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Antimo Buonocore^a & Robert D. McIntosh^b

^a Department of Psychology and Cognitive Science, University of Trento

^b Human Cognitive Neuroscience, Psychology, University of Edinburgh

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Attention modulates saccadic inhibition magnitude

Antimo Buonocore¹, Robert D. McIntosh²

¹Department of Psychology and Cognitive Science, University of Trento

²Human Cognitive Neuroscience, Psychology, University of Edinburgh

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Corresponding Author:

Dr Antimo Buonocore

Department of Psychology and Cognitive Science

University of Trento

Corso Bettini, 31

38068, Rovereto (TN)

Tel: +39 0464 808728

antimo.buonocore@unitn.it

Abstract

Visual transient events during ongoing eye movement tasks inhibit saccades within a precise temporal window, spanning from around 60-120 ms after the event, having maximum effect at around 90 ms. It is not yet clear to what extent this *saccadic inhibition* phenomenon can be modulated by attention. We studied the saccadic inhibition induced by a bright flash above or below fixation, during the preparation of a saccade to a lateralised target, under two attentional manipulations. Experiment 1 demonstrated that exogenous pre-cueing of a distractor's location reduced saccadic inhibition, consistent with *inhibition of return*. Experiment 2 manipulated the relative likelihood that a distractor would be presented above or below fixation. Saccadic inhibition magnitude was relatively reduced for distractors at the more likely location, implying that observers can endogenously suppress interference from specific locations within an oculomotor map. We discuss the implications of these results for models of saccade target selection in the superior colliculus.

Keywords: eye movements; saccadic inhibition; visual distractors; endogenous attention; exogenous attention

Introduction

As we explore the visual world, our planned eye movements are prone to interference from new visual events. Reingold and Stampe (2002, 2004) devised a simple paradigm to study such interactions. A visual transient was flashed while participants were engaged in reading, scene viewing, or discrete saccadic tasks. In all tasks, there was a dip in saccade frequency, relative to baseline behaviour, starting 60-70 ms after flash onset, and maximal around 90-100 ms. Although studied initially using large visual transients, we have shown that this *saccadic inhibition* (SI) phenomenon is a critical, and possibly the main, mechanism underlying the classical *remote distractor effect*, in which even a small distractor (e.g. a dot in the non-target hemifield) can increase average saccade latency (Walker et al., 1995; 1997; Buonocore & McIntosh, 2008; 2012). However, the SI profile, which is based on the distribution of latencies, offers greater insight into mechanisms of saccade target than does any simple measure of average saccadic reaction time (Buonocore & McIntosh, 2008; 2012).

The minimal latencies for the onset of the SI dip following a visual distractor (~60 ms, Buonocore & McIntosh, 2012; Bompas & Sumner, 2011; Reingold & Stampe, 2002) push the limits imposed by the neural architecture, which has been taken imply a subcortical substrate for the phenomenon in the oculomotor maps of the intermediate superior colliculus (iSC) (e.g. Reingold & Stampe, 2002). Dynamic neural field models of saccade generation, based on the physiology of the iSC can reproduce the SI signature, even though they were not designed with this purpose in mind. For instance, Bompas & Sumner's (2011) DINASAUR model yields plausible SI dips, assuming only a fast transient exogenous input (representing the visual stimulus), a sustained endogenous input (representing 'top-down' control), and lateral

inhibition and facilitation between saccade buildup neurons for different locations.

Distractor properties modulate the SI dip profile predictably. Increasing the *luminance* of the distractor increases the magnitude (i.e. depth) of the SI dip, and reduces its latency slightly (Bompas & Sumner, 2011). Distractor *size*, on the other hand, has its main impact on the magnitude of the dip, which increases as a logarithmic function of distractor size (Buonocore & McIntosh, 2012). These effects can be modelled by adjustments to (one or both of) the amplitude and latency parameters of the exogenous signal for the distractor (Bompas & Sumner, 2011). On the other hand, changing distractor *location* has consequences that are less obviously related just to the properties of the stimulus, and may require prior attentional allocation to be taken into account (Buonocore & McIntosh, 2012; Reingold & Stampe, 2004).

Reingold and Stampe (2004) found that, during reading tasks, a large distracting flash induced stronger and longer-lasting SI when its location was congruent with the direction of the upcoming saccade, than when it was directionally opposite. Reingold and Stampe (2004) called this the *congruency effect*, proposing that it relates to the participant's endogenous attentional state. Specifically, since attention is pre-allocated in the direction of a planned saccade (e.g. Deubel & Schneider, 1996), this may amplify the influence of unexpected events in the congruent (ipsilateral) direction. We further investigated the effects of distractor size and location in a discrete saccadic task (Buonocore & McIntosh, 2012), confirming that, beyond a certain size ($> 2^\circ$ of visual angle), ipsilateral distractors were more powerful than contralateral. Like Reingold and Stampe (2004), we suggested that top-down attention was critical, in that participants were obliged to attend to the target field but could voluntarily withdraw attention from the non-target field.

SI is a low-level oculomotor phenomenon, but the idea that it is modulated by top-down attentional factors is very plausible. The iSC integrates sensory afferents from the superficial superior colliculus (sSC) with cortical inputs from the frontal eye fields (FEF) and dorsolateral prefrontal cortex (dlPFC), as well as parietal and temporal regions (Clower, West, Lynch, & Strick, 2001).

Indeed, the capacity to make voluntary, rather than just reactive eye-movements, implies that endogenous inputs can bias saccade preparation; and endogenous inputs are built into dynamic neural field models of saccade generation (Bompas & Sumner, 2011; Satel, Wang, Trappenberg, & Klein, 2011). At a neurophysiological level, deactivation of dlPFC reduces pre-saccadic activity in the iSC suggesting the involvement of dlPFC in suppressing stimulus related saccadic responses. Moreover, task instruction such as preparing an anti-saccade, reduce the activity within the iSC during the instruction period for saccade buildup neurons and increase it for collicular fixation neurones, suggesting a modulation via top-down signals over the iSC (Koval, Lomber & Everling, 2011). Nonetheless, the behavioural evidence for SI modulation by top-down attentional factors is thus far limited to an indirect inference made from the congruence effect described above.

The purpose of this paper is to test directly the role of attention in modulating SI. Experiment 1 uses a peripheral cueing manipulation, inducing *inhibition of return* (IOR) for possible distractor locations (Posner & Cohen, 1984; Satel et al., 2011). Experiment 2 tests whether participants allocate attention endogenously according to the likelihood of distractors appearing at different locations. Our data show that both manipulations do modulate distraction effects, with SI magnitude (but not latency) reduced by IOR at the distractor location, and similarly reduced at more probable distractor locations.

Methods

Participants

Eight volunteers (aged 18-30 years) participated in *Experiment 1*, and six (aged 18-30 years) participated in *Experiment 2*. All had normal or corrected-to-normal vision. This study was conducted in accordance with the 1964 Declaration of Helsinki, with approval from the University of Edinburgh Psychology Research Ethics Committee.

General procedure

Grey fixation and target and white distractor stimuli on a black background were presented on a 17 inch CTR monitor (1024 x 768 pixels) at 100 Hz. Participants sat 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 horizontal-vertical calibration was run at the beginning of each session and after three consecutive trial blocks; additional calibrations were run if the participant moved their head from the chinrest. Each experiment lasted ~90 minutes per participant.

For each experiment, a preliminary block was run in which the target was always presented alone (T trials). Each trial began with drift correction and a tone accompanying the onset of a 0.5° central fixation cross. Participants were required to fixate the cross and to move their eyes to the circular target (0.5°) as soon as it appeared. There were 70 trials in the preliminary block, with the target appearing equally often at 5° eccentricity to the left or right, 500 ms after fixation onset. The

median baseline saccadic reaction time (SRT) of the last 50 trials was used to determine the timing of distractor (D) onset in the main experiment, according to the formula: D onset = median baseline SRT - 110 ms.

Procedure: Experiment 1 – inhibition of return (IOR)

In experimental trials, fixation was followed after 500 ms by the onset of a 0.5° cue (an asterisk) presented 5° above or below fixation for a duration that varied randomly between 200-300 ms. The saccadic target appeared after the cue onset, at 5° eccentricity to the left or right of fixation. In some trials, a distractor (2.5° wide square) was presented 5° above or below fixation, being either at the same location as the preceding cue (valid cue) or not (invalid cue). The delay between target and distractor was determined individually per participant from baseline SRTs (see General Procedure), and was 117.5 ms (SD 36.5 ms) on average. Fixation cross, target and distractor offset simultaneously, 700 ms after target onset. Note that, within this design, the delay of the distractor following cue onset was on average between 310 and 410 ms, ensuring that the distractor would appear during the time window for IOR (Posner & Cohen, 1984). Within each block of 48 trials, each of the three distractor conditions (target only, distractor valid and distractor invalid) occurred 16 times, with target side counterbalanced, and trial order shuffled randomly. There were 15 blocks for a total of 720 trials (240 target only, 240 validly-cued distractor, 240 invalidly cued distractor, collapsed by side), though three participants completed only 13 blocks, and one participant completed only 12.

Procedure: Experiment 2 - endogenous

Experimental trials for *Experiment 2* were similar to the above, except as stated. First, there was no cue; instead, the target appeared after a delay that varied randomly between 500-1000 ms after fixation onset. Target location was always 5° to the right of fixation. The delay between target and distractor was determined individually per participant from baseline SRTs (see General Procedure), and was 110 ms (SD = 26.1 ms) on average. When present the distractor appeared with a high probability (75%) above (or below) fixation, and with a low probability (25%) at the opposite location. The pairing of high and low probability with top and bottom locations was counterbalanced across participants. Within each block of 50 trials, there were 10 target only, 10 low probability distractor, and 30 high probability distractor trials. There were two sessions of ten blocks, for a total of 1000 trials (200 target only, 200 low probability distractor and 600 high probability distractor), though one participant completed only 17 blocks.

Results

Data screening

Saccades with a latency of less than 70 ms (Experiment 1: 1.86%; Experiment 2: 3.43%) or more than 500 ms (Experiment 1: 0.30%; Experiment 2: 0.43%), saccades made in the wrong direction (Experiment 1: 0.24%; Experiment 2: 0.22%), saccades of less than 1° amplitude (Experiment 1: 1.28%; Experiment 2: 0.70%) and time out trials (Experiment 1: 0.19%; Experiment 2: 0.13%) were excluded.

Results: Experiment 1 – inhibition of return (IOR)

Each participant's median saccadic amplitudes and SRTs were entered into separate repeated-measures ANOVAs by condition. Participants were generally accurate (median = 5.05°, SD = 0.68°) and saccadic amplitude was unaffected by distractor condition [$F(2,14) = 1.596$; $P = 0.24$]. SRTs were significantly affected by distractor condition [$F(2,14) = 4.739$; $P < 0.05$], with post-hoc paired comparisons showing that while the valid condition was only marginally affected by distractor onset, the invalid condition was significantly slower than the target-only condition (195 ms) [valid: 210 ms, $t = 2.14$; $df = 7$; $P = 0.07$; invalid: 212 ms, $t = 2.49$; $df = 7$; $P < 0.05$]. However, as we have demonstrated previously (Buonocore & McIntosh, 2008; 2012), SRT is a rather insensitive measure of distractor interference. More insight can be gained by considering the detailed SRT distribution using a SI analysis, described below.

For each participant and condition, a percentage frequency histogram of SRTs (bin width 4 ms) was created, and a seven-point moving-window-average smoothing function was applied. The smoothed histogram for the T condition was subtracted, bin-by-bin, from the histogram for each TD condition, giving a difference histogram. For each TD condition, these difference histograms were aligned to distractor onset and averaged across participants (Fig. 1A). Three key parameters were extracted from the difference histogram per condition per participant: (1) *magnitude* (minimum of the difference histograms), (2) *Lmax* (time to the minimum), (3) *duration* (the time spanning between 50% of the dip minimum on either side of the minimum).

The SI profiles in Fig 1a show that the magnitude of the dip is larger in the invalid (2.80%; SD: 0.87) compared to the valid condition (2.26%; SD: 0.97). Table 1 shows that a t-test on dip magnitude confirmed the significance of this difference, whilst the temporal parameters, *Lmax* and *duration*, were not affected by cue congruence. Inhibition is reduced for distractors at a cued location during the period

during which IOR is expected to apply to that location. Experiment 1 thus shows that the IOR modulates SI magnitude.

Results: Experiment 2 – endogenous

Analysis of median saccadic amplitudes and SRTs found no significant effects of distractor condition [amplitude: $F(2,10) = 0.769$; $P = 0.49$; SRT: $F(2,10) = 2.786$; $P = 0.11$], although the numerical trend for SRTs was towards increased latency in the low and high probability distractor conditions (212 and 210 ms respectively) relative to the target-only condition (199 ms).

Analysis of SRT distributions was performed to reveal the profile of SI in each distractor condition. Figure 1B shows that the magnitude of the dip was larger for the low than for the high probability distractor, and Table 1 confirms that this difference was significant. The effect, despite being small on average (0.54%, SD 0.62), was seen in five out of the six participants. As in Experiment 1, the attentional manipulation had no significant impact on the temporal parameters of the dip. Experiment 2 thus shows that participants are better able to suppress distractors at a location at which distraction is more likely.

Discussion

These experiments demonstrate that SI is modulated by IOR, and by manipulation of endogenous attention. In the first case, a non-informative cue drew attention to one of two locations, and the distractor was flashed at one of these locations ~310-410 ms later, thus within the temporal range of IOR. Consistent with IOR, the magnitude of SI was reduced for distractors at the cued location. In the endogenous case, distractors

were simply three times more likely to appear at one location than another. SI magnitude was reduced for distractors at the high probability location, consistent with a strategic withdrawal of attention from this location to resist distraction. Neither manipulation induced any significant change in the time-course of inhibition.

Experiment 1 used an irrelevant peripheral cue to induce IOR, reducing the impact of subsequent distractors at the cued location. IOR is a complex, non-unitary phenomenon, with dissociable neural substrates (Sumner, Nachev, Vora, Husain & Kennard, 2004; Taylor & Klein, 2000). Of particular relevance here is the distinction between an oculomotor component, which involves the SC and affects saccadic latency, and a cortical component, which does not affect saccades (Sumner, Nachev, Vora, Husain & Kennard, 2004). Oculomotor IOR does not entail inhibition only of locations that have been saccadic targets, but of any recently activated point in the oculomotor map. Consistent with this, Theeuwes and Godijn (2004) reported reduced oculomotor IOR (as measured by oculomotor capture, mean saccadic reaction time, and saccade trajectory veering) at previous target and distractor locations alike. Our Experiment 1 extends this general pattern to the related phenomenon of SI, which is similarly believed to reflect competitive oculomotor activations in the SC.

Even oculomotor IOR itself may have distinct subcomponents, respectively slowing saccades to cued locations, and speeding them to opposite locations (Fecteau & Munoz, 2005). The former effect, which is of most relevance to our result, correlates with attenuated target-related responses in the visual neurons of the superficial SC (sSC) and the visuomotor neurons of the intermediate SC (iSC) (Dorris et al, 2002; Fecteau & Munoz, 2005). However, the fact that SC neurons express IOR does not imply that they are the site of the inhibition (iSC neurons may actually be more and not less active after a cue within their receptive field; Dorris et al, 2002).

The attenuated responses may instead reflect reduced sensory signals, owing to short-term habituation of the target location in early visual areas that feed the sSC (Muller & Kleinschmidt, 2007; Prime & Jollicoeur, 2009), perhaps combined with additional cortical influences on the iSC (e.g. frontal eye fields, lateral intraparietal cortex). This suggests that IOR should weaken the exogenous signal for a distractor at an affected location, without changing its latency, predicting precisely the changes in SI that we observed in Experiment 1 (see Satel et al, 2011, for a compatible approach to modelling IOR).

Experiment 2 shows that distractor location probabilities similarly influenced SI; the more spatially-predictable the distractor, the less disruptive it was. Unlike IOR, which can be conceived of as modulation of the bottom-up distractor signal, the effect of target probability must reflect a strategic top-down modulation of SI. As described in the Introduction, such top-down modulation has been posited to explain the so called *congruency effect*, whereby a distractor ipsilateral to the saccade target has more influence than a distractor that is contralateral (Buonocore & McIntosh, 2012; Reingold & Stampe, 2004). The present study provides a more direct test and confirmation of top-down modulation, emphasising that a full understanding and modelling of SI must include such 'higher' influences.

Dynamic neural field models allow for top-down influences by the inclusion of a sustained endogenous signal for each location, via which the participant's goals can bias the outcome of sensory competitions between stimuli competing for saccadic initiation. Increasing the endogenous signal associated with the target provides a sustained boost to the target representation, allowing it to overpower competing distractors (e.g. Bompas & Sumner, 2011). Lateral interactions in the iSC, with local facilitation and longer-range inhibition, would suppress competing locations most

effectively at remote locations, which could give rise to the congruency effect (Reingold & Stampe, 2004). The present findings add important further detail to this idea by showing that, in addition to target enhancement, there can also be active suppression of the endogenous signals associated with non-target locations. This is not limited to coarse-grained inhibition of a whole collicular map (i.e. the non-target hemifield,) but can be selective within a map, as revealed by the relative suppression of distractors above or below fixation. This provides a strategic mechanism by which predictable sources of irrelevant interference can be more effectively ignored.

The strategic modulation of this low-level oculomotor response is consistent with a broad accumulation of evidence that top-down factors can affect all levels of visual processing. For instance, top-down attention can modulate the earliest component of the visual evoked potential (see Rauss, Schwartz, & Pourtois, 2011); and the responsiveness of iSC neurones during the presaccadic period varies in accordance with task instructions (Everling, Dorris, Klein, & Munoz, 1999) and target probabilities (Bell & Munoz, 2008) suggesting cortical modulation over the iSC.

Our findings may also offer further insight into some superficially puzzling patterns from neurological patients. Although patients with hemianopia may show oculomotor distraction effects for distractors in the blind field (Rafal, Smith, Krantz, Cohen, & Brennan, 1990; but see: Barbur, Forsyth, & Findlay, 1988; Walker, Walker, Husain, & Kennard, 2000), such effects have been absent in patients with visual neglect, despite the fact that subcortical *and* cortical visual routes are preserved in these patients (Van der Stigchel & Nijboer, 2010; Walker & Findlay, 1996). One possible interpretation for this pattern is that the cortical attentional bias of neglect suppresses oculomotor responsiveness for the neglected field (Van der Stigchel & Nijboer, 2010; Walker & Findlay, 1996); there would be no such suppression in

patients with hemianopia. The present study substantiates this interpretation, by confirming the capacity for active suppression of localised parts of the visual field. Nonetheless, we suggest that, even if there is usually no significant elevation of average SRT with neglected distractors, a detailed analysis of SRT distributions might have the sensitivity to reveal a muted SI signature.

In summary, these experiments demonstrate that attentional factors modulate SI. Manipulation of the exogenous signals by IOR, and manipulation of endogenous signals via changing distractor location probabilities, have similar effects upon the magnitude of the SI dip. Recent dynamic neural field models of saccade generation are well-equipped to incorporate these exogenous and endogenous attentional influences (e.g. Bompas & Sumner, 2011; Satel et al., 2011).

Figure Legends

Figure 1. Difference histograms for the two distractor conditions in the two experiments representing bin-by-bin subtraction of baseline histogram from distractor histogram for that condition. Data are aligned to distractor onset. A. Experiment 1. The dotted line represents the condition where the distractor was presented at valid cue location, the grey line at the invalid cue location. B. Experiment 2. The dotted line represents the high probability distractor location, the grey line the low probability distractor location.

Table 1. Dip parameters (Magnitude, L max, Duration) for each participant in the two experiments and overall Mean and Standard Deviation and statistical significance (t-test).

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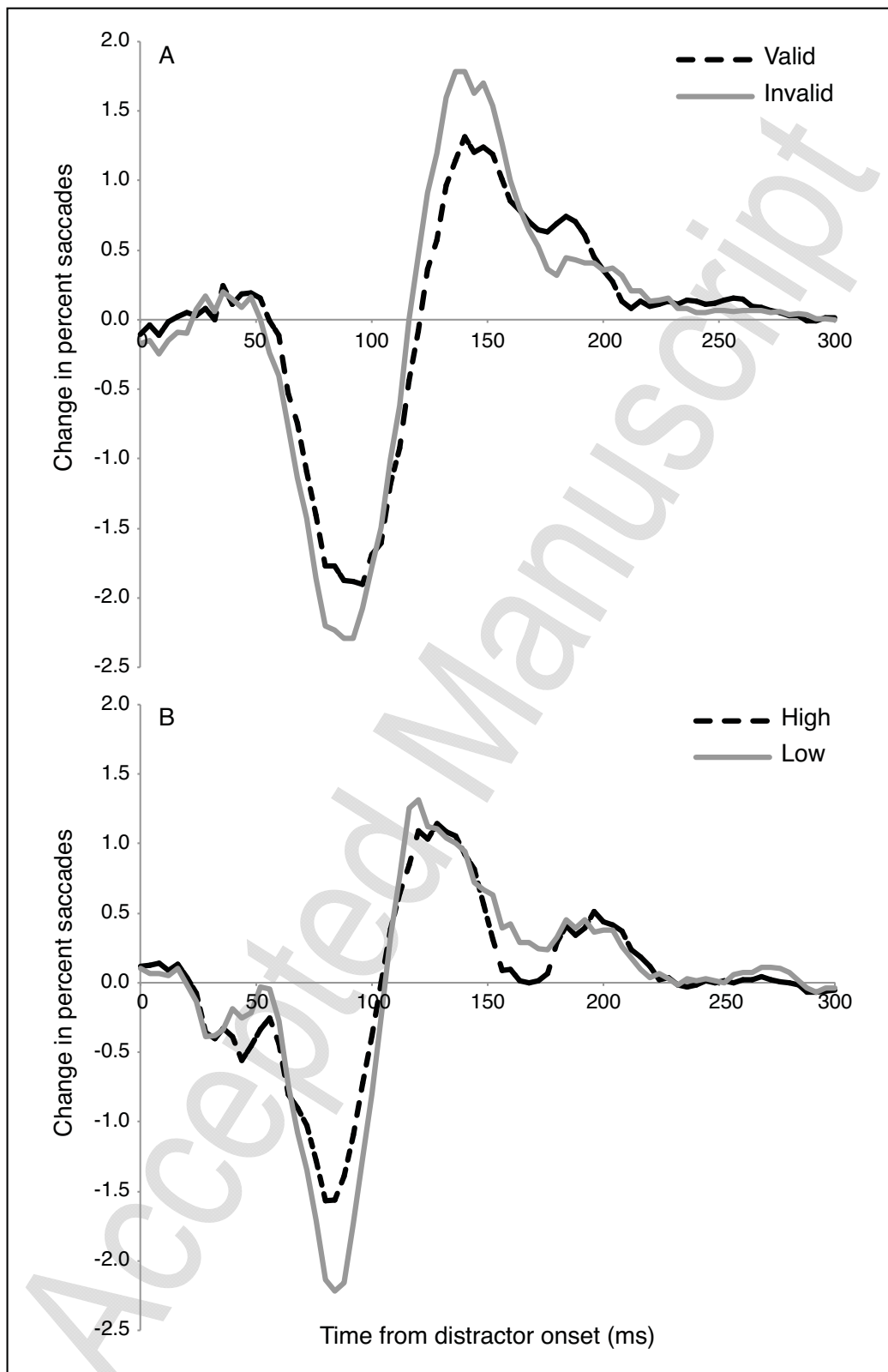
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		SI parameters					
		<i>Magnitude (%)</i>		<i>L max (ms)</i>		<i>Duration (ms)</i>	
Distractor:		Valid	Invalid	Valid	Invalid	Valid	Invalid
Experiment 1	S01	2.45	3.47	86	86	40	40
	S02	3.54	3.84	96	100	60	56
	S03	1.99	2.20	80	88	36	32
	S04	1.43	2.40	100	92	36	36
	S05	2.98	3.22	92	92	52	48
	S06	3.02	3.90	106	106	56	44
	S07	1.14	1.08	64	64	36	40
	S08	1.52	2.33	104	80	52	28
	Mean	2.26	2.80	91	88.50	42	36.50
	SD	0.87	0.97	14.02	12.77	14.03	12.93
<i>df</i> = 7		<i>t</i> = 3.69**		N.S.		N.S.	
		<i>Magnitude (%)</i>		<i>L max (ms)</i>		<i>Duration (ms)</i>	
Distractor:		25%	75%	25%	75%	25%	75%
Experiment 2	S01	1.90	2.13	90	78	28	32
	S02	3.38	1.96	80	72	44	36
	S03	1.22	0.89	90	86	36	44
	S04	3.59	2.88	86	86	36	46
	S05	2.21	1.21	82	82	52	36
	S06	1.81	1.78	88	92	24	32
	Mean	2.34	1.81	86	82.67	36.67	36
	SD	0.98	0.70	4.20	7.00	10.25	4.38
<i>df</i> = 5		<i>t</i> = 2.13*		N.S.		N.S.	

* $p < 0.05$ one tail; ** $p < 0.05$ two-tails