Full Publication Information: http://dx.doi.org/10.1016/j.neulet.2015.08.053

Cite as: .Maslovat, D., Drummond, N. M., Carter, M. J., & Carlsen, A. N. (2015). Startle activation is additive with voluntary cortical activation irrespective of stimulus modality. Neuroscience Letters, 606, 151-155. DOI: 10.1016/j.neulet.2015.08.053.

Startle activation is additive with voluntary cortical activation irrespective of stimulus modality

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Abstract

When a startling acoustic stimulus (SAS) is presented during a simple reaction time (RT) task it can trigger the prepared response through an involuntary initiation pathway. Previous research modelling the effects of presenting a SAS at various intervals following a non-startling auditory imperative signal (IS) suggested that involuntary initiation-related neural activation is additive with the voluntary initiation processes. The current study tested the predictions of this additive model when the SAS and IS are of different modalities by using a visual rather than auditory go-signal. Because voluntary RT latencies are delayed for visual stimuli compared to acoustic stimuli, it was hypothesised that the time course of additive activation would be similarly delayed. Participants performed 150 RT trials requiring a targeted 20° wrist extension task with a SAS presented 0 to 125 ms following a visual go-signal. Results were not different to those predicted by an additive model (p=.979), yet were significantly different to those predicted by a horse-race model (p=.037), indicating a joint contribution of voluntary and involuntary activation, even when the IS and SAS are of different modalities. Furthermore, the results indicated that voluntary RT differences due to stimulus modality are attributable to processes that occur prior to the increase in initiation-related activation.

Keywords: additive model; initiation; motor preparation; neural activation; startle

Abbreviations: ECR, extensor carpi radialis; FCR, flexor carpi radialis; IS, imperative stimulus; SAS, startling acoustic stimulus; SCM, sternocleidomastoid

Introduction

In a simple reaction time (RT) paradigm, the goal for the participant is to initiate a response as soon as possible following the appearance of an imperative stimulus (IS). To accomplish this goal, the required movement can be prepared in advance such that RT is considered to be indicative of simply the time required to detect the IS and perform the processes associated with response initiation. From a neural perspective, response initiation can be thought to occur when the activation of a group of cortical neurons responsible for the movement reaches an initiation threshold [16]. In these neural activation models [1, 4], advance preparation reduces RT by increasing activation to sub-threshold levels, with RT reflecting the time required to raise activation over the initiation threshold. One recent method used to examine activation related to response preparation and initiation involves the use of a startling acoustic stimulus (SAS) [see 1, 14 for recent reviews]. When a SAS is presented in place of the IS, the prepared response is typically initiated at a much faster latency [i.e., <80 ms; 15]. It is thought that the startle-related activation results in the involuntary triggering of

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prepared response because the RT latencies observed following a SAS appear to rule out typical voluntary initiation processes. One model suggests that neural activation associated with the startle reflex acts via a brainstem-mediated pathway to reach cortical neurons faster, resulting in an earlier and greater rate of activation increase as compared to voluntary response initiation processes [1].

Although different pathways may underlie voluntary initiation and SAS triggering, research has been conducted to determine whether the two processes are independent or interactive. In a previous paper [8], Maslovat et al. examined RT latencies following a SAS presented at various time points after a non-startling auditory IS to determine the relative contributions of voluntary and involuntary activation to the process of response initiation. In contrast to a "horse-race" model, which predicts that the RT latency is determined by whether the voluntary or involuntary process completes first, the results showed that delaying the SAS resulted in shorter than predicted RT delays, indicating that both sources of activation contributed to the observed RTs. Furthermore, the observed RTs closely matched those predicted by a linear additive model in which the rate of activation was summed during the time course in which both voluntary and involuntary activation increases were predicted to occur [8].

The use of a non-startling auditory IS in the previous study [8] resulted in relatively short voluntary RTs (127 ms), which limited the time frame in which additive initiation could occur. The purpose of the current study was to further investigate an additive model of initiation, using a visual go-signal paired with a SAS at various time points during the RT interval. When responding to visual compared to auditory stimuli, RT latencies are typically delayed [3]. This delay in voluntary activation would be expected to produce a similar delay in the time course of additive initiation, allowing for a more detailed examination of an additive model. However, previous research involving a SAS presented in 20 ms intervals following a visual IS [7] found that RT appeared to increase monotonically by approximately 20 ms, indicative of a horse-race between processes. While this may indicate that additive activation does not occur when the SAS and IS are of different modalities, a more detailed investigation is necessary to determine the relative contributions of voluntary and involuntary initiation processes. It was hypothesized that an additive model would provide a better fit to the observed results as compared to a horse-race model, providing additional support for the summation of voluntary and involuntary initiation processes irrespective of stimulus modality. This result would also provide indirect evidence that differences in visual versus auditory RT latencies are likely due to processes that occur prior to response initiation.

Materials and Methods

Participants

Data were collected from fourteen participants with no sensory or motor dysfunction and normal hearing. Four participants did not show startle response activation in the sternocleidomastoid (SCM) muscle [indicative of a reliable startle response; 2] in more than 50% of trials where SAS was presented concurrent with the go-signal, and were thus rejected from the data analysis, leaving ten participants (5F, 5M; M=25 yrs, SD=6). This exclusion criteria was not conducted for trials in which the SAS followed the IS as presenting a cue prior to a SAS can cause a reduction of the reflexive startle response (i.e., pre-pulse inhibition), although response triggering effects remain [9]. All participants gave written informed consent, the study was approved by and conducted in accordance with the ethical guidelines set by the Health Sciences and Science Research Ethics Board at the University of Ottawa, and conformed to the latest revision of the Declaration of Helsinki.

Apparatus and Task

Details of the experimental apparatus and recording equipment have been published previously [8]; thus, methods will be described here in brief. Participants sat facing a 24" LCD computer monitor with their right arm forearm parallel to the floor in a custom manipulandum

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that allowed wrist flexion and extension. Participants were required to perform a 20˚ wrist extension "as quickly as possible" following a visual IS. The starting position was 20˚ of wrist flexion and the target located at a position corresponding to a neutral wrist position. Feedback was provided on the computer monitor after each trial consisting of RT on that trial and accuracy with respect to the target. A points scheme was also provided to encourage fast RTs.

Instrumentation and stimuli

At the start of each trial a warning tone (100 ms, 200 Hz, 80 dB) sounded and a 5 cm x 5 cm grey box with a 3 mm black border appeared on the screen in front of the participant. This was followed by a variable foreperiod (2000 – 2500 ms), and finally a visual IS consisting of the box turning bright green. On 20% of trials a SAS (25 ms, white noise, 120 dB), was presented at six different intervals (0, 25, 50, 75, 100, 125 ms) following the go-signal. Participants performed up to two practice blocks of 10 trials (without SAS) which was then followed by 5 blocks of 30 RT trials including 24 visual IS only (control) trials and 1 SAS trial per interval. The SAS was amplified and presented via a loudspeaker located 30 cm directly behind the participant's head. Stimulus intensity was confirmed using a precision sound level meter located at the same distance from the loudspeaker to the ears (Casella CEL-254; A-weighted, impulse setting). Participants were told that on some trials they would hear a loud "static noise" sound that was irrelevant to the task. The SAS was presented pseudorandomly such that a SAS was not presented in the first two trials of a block or in any two consecutive trials.

Surface electromyographic (EMG) data were collected from the muscle bellies of the right extensor carpi radialis longus (ECR), right flexor carpi radialis (FCR), and left sternocleidomastoid (SCM) muscles using bipolar preamplified surface electrodes connected to an external amplifier system (Delsys Bagnoli-8). Wrist angular position data were collected using a potentiometer attached to the central axis of the manipulandum. On each trial, band-passed (20-450 Hz) EMG and raw position data were digitally sampled at 1 kHz (National Instruments PCI-6024E) for 3 sec beginning 500 ms prior to the go-signal using a customized program written with LabVIEW software (National Instruments).

Data Reduction and Analysis

Practice trials were not included in the analyses, nor were trials in which an error occurred (anticipation RT <50 ms: 50 trials; slow RT > 500 ms: 4 trials; movement error: 34 trials; no SCM when SAS presented concurrently with IS: 4 trials) resulting in 92 total trials excluded, for an inclusion rate of 94% (1408/1500). Peak displacement and peak velocity (differentiated from displacement) were defined as the maximal values attained for each measure following displacement onset. Muscle burst onsets were defined as the point at which the rectified and filtered (25 Hz low pass elliptical filter) EMG first began a sustained (>20 ms) rise 2 standard deviations above baseline levels (calculated from 100 ms prior to the go-signal) [5]. EMG onsets were visually confirmed and manually adjusted if necessary to compensate for any errors due to the strictness of the algorithm. Premotor RT was defined as EMG onset in the ECR muscle.

Model Predictions

When examining RT effects of responding to two stimuli, models typically hypothesize either independent streams of processing or some form of "co-activation" [10, 12]. The assumption of independence is based on the massively parallel nature of sensory processing, leading to a horse-race between inputs to determine the response latency [11]. For the current study this type of a model would predict that SAS-referenced RT values would linearly increase by 25 ms until SAS-referenced RTs were longer than the visual alone (control) RT value (i.e., once the voluntary process wins). An alternative view is that the two streams of input are facilitative in nature, such that the expected response latency would be considerably faster than from either input alone [10]. Although several forms of co-activation have been hypothesised, for the current study a linearly additive model initiation-related activation [8] was evaluated. In this model activation slopes are calculated for SAS+0 and control trials, then these slopes

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are added during the time period in which both voluntary and involuntary initiation processes are thought to occur. To determine "initiation time," it is necessary to subtract the physiological transmission time of the signals from the observed response latency. For startle trials, 20 ms are thought to be required for the auditory signal to reach areas related to initiation activation via a reticulo-thalamo-cortical circuit [1], and 25 ms are needed for conduction time from primary motor cortex to the arm muscles [13]. Once this 45 ms has been subtracted from the observed response latency, the remaining time is considered to involve an increase in activation from a baseline value (0%) to an arbitrary threshold (100%), providing a rate of involuntary (SAS) activation. For control trials, the rate of voluntary initiation-related activation was considered to be the same as that calculated by Maslovat et al. [8] whereby 67 ms were required to reach 100% of initiation activation (i.e., 1.49%/ms). This rate can then be back-applied to the observed RT to determine the time when voluntary activation begins to increase. As 25 ms of conduction time to the muscles is still required and 67 ms of "initiation time" are assumed, the remaining time is attributed to sensory processing of the visual stimulus. This assumption of a common voluntary initiation time/rate, irrespective of stimulus modality, is supported by research showing that visual and auditory RTs are similar when the pre-initiation process are equated by using a common stimulus intensity scale [6].

Statistical Analyses

In order to test the observed RT values against those predicted by both horse-race and additive models, a goodness-of-fit analysis was performed for the SAS conditions using calculated grand mean RT values. Specifically, a weighted sum of squared errors was constructed for each model and compared to that of a chi-squared distribution using the equation below (where O is the observed data, E is the theoretically predicted data, and σ2 is the variance between participant means for each of n conditions).

$$X^2 = \sum_{i=1}^{n} \frac{(O-E)^2}{\sigma^2}$$

In addition to the goodness-of-fit analysis, peak displacement and peak velocity were calculated for each participant and analyzed using one-way, 7 factor (SAS delivery: none, 0, 25, 50, 75, 100, 125 ms), repeated measures analysis of variance (ANOVA). Greenhouse-Geisser corrected degrees of freedom were used to correct for any violations of sphericity. Uncorrected degrees of freedom are reported, along with corrected p-values and partial eta squared (ηp2), to provide an estimate of the effect size. Tukey's HSD post-hoc tests were administered to determine the locus of the differences. For all analyses, differences with a probability of less than .05 were considered to be significant.

Results

Response Latency

Response latencies from the visual (control; M=183 ms, SD=17) and SAS+0 (M=85 ms, SD=16) conditions were used to calculate the predictions of the horse-race and additive models. The horse-race model would predict RTs of 110 ms, 135 ms, 160 ms, 183 ms, and 183 ms[1] for the SAS+25, SAS+50, SAS+75, SAS+100 and SAS+125 conditions, respectively. For the additive model, predictions are shown graphically in Figure 1, using colored slopes to represent rates of voluntary, involuntary, and additive activation increases. For the SAS+0 condition, activation in startle-reflex related structures would begin 20 ms following the SAS (point A) and reach activation threshold 25 ms prior to the observed RT of 85 ms (i.e., 60 ms, point B). Thus, 40 ms of initiation time are required, providing a rate of involuntary (SAS) activation increase of 2.50%/ms (100%/40 ms), which is modelled graphically as a red line between points A and B. Using the observed control RT of

[1] Predicted RTs rise by 25 ms until the point at which the voluntary RT of 183 ms is faster than the SAS-referenced RT and thus "wins" the horse-race for all subsequent conditions.

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183 ms, the 67 ms required to reach initiation threshold results in an activation increase beginning at 91 ms (point C), and reaching threshold at 158 ms (point D). This voluntary increase in activation of 1.49%/ms (100%/67 ms) is shown graphically as a black line between points C and D.

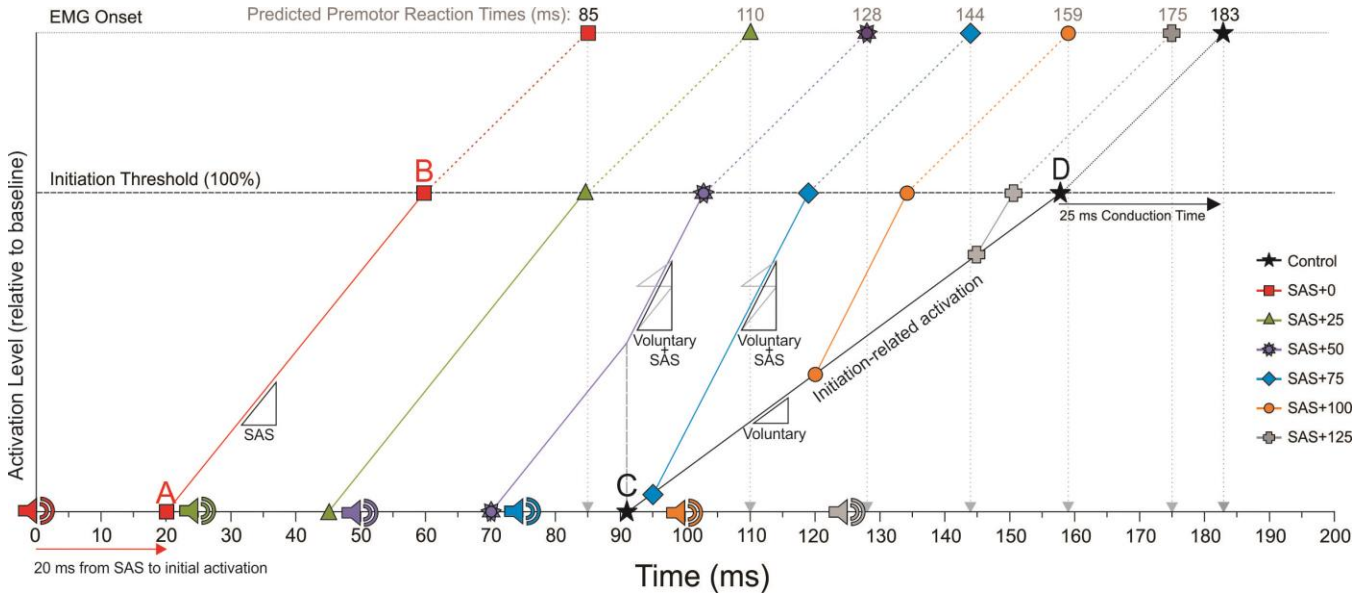

Figure 1. Additive model of initiation activation. Time (ms) is on the horizontal axis and neural activation on the vertical axis. Horn icons show times when a startling acoustic stimulus (SAS) was presented. Predicted premotor reaction time (RT) for each condition is shown at top. Sloped lines below the dashed initiation threshold line represent calculated initiation-related activation slopes. Dashed lines above threshold show 25 ms of nerve conduction time. For the SAS+0 condition (red squares), Point A represents when startle initiation-related activation begins to rise above baseline, Point B represents when startle activation has reached a threshold whereby motor commands are output from cortex to the muscles, with a calculated slope drawn between points A & B to represent the rate of increase in initiation-related activation following startle. For the control condition (visual IS only), the slope drawn between points C & D (black star) represents the rate of increase in voluntary initiation-related activation. Conditions in which a SAS was presented during the RT interval are modeled by adding the control and startle activation slopes during the time frame when both processes are occurring simultaneously (see slope triangles). See Methods and Results for further details.

Using these baseline slopes, expected RTs were calculated by determining the time period in which additive activation was expected. For example, in the SAS+25 condition (green triangles), initiation activation would begin to rise at 45 ms following the IS and threshold would be reached at 85 ms (prior to any voluntary activation beginning), resulting in a predicted premotor RT of 110 ms. For the SAS+50 condition (purple star), the SAS-related activation increase would begin 70 ms following the IS and increase at the SAS initiation rate until 91 ms. According to the additive model, at this point (dashed line extending vertically from point C) the voluntary activation slope would begin adding with the SAS initiation rate (steeper slope) until threshold would be reached at 103 ms, resulting in a predicted RT of 128 ms. Similar calculations for SAS+75 (blue diamonds), SAS+100 (orange circles), and SAS+125 (grey cross) provide predicted RT values of 144 ms, 159 ms, and 175 ms.

Observed premotor RT values are shown in Figure 2, including distribution boxplots for between-participant data (panel A) and mean RTs for each participant (panel B). RT predictions from both the horse-race (open circles) and additive (filled circles) models are also shown (panel A). The

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observed mean premotor RT for the SAS+25, SAS+50, SAS+75, SAS+100, and SAS+125 conditions of 108 ms (SD=13), 131 ms (SD=12), 148 ms (SD=14), 155 ms (SD=10), and 172 ms (SD=8) respectively, were significantly different to those values predicted by the horse-race model, X2(4, N=10) = 10.22, p=.037, yet were not different to those predicted by the additive model, X2(4, N=10) = 0.45, p=.979.

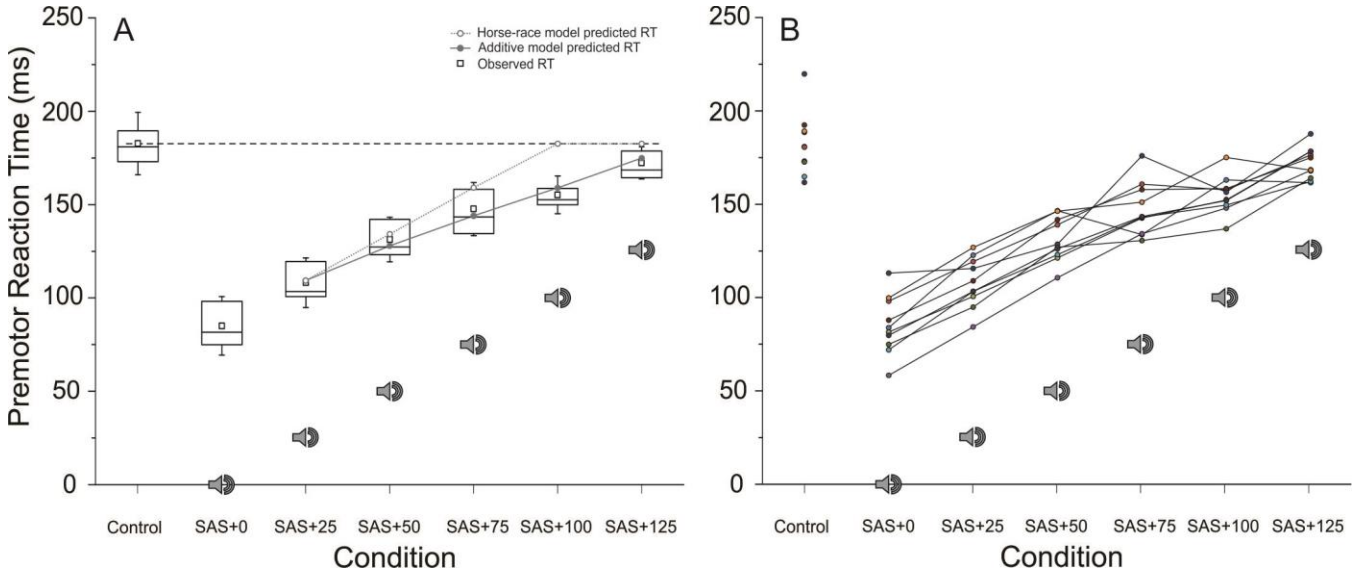

Figure 2. Premotor reaction time (RT) for control trials (visual go-signal) and trials where the startling acoustic stimulus (SAS; shown as speaker icon) was presented 0 to 125 ms following the visual go-signal. Panel A shows distribution boxplots with boundaries representing the first and third distribution quartiles (open squares = mean RT, horizontal line = median RT, error bars = 1 SD). Solid grey circles represent predicted RT values from an additive model (connected by solid grey line), whereas open grey circles represent the predicted RT values from a horse-race model (connected by dotted grey line). Panel B shows individual participant performance for each condition.

Response Characteristics

Kinematic variables were analyzed to determine if there were any differences in response output when participants were startled. Both peak displacement, F(6,54)=5.41, p=.008, η2p=.38, and peak velocity, F(6,54)=5.86, p=.008, η2p=.39, showed a main effect of SAS delivery time. Post hoc analyses confirmed these effects were due to significantly higher values on all startle conditions as compared to control trials, with no differences found between any startle conditions for both peak displacement (Control=27.1°[2] , SD=4.1; SAS+0=35.5°, SD=10.7; SAS+25=37.2°, SD=10.8; SAS+50=36.8°, SD=11.1; SAS+75=36.7°, SD=11.3; SAS+100=35.5°, SD=9.8; SAS+125=34.8°, SD=10.4) and peak velocity (Control=441°/s, SD=153; SAS+0=654°/s, SD=249; SAS+25=689°/s, SD=279; SAS+50=700°/s, SD=290; SAS+75=687°/s, SD=303; SAS+100=640°/s, SD=194; SAS+125=643°/s, SD=233).

[2] Note: peak displacement values are typically found to overshoot and then return to the 20° target, especially when speed of response is emphasized.

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Discussion

The purpose of this study was to test the predictions of an additive versus horse-race model of initiation activation using a SAS and IS presented via different sensory modalities. While previous work has provided evidence for additive activation when the SAS and IS are both auditory in nature [8], research involving a SAS presented following a visual IS [7] appeared to provide data suggestive of a horse-race model in which observed RTs reflected either the involuntary (SAS related) or voluntary initiation activation triggering the response, depending on which process reached threshold sooner. In the current study the observed RTs were significantly different to those predicted by a horse-race model ($p=.037$), but were not different to those predicted by an additive model ($p=.979$) (Fig. 2). This dichotomy, along with the large p-value obtained in the goodness-of-fit analysis for the additive model provides compelling evidence that when a SAS is presented, both voluntary and involuntary activation jointly contribute to response initiation, even when the IS and SAS are of different modalities.

Consistent with previous research examining visual versus auditory RT differences [3, 6], the visual IS resulted in a delayed voluntary RT (M=183 ms) when compared to the previously-reported auditory-based control RT (M=127 ms) [8]. This difference allowed for a more detailed examination of an additive model of initiation as additive effects were expected for all SAS presentation times greater than 25 ms following the IS. For example, in the SAS+75 condition (blue diamonds, Fig. 1), a near complete overlap of activation slopes would maximize additive initiation time. Consistent with an additive model, the SAS-referenced RT for this condition was 73 ms, representing a RT reduction of 12 ms compared to the SAS+0 condition (which was already executed at a very short latency of 85 ms). Furthermore, all conditions resulted in faster RTs than would be expected for either the control tone or SAS alone, providing additional support for additive initiation model. This is especially informative for the conditions of SAS+100 and SAS+125 as the horse-race model would predict RTs that are similar to those during control trials, which is clearly inconsistent with the data (Fig. 2).

Additional evidence supporting an additive model is provided by both peak displacement and peak velocity, which were larger for all SAS conditions compared to control trials. Previous startle studies have reported exaggerated response kinematics, which were attributed to additional activation of the nervous system caused by the SAS [e.g., 8]. This increased activation, and thus exaggerated kinematics, would be expected to occur in conditions where involuntary activation contributed to the initiation processes. While the additive model predicts that startle-related activation contributes to all SAS conditions, a horse-race model predicts that conditions where voluntary initiation processes complete first (e.g., SAS+100, SAS+125), no contribution of startle-related activation would be present in the produced movements. Thus, the increased peak displacement and peak velocity for all startle conditions (including SAS+100 and SAS+125) are more consistent with an additive activation model.

Although the current data strongly suggest that voluntary and involuntary initiation activation are additive (regardless of modality), this conclusion appears inconsistent with the data reported by Kumru and Valls-Solé [7] who employed a similar method (note that this study was not designed to test an additive model of initiation). However, Kumru and Valls-Solé reported considerably longer RTs for both control trials (M=201 ms) and the SAS+0 condition (M=101 ms), compared to the current study (control M=183 ms, SAS+0 M=85 ms). In terms of an additive model, these differences would result in a shallower SAS-related activation slope as well as an increased amount of time before additive activation would be predicted. Using the data provided by Kumru and Valls-Solé, predictions of both models can be made for their SAS+20, SAS+40, SAS+60, SAS+80 and SAS+100 conditions (horse-race model: 121 ms, 141 ms, 161 ms, 181 ms and 201 ms; additive model: 121 ms, 138 ms, 149 ms, 160 ms and 171 ms). Subjecting their reported results (119 ms, 129 ms, 150 ms, 165 ms, 188 ms) to a similar goodness-of-fit analysis as used in the current study, neither prediction is

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significantly different the observed values, although a better fit is found for the additive model, X2(4, N=10) = 0.99, p=.911, as compared to the horse-race model, X2(4, N=10) = 2.27, p=.687.

As a final note, the RT predictions of the additive model in the current study were based on using an initiation activation slope for the visual control trials that was the same as that calculated by Maslovat et al. [8] for auditory control trials. This value resulted in a close match between predicted and actual results for the current data, suggesting that an identical initiation activation slope is appropriate for both a visual and auditory IS. A common initiation time for different IS modalities implies that the typically observed differences in control RT between visual and auditory stimuli [3] are more likely due to processes that occur prior to response initiation. This result is consistent with previous research showing that visual-auditory RT differences can be negated when the stimuli are equated on a common intensity scale [6], suggesting it may be a difference in stimulus detection time that causes the often reported RT differences between a visual versus auditory IS.

Acknowledgements

Supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) discovery grant awarded to ANC (RGPIN:418361-2012).

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