

ORIGINAL ARTICLE

The interplay of perceptual processing demands and practice in modulating voluntary and involuntary motor responses

Welber Marinovic¹  | An T. Nguyen¹  | Ann-Maree Vallence² | James R. Tresilian³ | Ottmar V. Lipp⁴ 

¹School of Population Health, Curtin University, Perth, Western Australia, Australia

²School of Psychology and Exercise Science, Murdoch University, Murdoch, Western Australia, Australia

³Department of Psychology, University of Warwick, Coventry, UK

⁴School of Psychology and Counselling, Queensland University of Technology, Brisbane, Queensland, Australia

Correspondence

Welber Marinovic, School of Population Health, Curtin University, Perth, WA, Australia.

Email: welber.marinovic@curtin.edu.au

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Abstract

Understanding how sensory processing demands affect the ability to ignore task-irrelevant, loud auditory stimuli (LAS) during a task is key to performance in dynamic environments. For example, tennis players must ignore crowd noise to perform optimally. We investigated how practice affects this ability by examining the effects of delivering LASs during preparatory phase of an anticipatory timing (AT) task on the voluntary and reflexive responses in two conditions: lower and higher visual processing loads. Twenty-four participants (mean age = 23.1, 11 females) completed the experiment. The AT task involved synchronizing a finger abduction response with the last visual stimulus item in a sequence of four Gabor grating patches briefly flashed on screen. The lower demand condition involved only this task, and the higher demand condition required processing the orientations of the patches to report changes in the final stimulus item. Our results showed that higher visual processing demands affected the release of voluntary actions, particularly in the first block of trials. When the perceptual load was lower, responses were released earlier by the LAS compared to the high-load condition. Practice reduced these effects largely, but high perceptual load still led to earlier action release in the second block. In contrast, practice led to more apparent facilitation of eyeblink latency in the second block. These findings indicate that a simple perceptual load manipulation can impact the execution of voluntary motor actions, particularly for inexperienced participants. They also suggest distinct movement preparation influences on voluntary and involuntary actions triggered by acoustic stimuli.

KEYWORDS

acoustic eyeblink startle reflex, anticipatory timing, loud acoustic stimulus, movement preparation, perceptual load

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1 | INTRODUCTION

When engaged in a sensorimotor task, we need to identify and channel task-relevant sensory information to the response production mechanisms while ignoring or suppressing task-irrelevant information to prevent it from disrupting performance (Allport, 1993; Lamy et al., 2013). The process by which this is accomplished during the execution of voluntary actions corresponds, at least in part, to what is usually referred to as sensory (or perceptual) selective attention. Selective attention is imperfect or incomplete in the sense that not all task-irrelevant aspects of stimulation can be prevented from interfering with the on-going performance of a volitional action (e.g., Yantis & Jonides, 1984, 1990). For instance, while faint, weak, or otherwise obscure stimuli can be successfully ignored and prevented from influencing performance, intense or otherwise salient stimuli cannot, and for good reason: such stimuli are likely to require some kind of response, and ignoring them could have serious consequences. Sudden, loud, task-irrelevant sounds, for example, cannot be ignored; there is evidence that they are automatically processed (Yantis & Jonides, 1990), they disrupt on-going task performance and can elicit startle and/or orienting reactions that interfere with it (Blumenthal et al., 2015; Marinovic & Tresilian, 2016; Vlasak, 1969). In addition to these interference effects, sudden loud sounds can also involuntarily trigger prepared responses and increase their vigor when a person is in a state of readiness to perform them, as is the case in reaction time (RT) and anticipatory timing (AT) tasks (Marinovic et al., 2014; Valls-Sole et al., 1999). The triggering is known as the StartReact effect (Valls-Sole et al., 1999). The present study sought to investigate the role of attentional processes in determining the characteristics of the StartReact effect and the associated increased response vigor, extending our previous work on this topic (Marinovic et al., 2014).

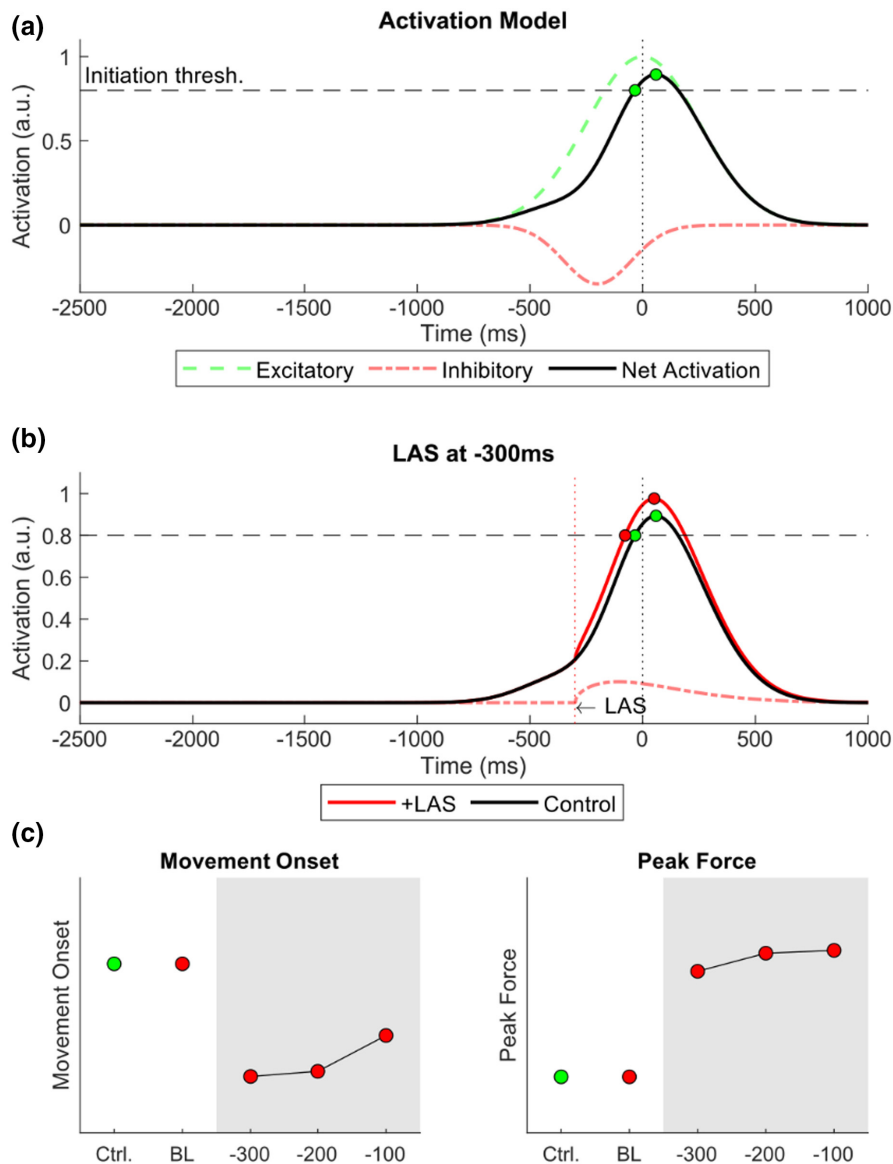
In both RT and AT tasks, a person is required to respond to a stimulus, either as quickly as possible (RT tasks) or at a specific moment (AT tasks). In the classic laboratory AT task, a sequence of discrete stimulus items is presented and the performer is required to time a response (e.g., a key press) such that it occurs at the same time as the final item in the sequence (Ghez et al., 1989). We previously studied how the modality of the stimulus sequence in an AT task influences the StartReact and response vigor effects (Marinovic et al., 2014) and found that the effects are larger when the stimulus sequence is auditory compared to when it is visual. We attributed this effect to selective attention: when the primary AT task requires attention to the auditory modality, the auditory system is more active and excitable than it is when the AT task requires attention to the visual modality. When the stimulus sequence is

visual, auditory stimulation is task irrelevant and the auditory system is subject to attentional processes directed at ignoring auditory stimulation and suppressing irrelevant auditory activation.

In previous work, we interpreted the effects of loud acoustic stimuli on the execution of prepared responses in terms of a simple model in which motor preparation is conceptualized as a build-up of activity in response production circuitry (Marinovic et al., 2013; Tresilian & Plooy, 2006). The response is initiated when the level of activity reaches a pre-established threshold at which point activity returns to the baseline level: a visual representation of the model is shown in Figure 1 (panel A). When the motor circuitry is in a high state of activation, the occasional delivery of a loud acoustic stimulus (LAS) can inject a transient surge of activity, pushing net activation over the initiation threshold, leading to earlier and more forceful responses (Figure 1b). Based on the amount of activation (relative to control trials), the excitability of response circuits can be estimated, and the time course of excitability changes can be mapped by delivering the LAS at different time points (Figure 1c). If attention is assumed to modulate the level of auditory activity evoked by stimulation, then more or less attention to the auditory modality would be expected to lead, respectively, to a larger or smaller injection of LAS-evoked activity into the motor circuitry and corresponding effects on the response. Thus, when attention is directed to the auditory modality, the LAS-evoked activity will be greater, and the effects on the response correspondingly larger, as reported by Marinovic et al. (2014). In the present study, we sought to investigate attentional effects further not by manipulating attention to the auditory modality, but by altering attentional demands in the visual modality.

As in our previous study, we employed an AT task in which participants were required to make an index finger movement response at the same time as the final stimulus item in a four-item sequence. Here, we added a condition in which there was the additional requirement that any differences between the items in the sequence be reported following the response (see methods for details). This secondary task imposes an additional perceptual demand on the participant: not only must they extract information concerning the timing of the items but also their form. The question of interest concerns the effect on the task-irrelevant auditory system: will additional visual demand reduce excitability in the auditory system and so reduce the effects of the LAS, will it increase excitability and do the opposite, or will it have no effect on auditory excitability? There are reasons for supposing that the answer is that the effects of the LAS will be reduced, implying a reduction in auditory excitability. Increasing the perceptual processing demands of a sensorimotor task has been found to

FIGURE 1 (a) Conceptual visualization of the activation model, depicting activation in the response circuits during an anticipatory timing task. The solid black line represents the net preparation-related activity which gradually increases as the expected time of the response approaches (0 ms). A response is initiated when net activation crosses the initiation threshold (dashed black line) and the green dots represent the time of movement onset and peak force, respectively. The red and green lines represent excitatory and inhibitory processes that contribute to the overall state of the motor system, with the red line depicting a phenomenon referred to as pre-movement inhibition. (b) Shows the effect of loud acoustic stimulation (LAS) on the motor response. The solid red line shows how the added activity from the LAS causes the net activity in the system to cross the initiation threshold earlier and peak higher, producing an earlier and more forceful response. (c) Shows how the time course of preparation can be characterized by positioning the LAS at different time points relative to the expected movement.



result in reduced perceptual processing of task-irrelevant stimulus information both within and between sensory modalities (Lavie, 2005; Molloy et al., 2015): when processing demands are high, perception is more selective in the sense that processing of unattended stimulation is reduced or prevented (Lavie, 2005). Based on these findings, we predict that the additional visual processing demand will decrease the effect of the LAS on the AT response.

We also expect that the time course of movement preparation will be reflected in the effects of an LAS on both the voluntary AT response and on involuntary, reflex responses. This prediction is based on previous findings of a rapid transition from suppression to facilitation of the spinal cord occurring in the last 300 ms prior to movement onset, as reported by us and others (Ibanez et al., 2020; Marinovic et al., 2011; Starr et al., 1988). If the effect of increased visual processing demand is to reduce the excitability of the auditory system, then not only would the

effects of a LAS on the voluntary AT response be correspondingly reduced but the reflex responses would be expected to show similar reductions (longer latencies and decreased vigor).

Finally, there is the possibility that over repeated trials, experience with the task will reduce the effects of the LAS in both the higher and lower processing load conditions. It is well established that one effect of experience with and practice of a novel task is that performance becomes more automatic (Fitts & Posner, 1967; Tresilian, 2012), which means (in part) that it becomes possible to perform other tasks at the same time with little or no interference. Automaticity is associated with a reduced reliance on cortical control processes and an increasing involvement of subcortical task-specific mechanisms that are well insulated against interference from task-irrelevant activity (Ashby et al., 2010; Dupont-Hadwen et al., 2019; McInnes et al., 2021). The expected result of changes of this kind is

that the effect of LAS delivery on the AT task response will be reduced and this is expected in both lower- and higher-load conditions.

2 | METHOD

2.1 | Participants

Twenty-four participants [$M(SD)_{age} = 23.12 (5.84)$, age range = 18–45 years, 11 females, 13 males] completed the experiment. This sample size was determined based on previous work, which utilized similar tasks, procedures, equipment, outcome measures, and analytical methods (Nguyen et al., 2023). This sample size was considered sufficient to estimate effects with trial-level data using linear mixed models, which provide increased statistical power by more effectively accounting for within-participant variability (Baayen et al., 2008). All participants reported being right-hand dominant, having normal or corrected vision, no history of significant head trauma, and no diagnosed neurological conditions. They received course credit for their participation. All participants provided

written informed consent before starting the experiment and the protocol was approved by the human research ethics committee of Curtin University (approval number: HRE2018-0257).

2.2 | Anticipatory timing task

Participants were presented with Gabor patches in a fixed temporal sequence of four flashes and were instructed to synchronize the onset of their voluntary response with the fourth flash (depicted in Figure 2). Participants completed two different blocks of trials—low and high perceptual load blocks—with block order counterbalanced across participants. In the low-load block, participants were instructed to ignore the orientation of the Gabor patches and simply perform the motor action. In the high-load block, participants performed the motor action while also reporting whether there was a change in the orientation of one of the two Gabor patches on the final flash (compared to previous flashes, see Figure 2). The orientation of Gabor patches is described in more detail below. In the high-load block, participants reported whether they observed

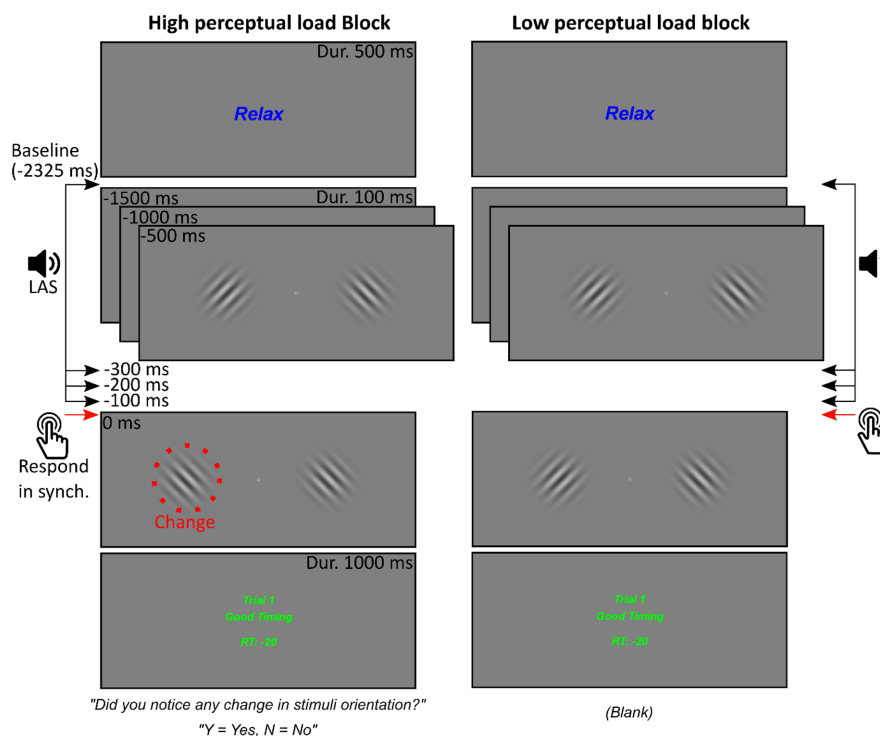


FIGURE 2 Sequence of key events in high (left) and low (right) perceptual load conditions. Participants were presented with a series of four Gabor patches (100 ms duration and 500 ms between stimuli) and were instructed to synchronize their response with the final flash (0 ms). The timing of events is depicted relative to the final flash. Attended block (left): In this block, participants had an additional requirement. They synchronized their response with the final flash and monitored the Gabor patches for orientation changes, reporting any changes they detected after the index finger movement occurred. Unattended block (right): Participants only synchronized their response with the final flash without monitoring for orientation changes. On 25% of trials, a loud acoustic stimulus (LAS) was pseudo-randomly presented at different times before the final flash (−2325, −300, −200, and −100 ms).

a change in orientation after they had made the voluntary response and received feedback about their temporal error (the difference between the onset of the fourth flash and movement onset time).

2.3 | Visual presentation

The task was presented using MATLAB 2015b and Psychtoolbox version 3.0.11 (Brainard, 1997; Pelli, 1997) on a 22-inch LCD monitor (Samsung Model 2233RZ, running at resolution of 1920×1080 and refresh rate of 120 Hz). Participants were seated ~70 cm from the monitor. Each trial began with the presentation of a “Relax” cue for 500 ms followed by a central fixation point (hollow white circle, 10 pixels in diameter) for a random jitter period of 0–400 ms plus 1000 ms. Participants were instructed to maintain fixation on this point, which also persisted during the Gabor flashes. Following this, two Gabor patches were briefly flashed on the left and right side of the display four times (500 ms intervals for a duration of 100 ms each). Each Gabor patch was 300 pixels in diameter (8 cycles, $\sigma=7$, with two randomly determined phase angles for each participant). The left and right patches were horizontally shifted by 250 pixels from the center of the display and were vertically centered.

In both high and low perceptual load blocks, the orientation of one patch was -45° from vertical and the other was $+45^\circ$, but the left–right location was randomized on each trial. On no-change trials, the same configuration was repeated for all four flashes. On change trials, one of the Gabor patches could be shifted by $+45^\circ$ or $+90^\circ$ in the clockwise direction. Change trials were present in both high and low perceptual load blocks.

2.4 | Loud acoustic stimulation

In each block, a LAS was pseudo-randomly presented on 25% of trials, consistent with recommendations for research on the StartReact phenomenon (Carlsen et al., 2011), at one of four predetermined time points: -2325 ms (baseline), -300 , -200 , or -100 ms before the expected time of response onset (i.e., onset of final flash). For each block, the LAS was presented 12 times at each time point. The pseudo-randomization occurred such that the LAS would not be presented in two consecutive trials but participants were unaware of any presentation schedule. The LAS was a 50 ms burst of broadband white noise presented at an intensity of 105 dBA, generated using an external custom-made white-noise generator, directly connected to high-fidelity headphones for low-latency presentation (Sennheiser Model HD25-1 II). Sound intensity

was measured with Brüel and Kjaer sound-level meter (Type 2205, A weighted) placed 2 cm from the headphone speaker. Stimulus rise time was measured to be 1.25 ms from the headphones.

2.5 | Response and feedback

Participants responded to the task by quickly and briefly pressing their right index finger on a force sensor (SingleTact, Model: CS8-10N) embedded in a shell resembling a computer mouse. Before the participants began practice trials, they experienced the LAS once to ensure they were comfortable proceeding. Participants then executed practice trials, with 25% of trials including the LAS, to become familiar with the task. As whole-body startle responses habituated quickly (Davis, 1984; Landis & Hunt, 1939), this approach ensured that participants could perform actions without being affected by exaggerated startle responses. Additionally, participants were instructed to generate quick responses that were comfortable for them, with a peak force range between 1 and 5 N. However, they were not given feedback on peak force during the experiment. Feedback about response time and timing accuracy was presented at the end of each trial (750 ms after the final flash for a duration of 1000 ms). If participants initiated their response within ± 50 ms of the final flash, “Good Timing” was presented. If they responded outside the 100 ms window, “Too Early” or “Too Late” was presented. If no detectable response was made on the trial, “No Response Detected” was presented. No feedback was presented on LAS trials and “Probe Trial” was presented instead. On high-load trials, “Did you notice any change in the stimuli orientation? (Y = Yes, N = No)” was presented after feedback offset, and participants indicated their response on a computer keyboard without a time limit. No feedback was presented on this response and the start of next trial commenced 500 ms after the response was made. This question was not presented in the low-load block.

2.6 | General procedure

After written informed consent was obtained, EMG electrodes were applied and participants were seated at the computer. Participants were then provided with on-screen and verbal instructions, followed by a demonstration of the trial sequence. Participants completed a practice block consisting of 10 trials (5 high and load perceptual load trials) in a fixed sequence with two LAS trials, followed by two experimental blocks consisting of 192 trials each, with a self-paced break in between. The block order was

counterbalanced across participants. The trial breakdown is shown in Table 1. The entire experiment took approximately 45 min to 1 h to complete.

2.7 | Force and EMG data acquisition, data reduction, and measurement

Force data acquired from the force sensor were continuously recorded for the duration of the trial, digitized at 2000 Hz using a National Instruments data acquisition device (Model: USB-6229 BNC multifunctional DAQ). The data were filtered using a low-pass second-order Butterworth filter with a cut-off frequency of 20 Hz. As our measure of response timing, we calculated movement onset time relative to the intercept from the tangential speed time series derived from the force data using the algorithm recommended by Teasdale and colleagues (Teasdale et al., 1993). This algorithm first determines the sample (S1) at which the time series first exceeds 10% of its maximum value. Then, working back from S1, it finds the first sample (S2) at which speed reaches 10% of the speed value at S1. Lastly, working back from S2, the algorithm locates the onset as the sample at which speed equals the average value plus the standard deviation between S1 and S2. Trials with onset latencies exceeding 300 ms before and after the final flash were excluded from further analysis (3.6% of trials discarded). We also used rate of force development as our measure of response vigor.

We recorded EMG activity from the right orbicularis oculi muscle using a pre-amplified bi-polar set-up. We used 8 mm Ag/AgCl sintered electrodes, one electrode was placed under the pupil, the second was placed laterally and slightly higher than the first electrode, approximately 1 cm edge-to-edge, and a ground electrode was placed on the right mastoid region. We used a Neurolog Systems Digitimer Pre-Amplifier (Model: NL820) and Amplifier (Model: NL905) with a 50–1000 Hz pass-band filter and gain set to 1000. These data were also digitized using the DAQ.

The EMG data were processed offline using a semi-automatic procedure in R. The data were down-sampled to 1000 Hz, rectified using the “rectification” function in “biosignalEMG” package (Guerrero & Macias-Diaz, 2018), and smoothed using 5-point moving average with the “rollapply” function in the “zoo” package (Zeileis et al., 2014). The Bonato method (Bonato et al., 1998) was

used to automatically detect the blink onset latency, using the “onoff_bonato” function in the “biosignalEMG package” (sigma $n=2$ times the standard deviation of activity within 0–200 ms prior to the LAS). Multiple passes of this step were run. If no onset was detected, another pass was run with the threshold gradually increasing (by increments of 0.2 times baseline variability, 10 times) and then decreasing (from 1 in increments of 0.2 times baseline variability, 2 times), until an onset was detected within 20–120 ms. We also measured baseline-to-peak EMG amplitude occurring after blink onset. Each trial was visually inspected, and corrections were made to onset and peak latencies where necessary. Acceptable onset latencies were within 20 to 120 ms from LAS onset; trials outside this window were excluded from further analyses of blink data (Blumenthal et al., 2005). Trials with a flat EMG response were classified as “non-response trials.” Trials containing excessive noise, artifacts, or voluntary activation before the eyeblink reflex were classified as “missing” trials. Non-response and missing trials were excluded in further analyses of blink data (6% of trials discarded). EMG amplitude was normalized within individuals by calculating t scores ($M=50$, $SD=10$) to account for individual differences in blink amplitude (Blumenthal et al., 2005).

2.8 | Statistical analyses

Statistical analyses were conducted in R Statistics (version 4.1.2) and R Studio (version 1.2.5033). To test our hypotheses, we employed both frequentist and Bayesian analytical approaches to take advantage of their complementary strengths, as recommended by Flores et al. (2022). We initially conducted linear mixed models using the “lmer” function from the “lmerTest” package (Kuznetsova et al., 2017) to obtain evidence for the main effects and interactions of interest in the framework of null hypothesis significance testing. The results are reported as F values using the “anova” function with Satterthwaite’s approximation for degrees of freedom. The dependent variables for voluntary responses were movement onset time and rate of force development, while for involuntary responses, they were blink latency and normalized blink amplitude. To strengthen the interpretability of our initial analysis, we conducted

| Condition | LAS position | | | | |
|-----------|--------------|------------------------|---------|---------|---------|
| | Control | Baseline (−2325 ms) | −300 ms | −200 ms | −100 ms |
| High | 144 | 12 | 12 | 12 | 12 |
| Low | 144 | 12 | 12 | 12 | 12 |

TABLE 1 Breakdown of control and LAS trials across perceptual load conditions (high, low). Time points are relative to the expected response time (i.e., onset of the final flash).

Bayesian linear mixed models using the “stan_lmer” function of the “rstanarm” package. Bayesian methods offer probability-based interpretations, are well-suited for complex designs and repeated measures, and allow us to quantify uncertainty in effects through the posterior distributions. Weakly informative default priors were used in the Bayesian models. Median effect estimates and 95% high-density intervals (HDI) were obtained using the “report” package. Highest posterior density interval (HPDI) estimates for specific pairwise contrasts were obtained using the “emmeans” package. We reasoned that the convergence of outcomes from these two analytical paradigms would enable a more detailed interpretation of the results and enhance confidence in our findings.

For both frequentist and Bayesian linear mixed models, we included perceptual load (high, low), control/LAS time points (control, -300 , -200 , and -100 for voluntary actions and baseline, -300 , -200 , and -100 for involuntary responses) as within-subjects fixed factors, and block order as a between-subject factor. Note that the different timings were entered in the model as categorical variables rather than numerical ones to allow comparisons across all pairwise conditions. Block order was included in the models as a fixed effect and as a random effect. Although we counterbalanced perceptual load blocks of trials across participants (e.g., half of the participants performed the low-load condition first while the other half performed the high-load condition first), we considered that the effects of perceptual load on movement preparation would be affected by practice (e.g., high-load may have a greater impact in the first block when the task is less practiced). Therefore, including block order as both a fixed and a random effect allows us to estimate the practice effect while also controlling for random variability in this factor that is not related to our research question. Note that the exclusion of the block order as a random effect did not change the qualitative pattern of results reported. All frequentist and Bayesian models successfully converged. Additionally, using control (no LAS) or LAS at -2325 ms as the baseline condition made no qualitative difference in the interpretation of results. However, we opted for the control condition (no LAS) as a better baseline to delineate the effects of the presence versus the complete absence of auditory stimuli.

3 | RESULTS

3.1 | Perceptual accuracy

During the high-load condition, participants correctly identified whether there was a change or not in the

orientation of Gabor patches on $\sim 80\%$ of trials. Perceptual accuracy did not differ between participants who completed the high-load condition in the first or second block (Welch two-sample t test: $T_{(21)} = 0.28$, $p = .77$, Mean (SE) Block 1 = 79.34 (2.45), Mean (SE) Block 2 = 80.9 (3.04)).

3.2 | Voluntary responses: Movement onset effects

Figure 3 presents the pattern results observed for both movement onset (Figure 3a) and rate of force development (Figure 3b). Focusing on the effects of movement onset, the linear mixed-model analysis revealed significant main effects of control/LAS time point ($F_{(3,8259)} = 22.06$, $p < .0001$) and block ($F_{(1,31.9)} = 4.90$, $p = .003$), but no main effect of perceptual load ($F_{(1,31.9)} = 2.60$, $p = .11$). Two-way interactions between Perceptual Load \times Control/LAS time point ($F_{(3,8259)} = 1.09$, $p = .35$) and Perceptual Load \times Block ($F_{(1,23.6)} = 1.77$, $p = .19$) failed to reach statistical significance. However, the two-way interaction between Control/LAS Time Point \times Block ($F_{(3,8259)} = 6.30$, $p < .001$) was significant, and so was the three-way interaction ($F_{(3,8259)} = 4.73$, $p = .0002$). The Bayesian linear mixed-model analysis supported the results of the frequentist approach, revealing three-way interactions. For the interaction among control/LAS time point at -300 , high load, and Block 2, the analysis yielded a median effect of -31.86 with a 95% high-density interval (HDI) of $[-51.38$ to $-12.36]$. Similarly, the control/LAS time point at -200 , high load, and Block 2 interaction showed a median effect of -18.67 and a 95% HDI of $[-37.28$ to $-0.27]$. These HDIs suggest credible intervals of the effects well away from zero, indicating substantial evidence for these interactions. Conversely, the interaction for control/LAS time point at -100 , high load, and Block 2 had a median effect of -0.07 with a 95% HDI of $[-18.75$ to $18.36]$, indicating a lack of credible evidence for a substantial effect in this case. These results illustrate how the relationship between perceptual load and block varies depending on the control/LAS time point. Figure 4 presents pairwise comparisons of these contrasts as estimated from the Bayesian model.

In Block 1, most of the prominent pairwise differences involved the -200 ms time point relative to movement onset time. As depicted in Figure 4a, the 95% HPDIs for the -200 ms time point did not overlap with those of all other time points in both high- and low-load conditions, providing strong evidence against the null hypothesis of no difference. The HPDIs for -200 and -300 ms in the low-load condition, however, did overlap, suggesting that responses were initiated early in both cases compared to control trials. In Block 2, the 95% HPDIs for the post hoc

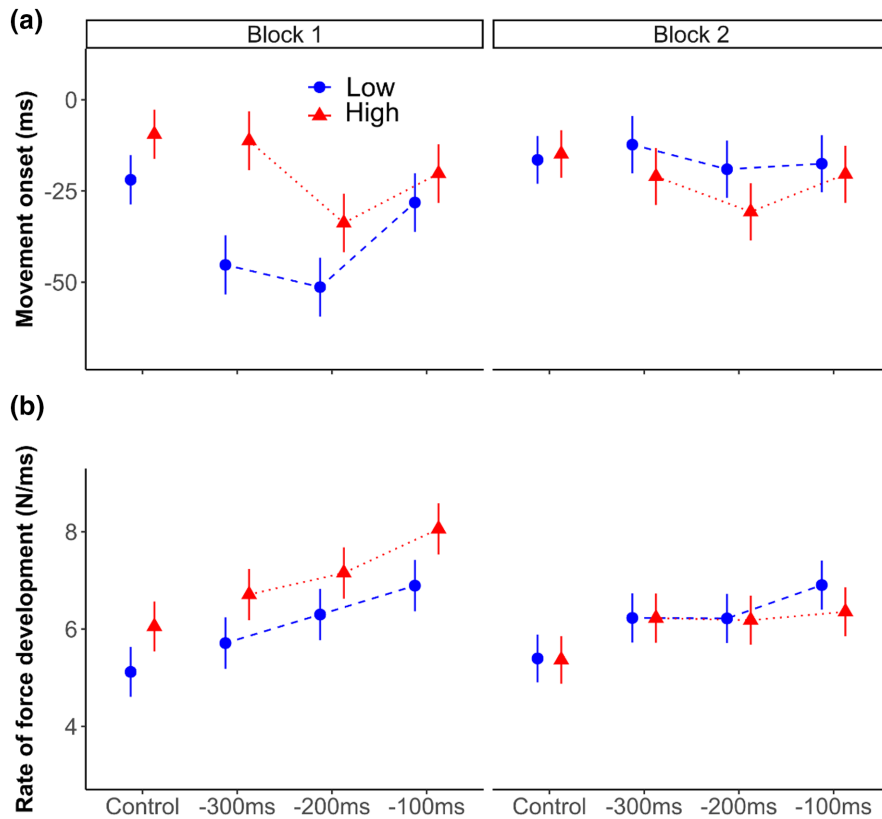


FIGURE 3 Estimated marginal grand means (with standard error bars) for voluntary responses. (a) Movement onset means across both blocks of trials. (b) Rate of force development across both blocks of trials. Control, -300 , -200 , and -100 ms in relation to the expected time of movement onset. Red triangles represent the means obtained during the high-load condition. Blue circles represent the means obtained during the low-load condition.

comparisons between high- and low-load conditions at all timepoints largely overlapped (Figure 4b). The only time point that exhibited non-overlapping 95% HPDIs was the -200 ms to movement onset in the high-load condition when compared to control trials, providing strong evidence against the null hypothesis for this specific comparison.

As shown in Figures 3a and 4, these results indicate that responses were more affected by LAS in the first block of trials. They also indicate that voluntary responses were more facilitated by LAS at 200 ms to movement onset time. The results seem to indicate there is an initial facilitation of movement onset from -300 to -200 ms, followed by a return to baseline levels at -100 ms, reflecting the dynamic changes that occur around the time of movement onset. This early facilitation at -300 ms was not present under the high-load condition, indicating an impact of perceptual load in the first block of trials.

3.3 | Voluntary responses: Rate of force development effects

Regarding the rate of force development (Figure 3b), the linear mixed model revealed a significant main effect of control/LAS time point ($F(3, 8259)=268.15$, $p<.0001$), but no main effects of block ($F(1, 23.3)=2.07$, $p=.16$) nor perceptual load ($F(1, 23.3)=2.36$, $p=.13$). The two-way interaction between control/LAS time point and block

was significant ($F(3, 8259)=10.87$, $p<.0001$), but the two-way interactions between perceptual load \times control/LAS time point ($F(3, 8259)=0.48$, $p=.69$) and perceptual load \times Block ($F(1, 22.2)=0.75$, $p=.39$) were not statistically significant. The three-way interaction among control/LAS time point, perceptual load, and block ($F(3, 8259)=2.78$, $p=.03$) was statistically significant. The Bayesian linear mixed-model analysis corroborated these results, suggesting relevant three-way interactions. For the interaction involving control/LAS time point at -300 , high load, and Block 2, the median effect was -0.05 with a 95% HDI of $[-0.57, 0.48]$. This HDI indicates a lack of credible evidence for a substantial effect in this case. Similarly, the interaction between control/LAS time point at -200 , high load, and Block 2 demonstrated a median effect of 0.07 with a 95% HDI of $[-0.45$ to $0.58]$, also suggesting an absence of evidence for this effect. However, the three-way interaction involving control/LAS time point at -100 , high load, and Block 2 showed a median effect of -0.75 with a 95% HDI of $[-1.26$ to $-0.23]$, providing support for the presence of this effect.

To visualize this interaction, we examined pairwise comparisons from the Bayesian model (Figure 5). This revealed that, in the low-load condition during Block 1, responses at -300 , -200 , and -100 ms were more forceful than control trials, as indicated by non-overlapping 95% HPDIs (control vs. -300 : median = -0.59 , 95% HDI $[-0.86$ to $-0.35]$; control vs. -200 : median = -1.18 , 95%

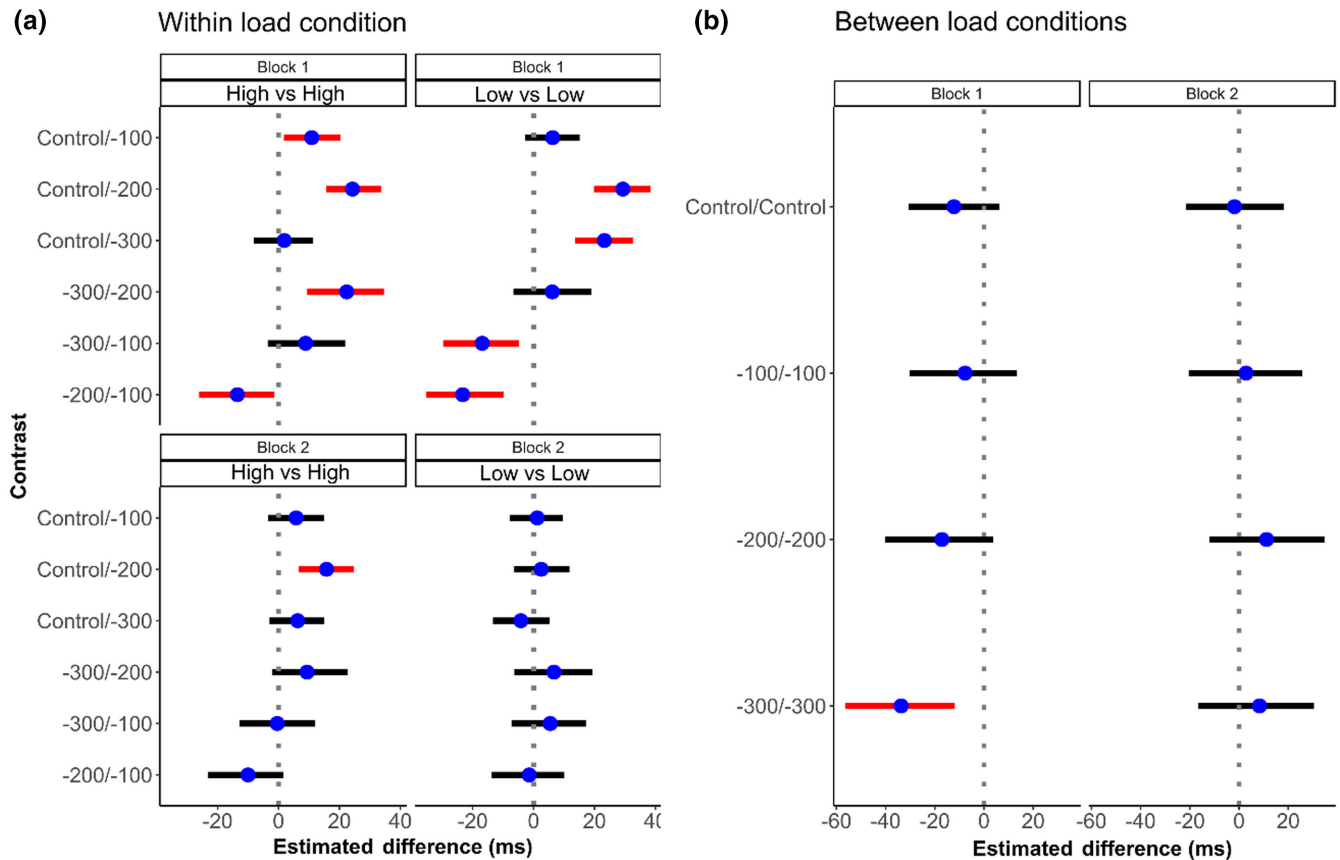


FIGURE 4 (a) Pairwise estimated differences in movement onset time among time points in Blocks 1 and 2 for both high- and low-load conditions. (b) Pairwise estimated differences in movement onset time between equivalent time points across load conditions. The circles represent the estimated mean difference between conditions. Bars represent the 95% highest posterior density intervals (HPDI) of marginal mean differences estimated from the Bayesian model through the R package “emmeans.” Red bars indicate significant differences where the 95% HPDI did not include zero, and black bars represent non-significant differences where the 95% HPDI included zero.

HPDI [−1.44 to −0.92]; control vs. −100: median = −1.77, 95% HPDI [−2.05 to −1.51]). Similarly, in the high-load condition during Block 1, responses at all LAS time points were more forceful than in control trials, also supported by non-overlapping 95% HPDIs (control vs. −300: median = −0.66, 95% HPDI [−0.92 to −0.41]; control vs. −200: median = −1.10, 95% HPDI [−1.35 to −0.85]; control vs. −100: median = −2.00, 95% HPDI [−2.27 to −1.76]). All pairwise comparisons among −300, −200, and −100 ms time points provided strong evidence for a difference for both high- and low-load conditions in Block 1 (see Figure 5a).

In Block 2, however, the −100 time point differed reliably from −200 and −300 ms only for the low-load condition, as indicated by non-overlapping 95% HPDIs (−100 vs. −300: median = −0.66, 95% HPDI [−1.01 to −0.34]; −100 vs. −200: median = −0.67, 95% HPDI [−1.02 to −0.33]). As shown in Figure 5b, none of the comparisons between equivalent timepoints across high and low loads provided strong evidence against the null hypothesis in Block 1. For Block 2, again there were no differences for which the 95%

HPDIs did not overlap between high and low load at any time point.

As depicted in Figures 3b and 5, these results indicate that responses were always more forceful when the LAS was delivered, irrespective of the time point the stimulus occurred. In the first block of trials, there is evidence that as the time of LAS occurred closer to movement onset time, there was a linear increase in response vigor. However, this was not apparent in Block 2, where only responses at −100 ms were more forceful than at −300 and −200 for the low-load condition.

3.4 | Involuntary responses: Blink onset latency effects

The frequentist linear mixed-model analysis found a significant main effect of control/LAS time point ($F_{(3,2018)} = 10.54$, $p < .0001$). However, the main effects of perceptual load ($F_{(1,21.7)} = 0.08$, $p = .77$) and block ($F_{(1,21.7)} = 0.03$, $p = .87$) were not statistically significant. The interaction between

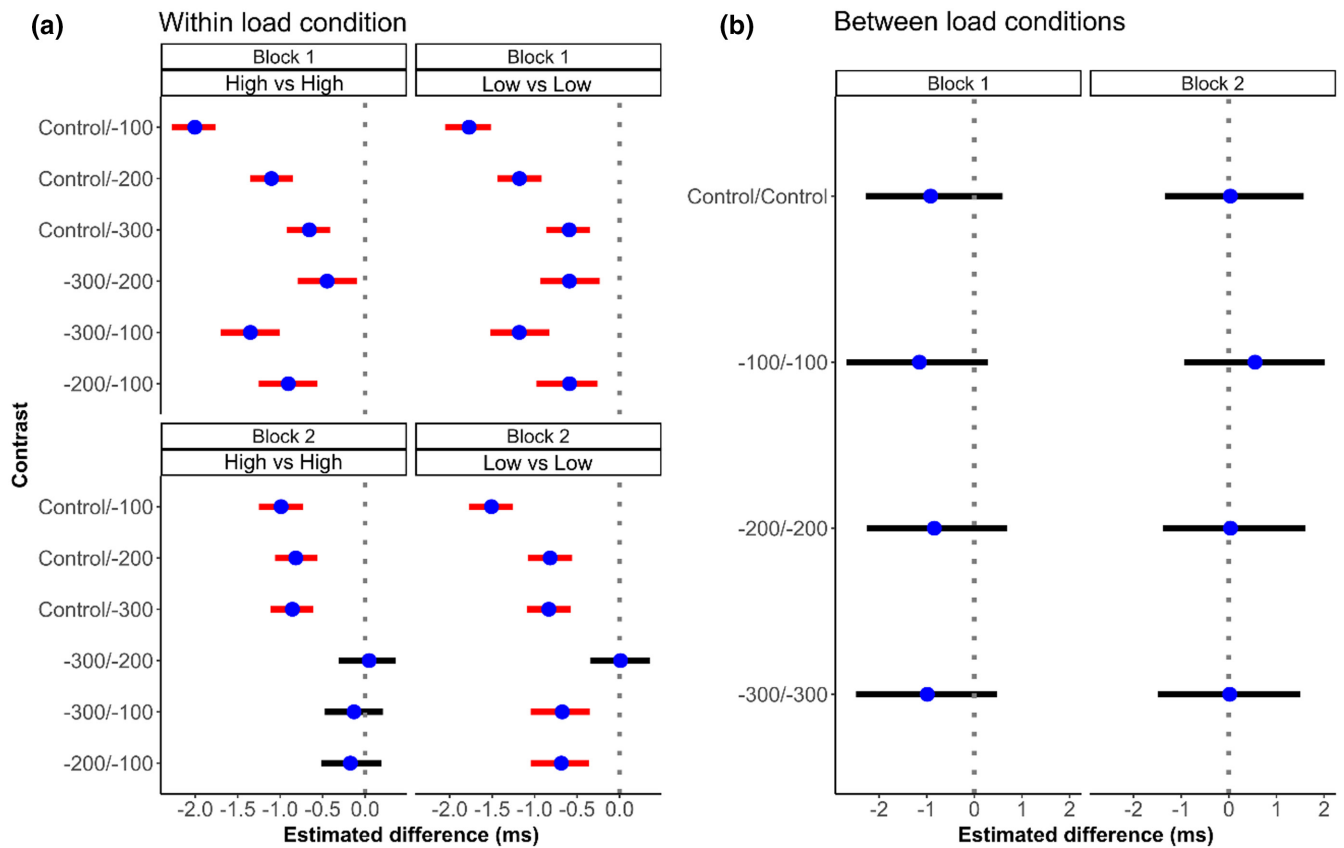


FIGURE 5 (a) Pairwise estimated differences in rate of force development among time points in Blocks 1 and 2 for both high- and low-load conditions. (b) Pairwise estimated differences in rate of force development between equivalent time points across load conditions. The circles represent the estimated mean difference between conditions. Bars represent the 95% HPDI of marginal means differences estimated from the Bayesian model through the R package “emmeans.” Red bars indicate significant differences where the 95% HPDI did not include zero, and black bars represent non-significant differences where the 95% HPDI included zero.

control/LAS time point and block reached statistical significance ($F_{(3,2020)} = 2.62, p = .049$). All other interaction terms were not significant (all $p > 0.44$).

The Bayesian linear mixed-model analysis provided mixed support for these findings. For the effect of block, the Bayesian model indicated an 85.5% posterior probability for the effect being different from zero (median = 3.30, 95% HDI [−2.04 to 9.13]), yet the inclusion of zero in the HDI suggests some uncertainty about this effect. Regarding the effect of perceptual load, the model estimated a median of 2.44 with a 95% HDI of [−2.47 to 7.38]. This result has an 82.53% probability of the effect being positive, a 77.75% probability of being reliable, and a 48.75% probability of being large, contrasting with the nonsignificant finding in the frequentist analysis.

Regarding two-way interactions between condition and block, the interactions at −300 and −200 at Block 2 showed medians of −1.75 and −1.62 with 95% HDIs of [−3.69 to 0.15] and [−3.47 to 0.30], respectively, suggesting some uncertainty for these effects due to the inclusion of zero. However,

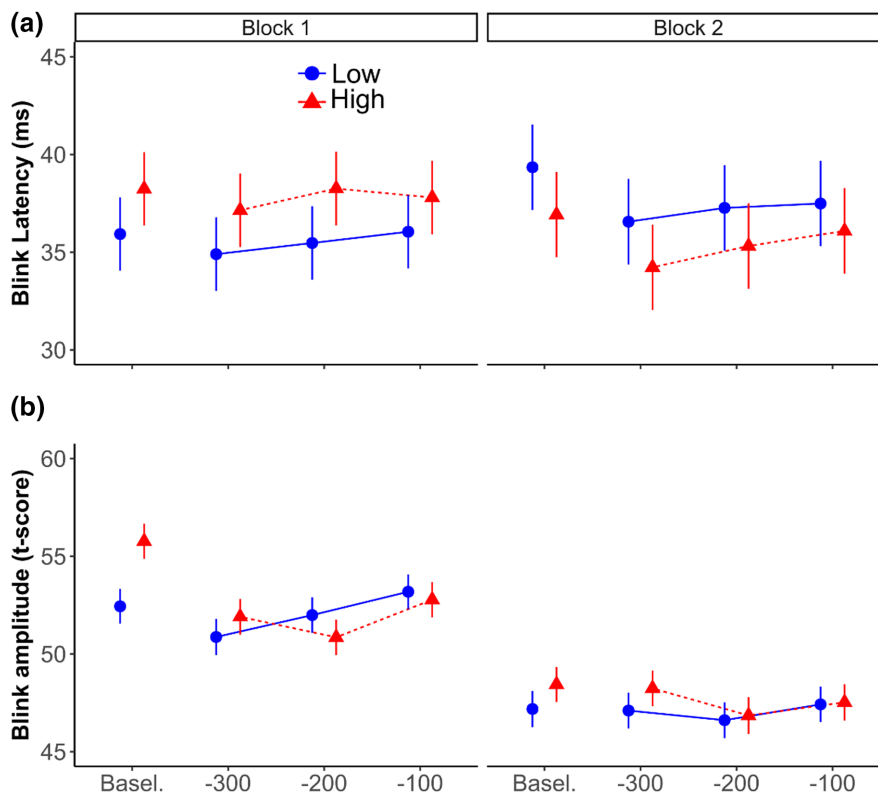
the interaction at −100 at Block 2 (median = −1.98, 95% HDI [−3.86 to −0.11]) does not include zero, indicating stronger evidence for this effect (see also Figure 7a,b).

In summary, both the frequentist and Bayesian analyses, as shown in Figures 6 and 7a, suggest an overall facilitation of blink latency during movement preparation relative to baseline. This facilitation was more pronounced in the second block of trials.

3.5 | Voluntary responses: Blink amplitude effects

The frequentist linear mixed model showed a significant main effect of control/LAS time point ($F_{(3,2041)} = 3.88, p = .008$). A significant main effect of block was also detected ($F_{(1,22.45)} = 59.4, p < .0001$), indicating that blink amplitudes were large in the first block of trials. The main effect of perceptual load ($F_{(1,22.45)} = 1.12, p = .30$) was not statistically significant. None of the interaction terms reached statistical significance (all $p > .07$).

FIGURE 6 Estimated marginal grand means (with standard error bars) for involuntary responses. (a) Blink latency means across both blocks of trials. (b) Normalized blink amplitude across both blocks of trials. (Baseline = Baseline, -300, -200, and -100 ms in relation to the expected time of movement onset). Red triangles represent the means obtained during the high-load condition. Blue circles represent the means obtained during the low-load condition.



Complementing this, the Bayesian linear mixed-model analysis confirmed a high posterior probability for the block effect (99.98% probability of an effect size different from zero, median = -5.24, 95% HDI [-7.71 to -2.69]) and for the effect at control/LAS time point -300 (82.17% probability, median = -1.57, 95% HDI [-3.87 to 0.76]). In addition, the Bayesian approach indicated a high probability (98.90%) that the effect of high load is credibly different from zero (median = 3.29, 95% HDI [0.94 to 5.84]). The model further identified likely interactions between control/LAS time points and high load, with the interaction at -300 showing an 86.4% probability of a non-zero effect (median = -2.22, 95% HDI [-5.49 to 0.89]). The interactions at time points -200 and -100 with high load also exhibited high probabilities of non-zero effects (99.12% for -200, median = -4.36, 95% HDI [-7.78 to -1.14]; 96.90% for -100, median = -3.71, 95% HDI [-7.06 to -0.35]), highlighting a consistent pattern in the data.

In sum, although the frequentist linear model did not find a statistically significant interaction between perceptual load and control/LAS time point ($p=0.079$), the Bayesian analysis suggested these effects are likely to be genuine. In particular, the Bayesian analysis indicated that the high-load condition resulted in lower blink amplitudes, particularly when comparing baseline blink amplitude and amplitudes at all LAS time points (-300, -200, and -100 ms, see also Figure 8a).

4 | DISCUSSION

The main purpose of this study was to examine the impact of visual processing demand on the preparation and execution of voluntary (finger flexion) and involuntary (blink reflex) motor responses. Previous research led to the prediction that increased visual demand would increase perceptual selectivity and so reduce the effects of a task-irrelevant LAS on the voluntary (anticipatory timing, AT) response and possibly result in a similar reduction in the reflex responses to the LAS as well. We also sought to characterize the time course of excitability changes over the last 300 ms of motor preparation: a critical interval where significant changes in corticospinal excitability are known to occur (Carlsen & Mackinnon, 2010; Ibanez et al., 2020; Marinovic et al., 2011; Marinovic et al., 2013; Nguyen et al., 2021). In addition, we sought to determine whether experience with the task (practice) over the course of the experiment would impact the initiation and execution of responses.

4.1 | Effects of visual processing load and practice—Voluntary responses

Consistent with the activation model (Figure 1) and previous findings (McInnes et al., 2021; Nguyen et al., 2021; Tresilian & Plooy, 2006), the delivery of the LAS during movement preparation led to AT responses occurring

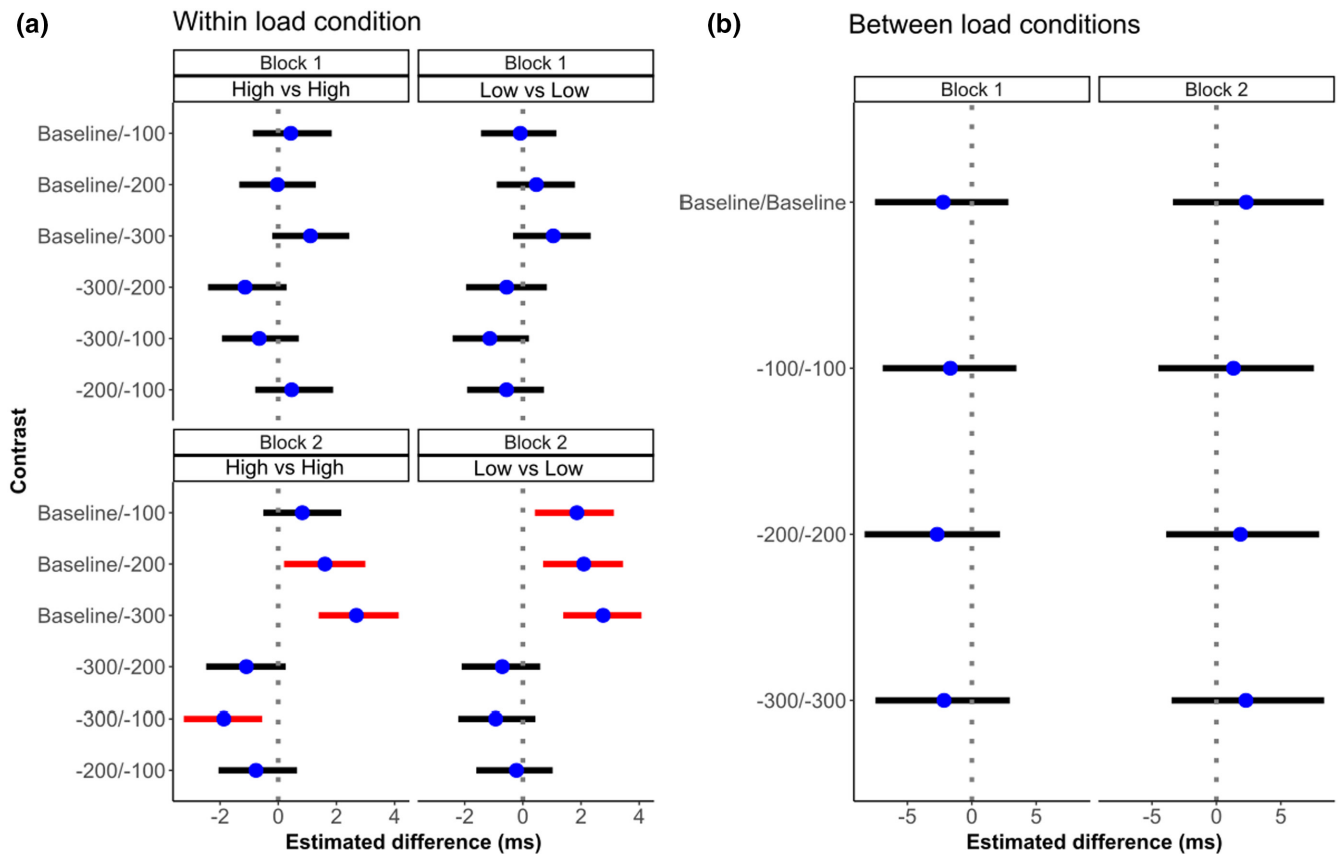


FIGURE 7 (a) Pairwise estimated differences in blink latency among time points in Blocks 1 and 2 for both high- and low-load conditions. (b) Pairwise estimated differences in blink latency between equivalent time points across load conditions. The circles represent the estimated mean difference between conditions. Bars represent the 95% HPDI of marginal means differences estimated from the Bayesian model through the R package “emmeans.” Red bars indicate significant differences where the 95% HPDI did not include zero, and black bars represent non-significant differences where the 95% HPDI included zero.

earlier. The magnitude of the timing effect was smaller than previously reported for reaction time tasks with more variable foreperiods, but of similar magnitude to those observed using anticipatory timing actions (Leow et al., 2018; Marinovic et al., 2014). We predicted that both greater processing load and task experience would reduce the effect of the LAS on the timing of AT task responses. These predictions were partially confirmed. Figures 3a and 4b show that in the first block of trials, responses occurred earlier (on average) in the lower-load condition than in the higher-load condition, with the greatest difference at the -300 ms LAS delivery time point. This meant that high-load responses were slightly more temporally accurate (closer to the time of the last stimulus item) than low-load responses in both control and LAS trials. However, the effect was small and there was no statistically significant main effect of perceptual load. The significant interactions and Bayesian analysis (Figure 4b) showed statistical evidence for the high-load benefit at the -300 ms LAS delivery time, but not in control trials or at the other two LAS delivery times (Figure 4b). In addition, Figure 3a shows that, on average, the effect of

the LAS on response timing was greatest at the -200 ms time. Statistically, the effects relative to control trials were significant in the lower-load condition at both the -200 and -300 ms LAS delivery times, but only at the -200 ms delivery time for the higher-load condition (Figure 4a), indicating that the effect of the LAS was greatest at the -200 ms delivery time, which aligns with the timing of the previously observed transition from net inhibition to facilitation of the corticospinal system (Ibanez et al., 2020). Thus, the overall pattern in the average data was consistent both with previous research and the prediction of smaller effects of the LAS in the high-load condition, but the latter effect only reached the criterion for statistical significance at the -300 ms delivery time.

With experience, the pattern shifted in the direction expected, as revealed by the differences between responses in Blocks 1 and 2 (Figures 3a and 4b, left and right panels). In Block 2, response timing in the lower-load condition was (on average) slightly more accurate than in the higher-load condition in LAS trials, a reversal of the pattern in Block 1. However, there were no statistically significant differences between the lower- and higher-load conditions

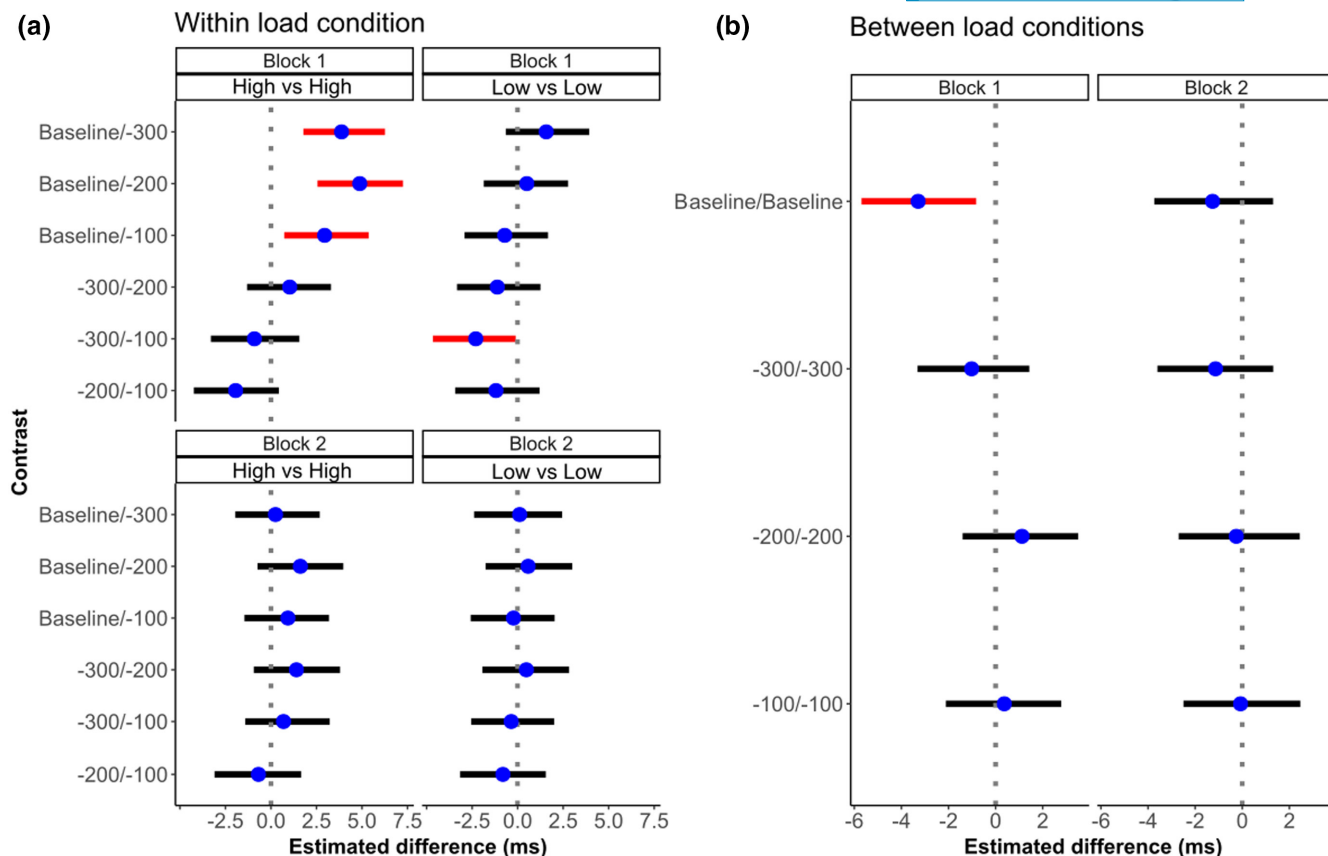


FIGURE 8 (a) Pairwise estimated differences in blink amplitude among time points in Blocks 1 and 2 for both high- and low-load conditions. (b) Pairwise estimated differences in blink amplitude between equivalent time points across load conditions. The circles represent the estimated mean difference between conditions. Bars represent the 95% HPDI of marginal mean differences estimated from the Bayesian model through the R package “emmeans.” Red bars indicate significant differences where the 95% HPDI did not include zero, and black bars represent non-significant differences where the 95% HPDI included zero.

(Figure 4b, right) and no significant differences between LAS timing conditions except in the high-load condition where the difference between control and LAS trials was still present at the -200 ms delivery time (Figure 4a, bottom). Once again, the overall pattern in the mean data was consistent with the prediction that differences in the effects of load condition should get smaller with experience and practice, and with the broader expectation that experience with the task would reduce the timing effect of the LAS regardless of perceptual processing load.

Response vigor (measured as rate of force development) showed a different pattern. Figure 3b shows that in LAS trials, responses were more vigorous than in control trials, consistent with previous work (Marinovic et al., 2013; McInnes et al., 2020; Tresilian & Plooy, 2006). In addition, the vigor was greater at shorter LAS delivery times in Block 1, as confirmed statistically (see Figure 5a, top). Specifically, a reliable linear trend in the rate of force development over time was observed (estimate = 13.81, SE = 3.24, $p < 0.001$, excluding control trials). This is predicted by our activation model (Figure 1) where response vigor is determined by the level of activation at the time

of response initiation and this activation increases as the time to expected movement onset gets shorter (Tresilian & Plooy, 2006). The pattern did not confirm our prediction concerning the difference between the higher- and lower-load conditions: the responses in Block 1 were (on average) slightly more vigorous in the high-load condition (which is the opposite of the prediction), although the effect was not significant. However, response vigor is not directly task related: the goal of the AT task is to achieve temporal coincidence of the response and the final stimulus item, which does not depend upon response vigor.

With experience (Block 2), responses in LAS trials were still more vigorous than in control trials. However, the trend for increasing vigor with later LAS delivery time was much reduced in Block 2 (Figure 3b). The linear trend in Block 2 (estimate = 7.46, SE = 2.13, $p < .001$) was approximately half the magnitude of that in Block 1. In the higher-load condition, the mean response times were almost exactly the same for all LAS delivery times and there were no significant differences (Figure 5a, bottom). In the lower-load condition, responses at -100 ms were still more vigorous than at the earlier delivery

times where the mean vigor was almost identical. These findings were broadly in line with the expectation that experience and practice would reduce the effects of the LAS on response parameters, although the effects were only observable at the earlier (-200 and -300 ms) delivery times. This pattern is consistent with the core concept of protective suppression proposed by McInnes et al. (2021), where practice enhances the ability to shield prepared actions from disruption. However, it is important to note that in McInnes et al. (2021) study, protection manifested as enhanced response vigor when a startling stimulus was presented during preparation, indicating an additive effect of the startling stimulus on the already prepared response (see also McInnes et al., 2020) as described in Figure 1 (see Introduction). The temporal difference between initiation and execution effects suggests partially independent underlying mechanisms, aligning with the conceptual model proposed by Haith et al. (2016), where *initiation* and *execution* processes can develop partially independently.

Danielson et al. (2024) recently provided evidence for subcortical involvement in force execution for finger muscles, showing that activity within the pontine reticular nucleus scales with handgrip force in humans. This finding, combined with our observation of a later peak in response vigor compared to movement initiation, suggests that the LAS might be acting on distinct cortical and subcortical pathways. More specifically, the LAS may facilitate action triggering cortically, leading to earlier movement onset, while simultaneously increasing force output via a subcortical pathway, potentially the reticulospinal tract. This observation is further supported by our finding that the vigor effect persisted even with practice, suggesting that the subcortical force-related pathway remains sensitive to the excitatory influence of the LAS even as the timing of initiation becomes more shielded from disruption. The -100 ms peak in vigor aligns well with the known time course of LAS effects on spinal excitability, which is maximal around 80 ms after LAS onset (Furubayashi et al., 2000). Note, however, that while this interpretation suggests a degree of independence between cortical and subcortical contributions to movement initiation and vigor, we must recognize that these systems interact dynamically to support goal-directed actions (Danielson et al., 2024; Nguyen et al., 2023).

4.2 | Involuntary responses: Time course and effect of visual processing load

In the absence of a specific hypothesis concerning the mechanism by which visual processing load influences sensory selectivity, we did not describe any predictions

concerning load conditions on eyeblink reflex responses to the LAS in the introduction. It might seem that if auditory excitability is lower in the higher-load condition, then eyeblink reflex responses to the LAS should be less pronounced (longer latencies and smaller amplitudes). However, the same result could occur due to blink suppression to avoid contrast sensitivity reductions led by eyelid blinks (Ridder III & Tomlinson, 1993) that could otherwise interfere with processing of the Gabor stimulus orientation, which is only task relevant in the higher-load condition. On this basis, it would be expected that blink suppression is greater in the higher visual load condition. Alternatively, suppression could occur because of an effect of the third Gabor flash suppressing reflexes upon presentation of the LAS (Lipp et al., 2001). In this case, suppression should be similar for both visual load conditions.

Figure 6a shows the average latency data. In Block 1, mean blink latencies were slightly greater in the higher-load condition than in the lower-load condition, both at baseline and in the interval prior to AT response production (Figure 7a, top left). This could either be due to reduced auditory excitability or to greater blink suppression in the higher-load condition as mentioned above. Either way, the effect did not meet the threshold for statistical significance. There was also no evidence for any differences in blink latency between times of LAS presentation in block 1.

In Block 2, the pattern shifted similarly to the shift observed in the timing of the voluntary response: the mean latency was greater in the lower-load condition in both baseline and later LAS delivery times (Figure 6a, top right), but the difference between conditions did not meet the threshold for statistical significance according to the frequentist approach. However, the Bayesian analysis (see Figure 7a, bottom) suggested that blink latency was slightly shortened for both processing load conditions relative to baseline levels. Specifically, for the baseline/ -100 , baseline/ -200 , and baseline/ -300 contrasts, the Bayesian analysis indicated that the lower-load condition had consistently shorter blink latencies compared to the high-load condition (Figure 7a, bottom), with credible intervals not overlapping zero, highlighting a meaningful difference between conditions. Specifically, in the high-load condition, significant differences with shorter latencies were observed for baseline/ -100 , baseline/ -200 , and baseline/ -300 contrasts, whereas in the low-load condition, significant differences were observed for baseline/ -200 and baseline/ -300 contrasts, as indicated by credible intervals not overlapping zero.

The effects on blink amplitude were more apparent than those on eyeblink latency, particularly showing the generic effect of habituation from Block 1 to Block 2 (Sanes & Ison, 1983). Figure 6b shows an overall suppression of

blink amplitude in comparison to baseline in Block 1, particularly for the high-load condition. As mentioned above, this could be related to either blink suppression to enhance stimulus visibility or to suppression of the task-irrelevant auditory channel. Although our frequentist analysis did not reveal a clear role for high processing load, our Bayesian analysis suggests a more nuanced picture, as shown in [Figure 8a](#). Specifically, the Bayesian analysis suggested visual processing load may interact with the time of LAS presentation in the modulation of blink amplitude, with greater suppression observed under high processing load. This result is inconsistent with a suppressive mechanism associated with the third Gabor flash (Lipp et al., 2001).

The findings described above are interesting when compared with the effects on voluntary responses. In Block 2, the effects of LAS on movement onset were smaller compared to Block 1, but effects on blink latency were larger. Specifically, our Bayesian analysis suggested that blink latency was shortened for both processing load conditions in relation to baseline levels, with this effect being more pronounced in Block 2 than in Block 1. It is tempting to suggest that practice serves to guarantee that planned responses are executed as intended and at the appropriate time. This likely involves a steeper release of preparatory suppression after practice, as observed using transcranial magnetic stimulation (Dupont-Hadwen et al., 2019). However, this likely strategic maintenance of the voluntary response does not extend or protect involuntary responses. This interpretation is consistent with recent results we obtained when correlating EEG and eyeblinks measures in the context of the StartReact effect (Nguyen et al., 2023).

5 | CONCLUSIONS AND BROADER IMPLICATIONS

The results show that visual processing load had an influence on the effects of a task-irrelevant LAS delivered shortly before the voluntary response in an AT task. There was a reduction in the effect of the LAS on AT response timing such that the timing error produced by the LAS was smaller in the higher-load condition. This can be interpreted as a consequence of a previously established effect of perceptual processing load: Greater processing load reduces the effects of task-irrelevant stimuli on task performance, implying increased perceptual selectivity (Lavie, 2005). This is usually framed in terms of attentional resources (Lavie, 2005; Lavie, 2010; Murphy et al., 2016): Attention is a limited resource that can be allocated to different sensory modalities and perceptual channels depending on the task requirements. If there is a higher visual processing load, more of the attentional resource must

be allocated to vision, leaving less left over for monitoring other sensory modalities, so attenuating the effects of non-visual, task-irrelevant stimuli. This lack of attention could manifest as simply less excitability in the task-irrelevant modality, which would predict that reflex responses to the LAS would be reduced in the higher-load condition. There was no evidence to support this prediction as any reduction in blink reflex excitability could be due to blink suppression.

It is relevant to place our findings within a broader theoretical framework that has implications for both understanding basic mechanisms of movement control and clinical applications. Research has shown that the prefrontal cortex (PFC) plays a crucial role in attentional control, directing the processing of sensory information based on goals and task demands (Corbetta & Shulman, 2002; Watanabe, 2021). Increases in perceptual load have also been associated with increased PFC activation (Agbangla et al., 2022). Given the role of PFC in attentional control, it is reasonable to assume that our task manipulation required changes in PFC function, suggesting a connection between PFC and “protective suppression.” Protective suppression describes a mechanism that enables prepared responses to be initiated and executed as planned even when external stimuli can disrupt them (McInnes et al., 2021). This suggestion is supported by our observation that processing load made voluntary responses more susceptible to the effects of the LAS during early practice, particularly with regard to their onset time. In contrast, although the linear increase in response vigor as the expected time of movement onset approached halved after practice and experience with the task, LAS was still effective in producing more forceful responses. This indicates the effects of LAS on response vigor may not be part of the StartReact effect, but rather a stimulus intensity effect (Cattell, 1886; Jaskowski et al., 1995; Jaskowski et al., 2007; Pieron, 1914) that is more difficult to filter out or extinguish.

If the onset and vigor of voluntary responses are affected by distinct mechanisms, one must consider whether it is necessary to always use a very loud auditory stimulus if the main goal of the research is to increase response vigor. The StartReact effect has been tested as a possible tool to assist with movement recovery in stroke survivors (Celinskis et al., 2018; Honeycutt et al., 2015; Rahimi & Honeycutt, 2020; Swann et al., 2022). However, loud sounds are aversive, and many participants may not tolerate them. Therefore, researchers must consider which mechanisms require enhancement: initiation or execution. Our results indicate these mechanisms may operate independently. Given that auditory stimulus intensity effects on force execution can be obtained with much lower intensities (<80 dBa) (Jaskowski et al., 1995), this aspect needs to be more thoroughly examined.

If the ability to protect responses from interference is strategic (McInnes et al., 2021) and limited by the availability of processing resources controlled by the PFC (Agbangla et al., 2022; Lavie, 2005; Lavie, 2010; Murphy et al., 2016), one would predict that any condition affecting PFC function would also affect protective suppression. This prediction has been confirmed by the results of Wilhelm et al. (2022) and Grandjean and Duque (2020), who both observed abnormal preparatory suppression in conditions known to affect PFC function: Parkinson's disease (Wilhelm et al., 2022) and binge drinking (Grandjean & Duque, 2020). These findings lend additional support for the role of the PFC in maintaining protective suppression and suggest that any disruption to PFC activity, whether through perceptual load and inexperience with a task (current study), neurodegenerative disease, or substance abuse can impair the ability to shield motor responses from interference.

AUTHOR CONTRIBUTIONS

Welber Marinovic: Conceptualization; data curation; formal analysis; funding acquisition; project administration; supervision; writing – original draft; writing – review and editing. **An T. Nguyen:** Conceptualization; data curation; formal analysis; methodology; writing – original draft. **Ann-Maree Vallence:** Conceptualization; writing – review and editing. **James R. Tresilian:** Conceptualization; writing – review and editing. **Ottmar V. Lipp:** Conceptualization; funding acquisition; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Welber Marinovic  <https://orcid.org/0000-0002-2472-7955>

An T. Nguyen  <https://orcid.org/0000-0001-5966-9903>

Ottmar V. Lipp  <https://orcid.org/0000-0001-6734-8608>

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