace, 2006). First, a difference curve was calculated for each participant, by subtracting the predicted

summed probability (RM) from the multisensory (AV) probability at each time bin (Figures 3c and 3d). A one-sample t-test was then performed at each time bin, to compare this difference to zero, and significant ($p < 0.05$) deviations were identified. Multisensory integration in the target-only condition was significant over a broad temporal range (136-204 ms), with a peak of 12.82 % performance benefit at 172 ms (Figure 3c). In the D condition, the latencies of saccade responses to multisensory exceeded those predicted by the race model in a narrower temporal range, ranging from 168 to 192, with a maximum gain in performance of 10.75 % benefit at 180 ms (Figure 3d).

These data demonstrate that MI did occur. Beyond this, it might seem tempting to conclude that MI was partially disrupted by the presence of a distractor, since violations of the race model were less extensive in distractor conditions. However, we must caution against this conclusion. Our method demanded that the distractor was onset at different times in the A+D, V+D and AV+D conditions, with the earliest distractor onset in the AV+D case, to compensate for the speeding of baseline SRTs for multisensory targets. Thus, the AV+D distribution in Figure 3b is measured in the context of a distractor that onset (on average) around 97 ms after the target, but the RM distribution against which it is compared is calculated by summing A+D and V+D distributions measured in the context of distractors that onset relatively later (153 and 142 ms after the target respectively). Thus, the A+D and the RMD distributions have not been obtained under comparable distractor conditions, rendering any direct comparison (at least beyond the start of the distractor influence) problematic. For this reason, we make no attempt to formally compare the extent of RM violation between the target-only and D conditions.

Distributional analysis of SI profile

SRT distributions were analysed in order to detect SI. For each participant and condition, a percentage frequency histogram of SRTs (bin width 4 ms) was created, and a 7-point moving-window-average smoothing function was applied. The proportional difference of distractor from baseline frequency was calculated for each bin according to the formula: $(baseline-distractor)/baseline*100$ (Bompas & Sumner, 2011). As noted in the Introduction, the use of a proportional difference measure has the effect of normalising relative to the baseline, allowing us to be confident that any observed difference in SI between conditions is genuine, and not induced by differences in the underlying baseline distributions. To avoid artefacts caused by dividing by a very low baseline frequency, we excluded (early and late) portions of the distributions for which the baseline frequency was lower than 1%. Three parameters were then extracted for each participant in each condition: the magnitude of the inhibition (maximum of the proportional difference histograms), the latency of the inhibition (time to the maximum) and the duration (the time spanning between 50% of the dip minimum on either side of the minimum). To illustrate the overall patterns, the group average proportional difference histograms per condition are shown in Figure 2b.

Figure 2 about here

Separate repeated measure ANOVAs by target modality (V, A, M) were run on the three parameters (Table 1). Inhibition magnitude did not differ between the three target modalities ($F(2,16) = 1.72$, $MSE = 130.82$, $p = .17$, $\eta_p^2 = .17$), and nor

did its latency ($F(2,16) < .00$, $MSE = 1298.58$, $p = .99$, $\eta_p^2 = .001$). However, the duration of inhibition was significantly affected by target modality ($F(2,16) = 10.3$, $MSE = 760.70$, $p < .001$, $\eta_p^2 = .56$). The duration of the inhibition was shorter for saccades to M targets than those to A and V targets ($t(8) = 6.83$ and $t(8) = 3.76$ respectively, both $p < .01$). We did not find any difference between A and V targets ($t(8) = 1.40$, $p = .23$). Multisensory targets were thus more robust to inhibition in the sense that SI was more transient, suggesting that an inhibited saccade plan could be re-established more rapidly to a multisensory target.

Discussion

We investigated the influence of visual distractors on the execution of saccades toward multisensory targets. We first replicated the finding that saccades to multisensory targets were faster than their unisensory counterparts, showing evidence of multisensory integration (Colonius & Diederich, 2004). This MRE was due to the multisensory integration rather than statistical facilitation, as confirmed by a significant violation of the RM, diagnostic of an underlying neural summation (or co-activation) prior to saccade initiation (Hughes et al. 1994; Nozawa et al. 1994).

Further analysis focused on a detailed distributional analysis of SRT. The characteristic SI profile was observed following the visual distractor, being maximal on average at 97 ms after flash onset (cf. Reingold & Stampe, 2002; Buonocore & McIntosh, 2008), and this time-course did not differ significantly according to the unisensory or multisensory nature of the targets. It is worth noting that, if the distractor had been onset an equal delay following the target, then the influence of the distractor would have affected different portions of the underlying response distribution, which was shifted relatively earlier in the multisensory condition. Our

method explicitly took account of baseline SRT differences, timing the distractor to onset correspondingly earlier in the multisensory target condition, so that a reliable proportional SI profile could be obtained relative to the central part of the baseline distribution. Using these methods, we found that saccades to multisensory targets were not less vulnerable to distraction than their unisensory counterparts. This is consistent with SI acting within the oculomotor neurons of the intermediate SC, probably via lateral inhibition mechanisms (Olivier, Dorris, & Munoz, 1999), so that a visual distractor exerts equivalent suppression on a target representation, regardless of the sensory modality of the target. Indeed, we found that a distractor in one modality (visual) can produce a typical SI profile for saccades to targets in another modality entirely (auditory) (see also Ten Brink, Nijboer, Van der Stoep, & Van der Stigchel, 2014). Congruent with this cross-modal equivalence, Edelman and Xu (2009) showed a strong but typical SI for endogenously generated saccades to a memorised target. The suppressive component of SI may thus impact similarly within the intermediate SC regardless of the sensory inputs that elicit the target activation.

On the other hand, the recovery component of SI may differ according to the sensory inputs, having an influence on the duration of the inhibition. Specifically, we found that the SI duration was reduced for multisensory targets compared to the unisensory conditions ($A+D= 120$; $V+D= 105.78$; $M+D= 63.33$ ms). The interpretation of the *duration* of SI is still not well established in the literature. We suggest that our data might imply that saccade plan to multisensory target signal can recover more rapidly following distraction, presumably because of the increased number of excitatory inputs at the location of the saccade target. We infer that the nature of SI is fundamentally the same across the different conditions, but the multimodal target has a faster recovery from suppression for much the same reason as

SRTs are generally shorter to multisensory targets. Such an interpretation will however need to be established by further investigations.

Notably, this is the first study within the SI literature manipulating the physical characteristics of the target. So far, studies on SI have been manipulating mainly distractor related characteristics and have often reported an effect on the SI parameters extracted by the inhibitory profiles (Bompas & Sumner, 2009; Buonocore & McIntosh, 2012). Here, by manipulating the characteristics of the target we observe an effect on the overall duration of the inhibition. The present results have been obtained for multimodal targets and it remains to be seen whether they are specific to multimodal targets, or would apply to any manipulation enhancing the strength of the target representation (e.g. target salience). Moreover, given the spatial disparity between the visual and auditory source during the audio-visual target presentation, future studies should also evaluate the effect of multiple sources of unisensory targets (i.e. both visual or auditory) on SI, to compare with the multisensory condition.

On a neurophysiological level our main findings can perhaps be explained by lateral interactions in the SC, which are known to have a local facilitation and a longer-range inhibition effect (Munoz & Istvan, 1998). We suggest that MI can increase the excitatory inputs related to the target and the inhibitory inputs related to the distractor; in our particular experiment it was the target representation that received the multisensory boost. Our behavioural data mimic the pattern of single-cell activations within the intermediate and deep layers of the SC. While recording from this site, Bell, Meredith, Van Opstal, & Munoz (2005) described how the neural activity elicited by an auditory stimulus located in the hemifield contralateral to the multisensory target, produced a competition between neuronal activities in the two different locations (see also Munoz & Istvan, 1998). This inhibitory long distance

mechanism might potentially be the source of the longer SRTs observed in our study. Pluta et al., (2011) addressed a similar question via single cell recordings from SC neurons, showing that the MI is reflected in enhanced activity in SC motor maps, and that such multisensory neuronal responses are more resistant to inhibition than those evoked by unisensory targets. (Pluta et al, 2011).

Alternatively, a faster recovery of the multisensory guided saccades might be due to a higher attentional allocation toward multisensory targets. The automatic capture of attention by multisensory events is well described in the literature (for a review, see Koelewijn, Bronkhorst & Theeuwes, 2010). Buonocore and McIntosh (2013) showed that both endogenous and exogenous allocation of attention can modulate SI magnitude. One could argue that the accessory tone added in the multisensory condition aided the automatic capture of attentional resources, enhancing the target representation in such a way that the flash event would have been less salient. However, our result showed a similar SI magnitude across the three conditions, in contrast with the effect reported by Buonocore and McIntosh (2013) where the magnitude itself was modulated by attentional factors. On this basis, we strongly favour the alternative hypothesis, whereby the main factor driving the shorter SI duration is the multisensory integration of the target representation.

In conclusion, our data indicate that MI can influence the SI effect by reducing the duration of the inhibition, partially confirming single neuron recordings in primates SC (e.g. Pluta et al., 2011). Furthermore, SI has appears to have a cross-modal equivalence, being essentially oculomotor in nature, rather than a purely visual phenomenon.

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Table 1. Mean and standard deviation for the inhibition parameters (magnitude, Lmax and duration)

SI parameters							
	<i>SRT -preliminary trials (ms)</i>	<i>Distractor onset</i>	<i>SRT-experimental trials (ms)</i>	<i>Amplitude (deg)</i>	<i>Magnitude (%)</i>	<i>L max (ms)</i>	<i>Duration (ms)</i>
A	242.78 (45.08)	152.78 (45.11)	253.97 (18.02)	4.86 (0.37)	-	-	-
V	232.11 (59.64)	142.11 (59.62)	242.35 (22.61)	4.61 (0.17)	-	-	-
M	186.55 (37.47)	96.57 (37.47)	190.05 (14.57)	4.59 (0.25)	-	-	-
A+D	-	-	263.70 (18.28)	4.82 (0.25)	62.62 (20.54)	77.33 (39.75)	120.00 (64.97)
V+D	-	-	258.90 (19.74)	4.58 (0.12)	68.35 (21.62)	77.44 (64.55)	105.78 (56.16)
M+D	-	-	205.04 (13.83)	4.67 (0.24)	58.36 (18.54)	79.34 (35.77)	63.33 (44.13)

Note: SI=saccadic inhibition; magnitude=minimum of the difference histograms; Lmax=time to the minimum; duration=time spanning between 50% of the dip minimum on either side of the minimum.

Figure 1.

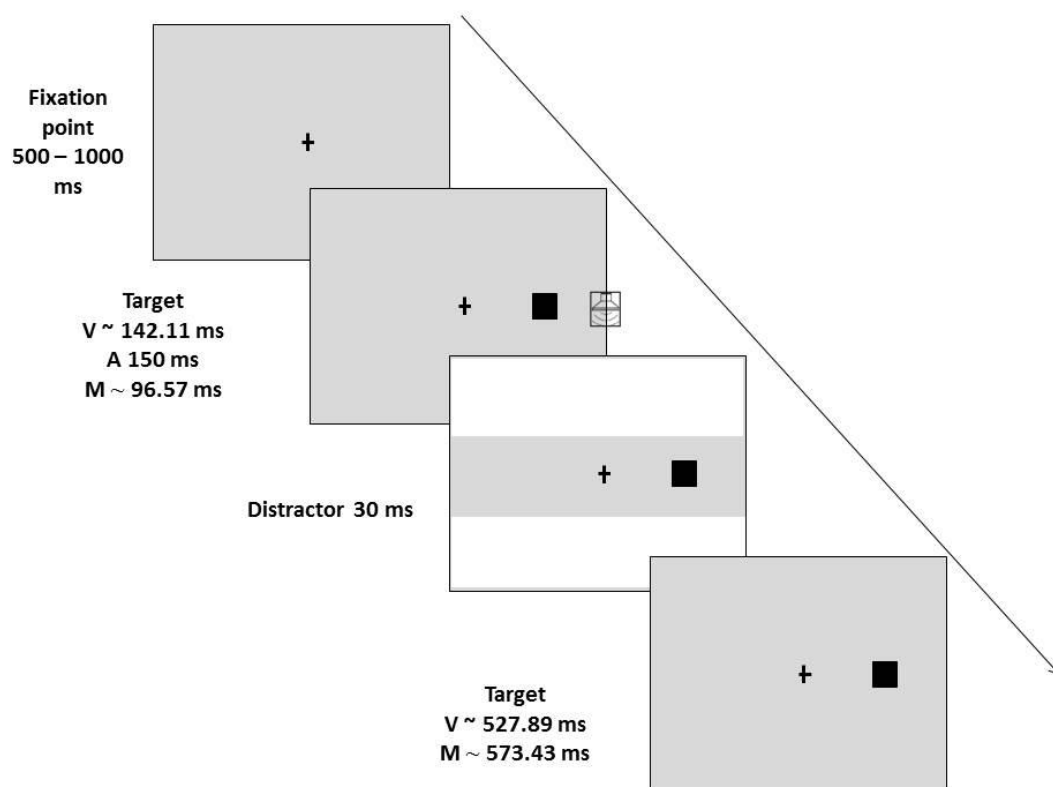


Figure 1. Representation of a typical experimental distractor trial with the timeline (not in scale). The initial fixation cross (500-1000 ms) was followed by the target (visual= V, auditory= A, multisensory= M), appearing randomly on the left or right side. The V target was followed by a white 30 ms flashing zone (Distractor; see Reigold & Stampe, 2002 for similar setup) on average after 142.11 ms, and offsets after 700 ms. The A target offsets after 150 ms and was followed by the distractor on average 152.78 ms after its onset. The M target consisted of V and A stimuli presented simultaneously, and was followed by a distractor on average after 96.57 ms. Similarly to unisensory conditions, the V stimulus composing the M target offsets after 700 ms whereas the A stimulus after 150 ms.

Figure 2.

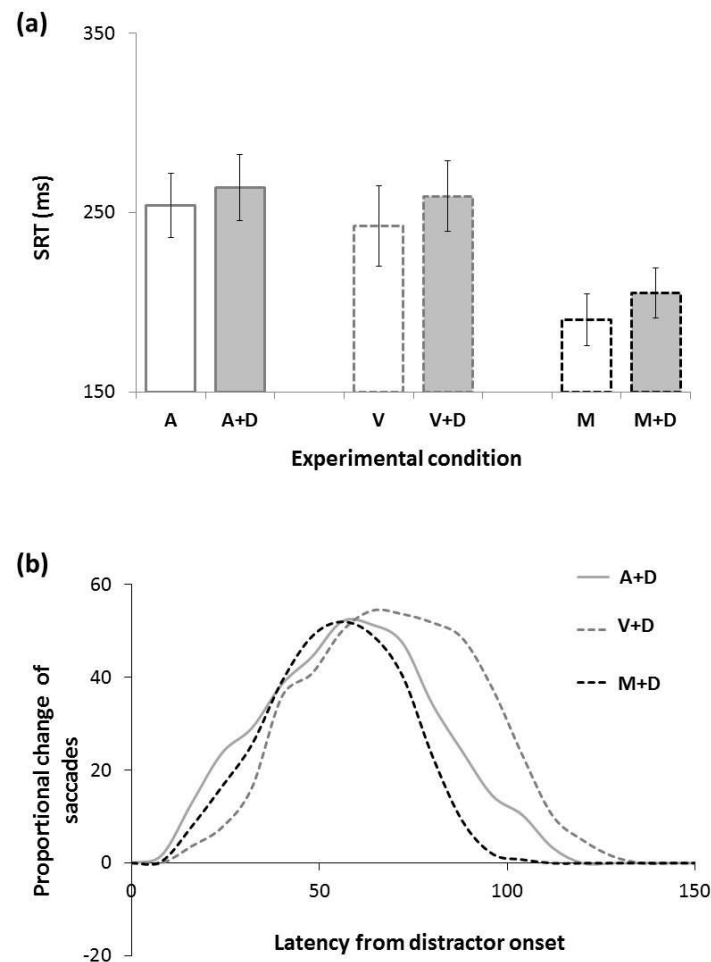


Figure 2. a) Average SRTs (ms) for the auditory (A), visual (V) and multisensory (M) target and target + distractor (A + D, V + D, M + D). **b)** Average proportional difference histogram of the magnitude of inhibition the three targets and distractors. Note that the analysis was not performed on the overall average histogram (which is shown only for illustrative purposes) but on parameters extracted from individual participants' histograms, reported in Table 1.

Figure 3.

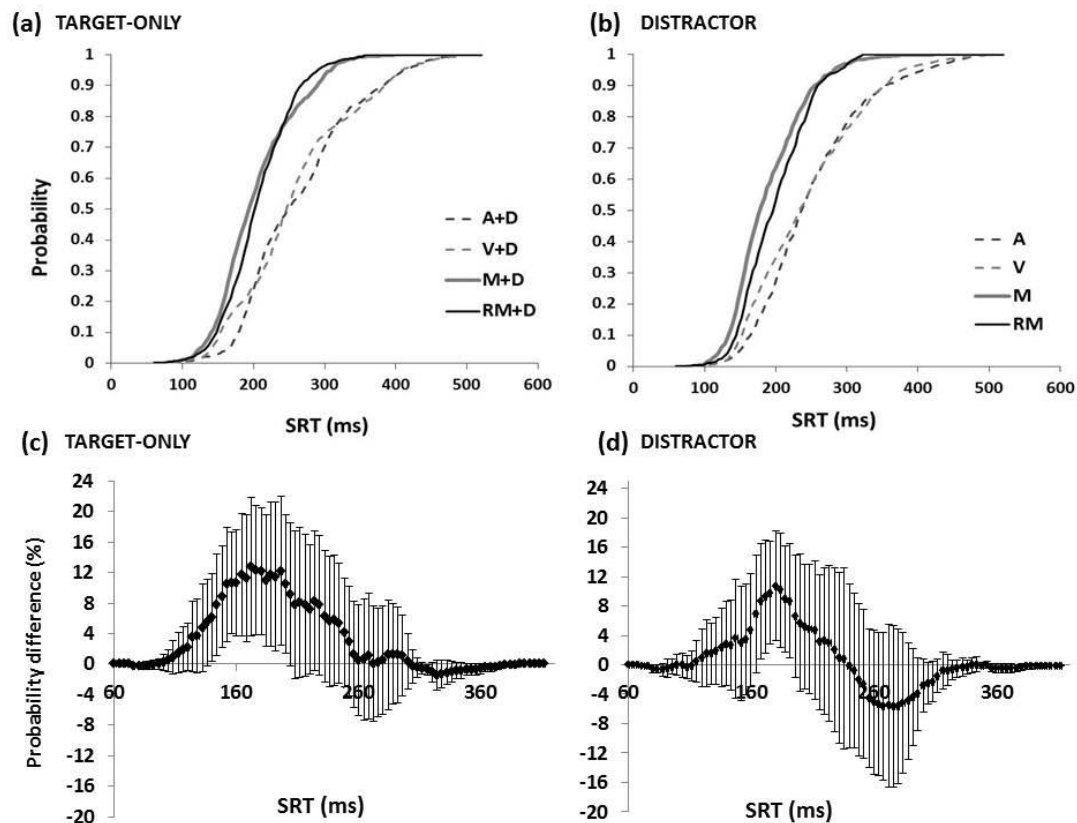


Figure 3. Cumulative SRT distributions (averaged across participants) for the three target conditions and the upper boundary of the RM, both for target-only (RM; **a**) and distractor (RM+D; **b**) conditions. (**c**, **d**) The cumulative probability difference (95% confidence interval) curve illustrates the enhancements under multisensory conditions when compared to the race model prediction for target-only (**c**) and distractor (**d**) condition.