

Unexpected sounds induce a rapid inhibition of eye-movement responses

Martin R. Vasilev^{1*}

Zeynep G. Ozkan²

Julie A. Kirkby³

Antje Nuthmann⁴

Fabrice B. R. Parmentier^{5,6,7}

1. Department of Experimental Psychology, University College London, UK

2. Department of Methodology and ERI-Lectura, Universitat de València, Spain

3. Department of Psychology, Bournemouth University, UK

4. Department of Psychology, Kiel University, Germany

5. Department of Psychology and Research Institute for Health Sciences (iUNICS), University of the Balearic Islands, Palma, Spain

6. Balearic Islands Health Research Institute (IdISBa), Palma, Spain

7. School of Psychology, University of Western Australia, Perth, Western Australia, Australia

* corresponding author at m.vasilev@ucl.ac.uk

Co-authors' email: zeynep.ozkan@uv.es ; jkirkby@bournemouth.ac.uk ;

nuthmann@psychologie.uni-kiel.de ; fabrice.parmentier@uib.es

ORCID:

Martin R. Vasilev: 0000-0003-1944-8828

Zeynep G. Ozkan: 0000-0002-8684-5789

Julie A. Kirkby: 0000-0001-6502-0676

Antje Nuthmann: 0000-0003-3338-3434

Fabrice B. R. Parmentier: 0000-0001-7439-0097

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Abstract

Unexpected sounds have been shown to trigger a global and transient inhibition of motor responses. Recent evidence suggests that eye movements may also be inhibited in a similar way, but it is not clear how quickly unexpected sounds can affect eye-movement responses. Additionally, little is known about whether they affect only voluntary saccades or also reflexive saccades. In this study, participants performed a pro-saccade and an anti-saccade task while the timing of sounds relative to stimulus onset was manipulated. Pro-saccades are generally reflexive and stimulus-driven, whereas anti-saccades require the generation of a voluntary saccade in the opposite direction of a peripheral stimulus. Unexpected novel sounds inhibited the execution of both pro- and anti-saccades compared to standard sounds, but the inhibition was stronger for anti-saccades. Novel sounds affected response latencies as early as 150 ms before the peripheral cue to make a saccade, all the way to 25 ms after the cue to make a saccade. Interestingly, unexpected sounds also reduced anti-saccade task errors, indicating that they aided inhibitory control. Overall, these results suggest that unexpected sounds yield a global and rapid inhibition of eye-movement responses. This inhibition also helps suppress reflexive eye-movement responses in favour of more voluntarily-generated ones.

Keywords: saccades, inhibition, novelty distraction, pro-saccade, anti-saccade

Word count: 199 words

Novel or unexpected sounds that deviate from a repetitive sound sequence cause distraction in unrelated tasks (Berti, 2012; Dalton & Hughes, 2014; Escera et al., 1998; Horváth et al., 2008; Parmentier, 2014; Schröger, 1996; Schröger & Wolff, 1998). Novel sounds are distracting not due to their novelty *per se*, but because they violate predictions that another repeated sound will be presented (Parmentier et al., 2011). Specifically, the violation of expectations is thought to elicit an obligatory orientating response (Sokolov, 1963, 2001) towards the novel sound, which temporarily disengages attention from the task at hand and leads to distraction (Escera et al., 1998; Parmentier, 2014; Schröger, 1996; Schröger & Wolff, 1998).

Recent evidence has suggested that novel sounds also induce global inhibition of motor responses in addition to the attention orienting response (Wessel, 2017, 2018b, 2018a). For example, TMS stimulation of the cortical representation of task-irrelevant muscles has shown that novel sounds lead to a reduction in motor-evoked potentials (MEPs) some 150 ms after their presentation (Dutra et al., 2018; Iacullo et al., 2020; Wessel & Aron, 2013). Similar non-selective inhibition of MEPs has also been observed following the successful stopping of actions (Badry et al., 2009; Cai et al., 2012; Majid et al., 2012), indicating that novel sounds may activate the same neural networks involved in action stopping. This is thought to occur via a fronto-basal network that includes the right inferior frontal cortex (rIFC), the pre-supplementary motor area (pre-SMA), and the subthalamic nucleus (STN) (Wessel & Aron, 2013, 2017). This global inhibitory response may serve to stop ongoing actions in order to facilitate the attention orienting response and process the unexpected stimulus (Wessel, 2017, 2018a).

Interestingly, there is evidence that unexpected sounds may induce similar motor inhibition in eye-movement planning. It is well-established that remote visual distractors (Bompas & Sumner, 2009; Buonocore & McIntosh, 2012; Walker et al., 1997), as well as large

transient displacements of visual information (Reingold & Stampe, 2000, 2004), lead to saccadic inhibition¹, i.e. a decrease in the proportion of terminated fixations and, therefore, greater latency in making the next eye-movement (see Buonocore & Hafed, 2023 for an overview). However, sounds can also cause such inhibition. For example, microsaccades (miniature eye-movements occurring within a fixation) are inhibited by both a repeated standard sound (Rolfs et al., 2008) and pitch deviants (Kadosh & Bonneh, 2022b; Valsecchi & Turatto, 2009; Widmann et al., 2014). Additionally, the amount of inhibition is related to the perceived saliency of the unexpected sound. Environmental sounds with greater acoustical salience are associated with greater microsaccade inhibition (Zhao et al., 2019) and pitch deviants with larger acoustical deviation also show inhibition that is both larger in its magnitude and earlier in its onset (Kadosh & Bonneh, 2022b).

Evidence from active vision tasks also shows similar results. For example, the presentation of a single pitch deviant sound during a scene viewing task leads to saccadic inhibition some 90 to 150 ms after the sound onset (Graupner et al., 2007). Additionally, the presentation of a deviant or novel sound during sentence reading leads to an immediate increase in fixation durations (Rettie et al., 2024; Vasilev et al., 2019, 2021). This effect is largely constrained only to the fixation during which the sound is played and already disappears by the next fixation (though see Rettie et al., 2024). Furthermore, distraction does not appear to be related to the processing of text meaning, but occurs even when scanning meaningless letter strings (Vasilev et al., 2023).

¹ This effect has also been called “oculomotor freezing” (White & Rolfs, 2016) and “oculomotor inhibition” (Bonneh et al., 2016).

Overall, these findings suggest that unexpected sounds inhibit the planning stages of the next eye movement. This may occur either due to a brief pause in saccade programming or due to slower accumulation of the neural signals leading up to a saccade. Despite this, once the saccade is executed, there is no evidence of inhibition as key saccadic metrics such as amplitude, duration, and velocity are unaffected (Vasilev et al., 2021). Therefore, the available evidence suggests that only the planning but not the execution of saccades is inhibited. This may be because saccades are ballistic in nature and their velocity and duration are not under conscious control (Leigh & Zee, 1999).

The inhibition of saccade planning by unexpected sounds could be explained by Wessel and Aron's (2013, 2017) global motor inhibition account as the planning of motor actions may be briefly put on hold to allow for processing of the unexpected sound stimulus. Interestingly, data from MEPs indicate that inhibition is observed at 150 ms after the sound's onset, but no inhibition occurs in the 25ms window before or after that (Dutra et al., 2018; Iacullo et al., 2020; Wessel & Aron, 2013). This suggests that the inhibition is relatively transient, even if most studies have used a limited number of sound onsets. However, evidence from frontal beta-bursts (Tatz et al., 2023) and isometric force exertion (Novembre et al., 2018) suggests that inhibition may start as early as 100 ms after the sound onset. Additionally, the P3 response (typically starting around 200-250 ms; Wessel, 2018a) suggests that the effect may be observed even later in time. Therefore, while data from MEPs suggest transient inhibition, there is a relatively wide time window in which the effect could occur.

Evidence from eye-movements also suggests variable time onsets for inhibition: some studies place it as early as 60 ms after sound onset (Vasilev et al., 2021), others around 80-100 ms (Graupner et al., 2007; Widmann et al., 2014) or 100-200 ms (Kadosh & Bonneh, 2022b;

Valsecchi & Turatto, 2009), and yet others around 180 ms (Vasilev et al., 2019). The difference between sound onset and fixation onset appears to be a key variable in explaining its temporal dynamics (Vasilev et al., 2021). Therefore, there is a lot of uncertainty in how quickly novel sounds can affect eye-movements. In this study, our main goal was to examine the timeline of novelty distraction in a more controlled environment.

One limitation of previous studies is that they have either used central stimuli presented at fixation (e.g., Kadosh & Bonneh, 2022b; Valsecchi & Turatto, 2009) or active vision tasks (e.g., reading, scene viewing). In both cases, the experimenter has no control over when participants make their next saccade or microsaccade. Therefore, while some of these tasks have greater ecological validity, they make it harder to determine the exact temporal onset of the effect. For this reason, the present study used simple saccade tasks that allow for greater temporal control in order to understand the time course of inhibition by novel sounds.

A secondary goal of the study was to examine whether unexpected sounds affect both voluntarily-generated and more involuntarily-generated saccades. Many human actions, such as driving, waving, and writing, are considered voluntary behaviours that are under conscious control. Conversely, involuntary behaviours, such as blinking, can arise in response to environmental factors. The pro-/anti-saccade task (Hallett, 1978; Hallett & Adams, 1980; Munoz & Everling, 2004) is a highly-controlled experimental paradigm that offers a unique opportunity to study the dichotomy between these two types of behaviour in the context of eye movements, which represents one of the fastest motor responses in humans.

The pro-saccade task involves the generation of a reflexive (somewhat involuntary) saccade towards a peripheral target location, facilitated by the oculomotor system's dominant feature of prioritizing sudden onset stimuli (Pratt & Trottier, 2005). The anti-saccade task, on the

other hand, involves the execution of a voluntary saccade in the mirror-opposite direction of where the peripheral target appeared. Therefore, anti-saccades require two separate actions: 1) inhibition of the reflexive response (pro-saccade) to follow the peripheral stimulus; and 2) the translation of sensory-motor plans to execute a voluntary saccade in the opposite direction (Munoz & Everling, 2004). As such, the anti-saccade task is often considered as a measure of response inhibition that requires some amount of executive control. However, participants are not always successful in inhibiting the automatic response and make an error (i.e., execute a pro-saccade instead of the required anti-saccade) about 10-30% of the time (Ettinger et al., 2003; Koval et al., 2004; Pierce & McDowell, 2016).

Interestingly, there is an overlap in the neural circuits involved in saccadic control in the pro-/anti-saccade task and the purported fronto-basal action stopping network that is activated by unexpected events (Wessel, 2018a; Wessel & Aron, 2013). In particular, performance on the pro-/anti-saccade task also recruits frontal and parietal areas, as well as the basal ganglia (BG) (Coe & Munoz, 2017). This suggests that the activation of frontal areas and BG (particularly the STN) by unexpected sounds may lead to saccadic inhibition in these tasks due to them sharing common and interconnected brain networks.

Present Study

We asked participants to perform the pro-saccade and anti-saccade task while listening to expected and unexpected sounds. We were interested in whether saccadic inhibition by unexpected sounds differs when performing the more reflective pro-saccades versus the more voluntarily-generated anti-saccades. Critically, to test the time course of saccadic inhibition, we also manipulated the timing of the sound relative to the appearance of the saccade cue, starting from 150 ms before the cue to 25 ms after the cue.

Consistent with previous work (Graupner et al., 2007; Kadosh & Bonneh, 2022b; Valsecchi & Turatto, 2009; Vasilev et al., 2019, 2023; Widmann et al., 2014), we expected that novel sounds would lead to longer saccadic reaction times (SRTs) in both the pro-saccade and anti-saccade trials compared to standard sounds. Additionally, we expected that the inhibition would be transient and mostly occur when the sound is presented between 150 to 100 ms before the saccade cue. This is because the sound has been observed most commonly around that time in eye-movements (e.g., Graupner et al., 2007; Kadosh & Bonneh, 2022b; Widmann et al., 2014). Furthermore, data from MEPs too (Iacullo et al., 2020; Wessel & Aron, 2013) suggests a similar onset. Nevertheless, it is important to note that MEP studies have used different tasks and effector muscles, so the onset of inhibition in eye-movements may not be identical.

In terms of differences between pro-saccades and anti-saccades, we expected greater inhibition by unexpected sounds in the anti-saccade task because it involves greater recruitment of frontal areas compared to the pro-saccade task (DeSouza & Everling, 2002; Furlan et al., 2016). Finally, because correct anti-saccade performance requires inhibition of the reflexive pro-saccade response, unexpected sounds may *improve* anti-saccade accuracy if they are successful in inhibiting the oculomotor system. Therefore, novel sounds may lead to fewer anti-saccade errors compared to standard sounds in the same way that they help behavioural stopping in the Go/No-Go task (Wessel, 2017).

Method

The study had a 2 (*task*: pro-saccade, anti-saccade) \times 2 (*sound*: standard, novel) \times 8 (*sound onset*: -150, -125, -100, -75, -50, -25, 0, +25 ms relative to visual target onset) within-subject design.

Participants

Seventy-two members of the Bournemouth community (46 women)² took part in return for 3.5 course credits or a £35 Amazon voucher. Their average age was 27.1 years ($SD= 8.05$ years; range: 18- 49 years). Participants reported normal (or corrected-to-normal) vision, normal hearing, and no prior diagnosis of neurological disorders. All participants were naïve as to the purpose of the experiment and provided written informed consent. The study was approved by the Bournemouth University Research Ethics Committee (ID: 42319).

Sample size was determined *a priori* based on statistical simulations using the simR package (Green & Macleod, 2016) on previous data (Vasilev et al., 2021). With an α level of 0.05 and 30 novel sounds per condition per participant, the simulations suggested that about 50 participants were needed to achieve 95% power of detecting 75% of the expected effect size ($d \approx 0.15$). However, there is uncertainty in the true size of the novelty distraction effect (and its potential interactions) in new and previously untested tasks, as well as potential data loss (e.g., due to blinks). Therefore, we decided to be more conservative and set the sample size to 72 participants prior to data collection.

Apparatus

Participants' eye-movements were recorded with the Eyelink 1000 system (SR Research, Ontario, Canada), which is a video-based eye-tracker with a sampling frequency of 1000 Hz. The average horizontal accuracy of the system was 0.25 - 0.5°. While viewing was binocular, only the right eye was recorded³. Participants' heads were stabilised with a forehead-and-chinrest. Testing was done in a small room illuminated by an overhead LED lamp. The visual stimuli were presented on a 24.5" Alienware 25 LCD monitor (resolution: 1920 × 1080; refresh rate: 244 Hz).

² A further three participants dropped out after the first session and were replaced.

³ For 7 participants, the left eye was used instead due to tracking issues with glasses/ contact lenses.

The distance between the eye and the monitor was 62 cm. All sound stimuli were played on a Creative Sound Blaster Z soundcard (SB1500) at 65 ± 1.5 dB(A) through Bose QuietComfort 25 noise-cancelling headphones.

The experiment was programmed in Matlab 2021b (MathWorks, 2021) using the Psychophysics Toolbox v.3.15 (Brainard, 1997; Cornelissen et al., 2002; Pelli, 1997). The experiment was run on a Windows 10 PC (64 bit). The screen refresh latency was 8ms and the sound output latency was 28ms (measured with the Black Box ToolKit v2, Sheffield, UK). The software took these delays into account and ensured that the physical onset of the sound relative to the visual target onset corresponded exactly to the experimental sound onset condition (accuracy was measured to be within 1 ms, on average).

Stimuli

Sounds. In 83.3% of all trials, participants heard the same (expected) “standard” sound. This was a 400 Hz sine wave tone that was 150 ms long with 10 ms fade-in/ fade-out ramps. In the remaining 16.7% of trials, participants heard an unexpected “novel” sound. The novel sounds were also 150ms long and consisted of 240 unique environmental and nature sounds (e.g., a door closing, a bell, a siren, sea waves, city noises, as well as various animal sounds, such as a cat, dog, goat, birds, etc.). Ninety-eight sounds were taken from Andrés et al. (2006) (originally from Escera, Alho, Winkler, & Näätänen, 1998); the remaining were created for this study (see <https://osf.io/ph7te/>). The novel sounds were presented in random order for each participant (once per task). All sounds were sampled at 44.1 kHz (stereo, 16-bit).

Pro-saccade task. The two tasks, illustrated in Figure 1, followed Antoniades et al.'s (2013) standardised protocol. In the pro-saccade task, participants made horizontal saccades to targets of 10° eccentricity relative to the centre of the screen. An equal number of targets were

presented to the left and to the right. The target was a circle with a diameter of 0.5°, coloured dark red (RGB: 149, 0, 0) and presented against a white background. Trials started with a fixation dot (same as the target) at the centre of the screen. The fixation dot remained on the screen for 1000 - 2000 ms (randomly drawn from a uniform distribution), after which it disappeared, and the target was presented either to the left or to the right for 1000 ms. The sound was presented in steps of 25 ms, starting from -150 ms before the target to +25 ms after the target appearance.

Anti-saccade task. The anti-saccade task was identical to the pro-saccade one, except that participants were instructed to execute a saccade in the *opposite* direction of the target step. For example, if the dot moved to the left of the screen, they were required to move their eyes to the right of the screen (and vice versa). Feedback was provided during the practice period and whenever participants made four consecutive mistakes in a row in the experimental blocks, to remind them of the instruction (Antoniades et al., 2013).

Procedure

Participants were tested in two sessions on two separate days (the average time between sessions was 5.15 days; $SD= 7.08$ days; range: 1- 37 days). Each task was completed in a separate session block and their order was counter-balanced across participants. We preferred a blocked design because interweaved trial presentation can affect response accuracy and the difference in SRTs between anti-saccades and pro-saccades (Zeligman & Zivotofsky, 2017). As such, the blocked presentation allowed us to maximise the differences between the two tasks in order to test how they are affected by unexpected sounds.

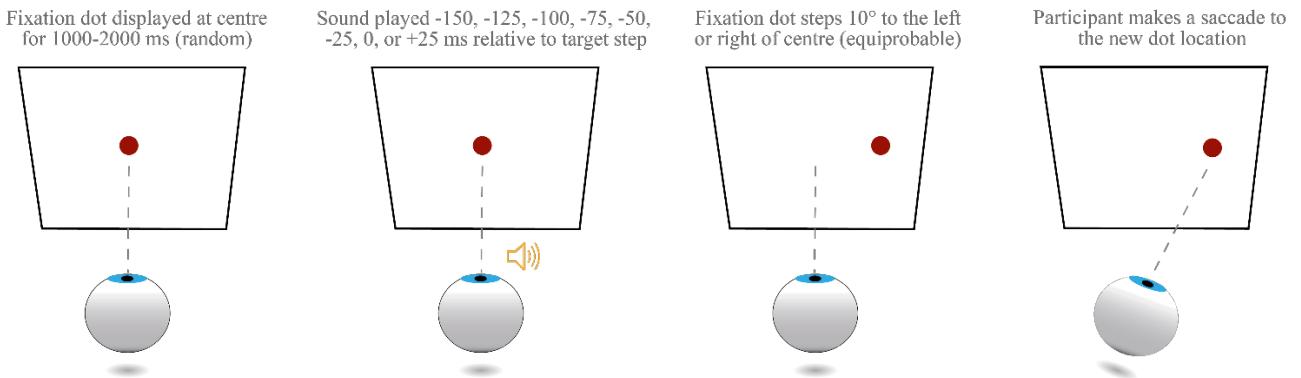
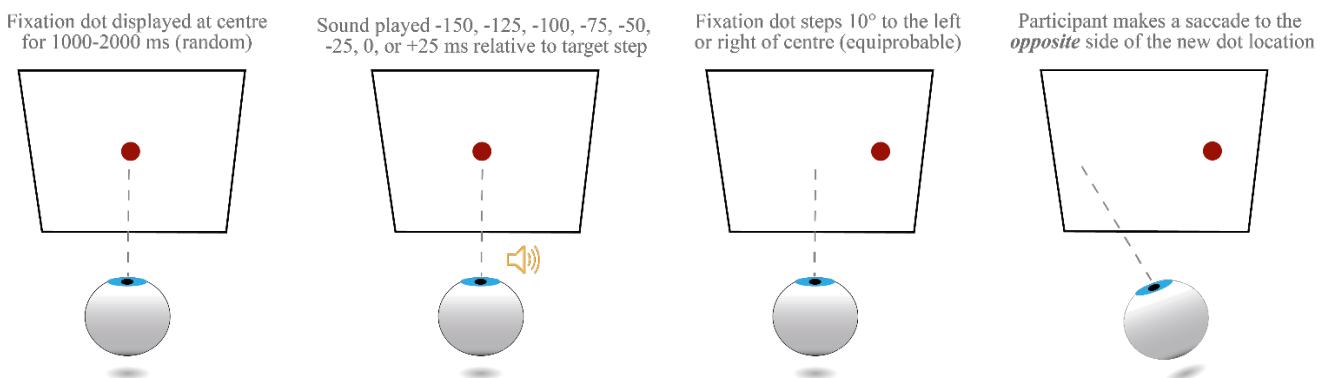
A) Pro-saccade trials**B) Anti-saccade trials**

Figure 1. An illustration of the pro-saccade (panel A) and anti-saccade (panel B) tasks used in the experiment.

Within each task block, the trials were randomised with the constraint that no two novel sounds were played one after another and that the first five sounds and the last sound in the block were always standard ones. The randomization was done by grouping trials into sets of 48 (8 novel and 40 standard ones, corresponding to a single run of all conditions within a task). Participants

completed 10 practice trials before the experimental ones. The experimental trials were then grouped into 10 smaller blocks of 144 trials each. Overall, in each experimental condition, participants completed 30 trials with a novel sound and 150 trials with a standard sound.

The task instructions were taken verbatim from Antoniades et al. (2013). In the pro-saccade task, participants were instructed to look at the peripheral target as quickly as possible. In the anti-saccade task, participants were instructed to look in the opposite direction of the target as quickly as possible. Note that the instructions did not emphasise making exact mirror saccades. Additionally, participants were told that they would hear different sounds but that they should try to ignore them and focus on the task.

Each testing session started with a 9-point calibration and validation grid. Calibration accuracy was then monitored with a drift check every 15 trials and participants were re-calibrated whenever necessary (but at least every 144 trials). Calibration accuracy of $< 0.5^\circ$ was maintained throughout the experiment. There was a short break between each block and a longer break halfway through the session. Each session lasted about 1.5 to 1.75 hours.

Data Analysis

Saccades were detected with the Eyelink software algorithm. Samples were detected as saccades when they exceeded a velocity threshold of $35^\circ/\text{s}$ and an acceleration threshold of $9500^\circ/\text{s}^2$. The dependent variables were: *saccadic reaction time* (the time difference between the onset of the peripheral target and the onset of the next saccade), *saccade amplitude* (the distance in visual angle that the eye travelled from the start of the saccade until the end of the saccade), and *anti-saccade error rate* (proportion of trials where an incorrect response was executed).

Statistical analysis was done on the raw (unaggregated) data with (Generalised) Linear Mixed Models ((G)LLMs) using the lme4 package v.1.1-34 (Bates et al., 2015) in the R software v. 4.31 (R Core Team, 2024). Fixed effects were Sound Onset (-150, -125, -100, -75, -50, -25, 0, 25 ms), coded using successive differences contrast coding, and Sound (novel: 1, standard: -1) and Task (anti saccade: 1, pro saccade: -1), both coded using sum contrast coding. To test for more fine-grained changes in the timeline of the effects, a post-hoc analysis was also conducted where Sound Onset was treated as a continuous variable (including both linear and quadratic terms). The full results from these models are reported in the Supplementary Materials and we only highlight notable differences from the main model in the text.

Participants were included as a random intercept in the models (Baayen et al., 2008). Additionally, random slopes for Task, Sound, and Sound Onset were included (Barr et al., 2013). If the model failed to converge, the slopes were removed one by one until convergence was achieved. The formulas for each model were:

- SRT: lmer(log(SRT) ~ sound*task*onset +(task|sub), data= dat)
- Saccade amplitude: lmer(sacc_ampl ~ sound*task*onset +(sound|sub), data= dat)
- Error rate: glmer(error_rate ~ sound*onset + (1|sub), data= subset(dat, task == "ANTISACC") , family = binomial(link = "logit")).

Saccadic reaction time was log-transformed to improve the distribution of residuals. A Bonferroni correction was applied due to the use of 3 dependent variables. The results were considered as statistically significant if the p -value was ≤ 0.016 ($0.05/3$). Significant interactions were followed up with Bonferroni-adjusted t-tests using the emmeans R package v.1.10.1 (Lenth, 2024). Empirical effect sizes are reported in Cohen's d (Cohen, 1988).

Results

During data pre-processing, trials with blinks were removed ($N = 8152$, 3.94%), as well as trials with saccade latencies smaller than 50 ms ($N = 4961$, 2.4%) or saccades with amplitude 2 SDs above/below the target eccentricity of 10° ($N = 13217$, 6.39%) (Wenban-Smith & Findlay, 1991). This left 87.4% of the data for analysis. Descriptive statistics are shown in Table 1 and the key results are visualized in Figures 2-3.

Table 1

Mean Saccadic Reaction Time, Saccade Amplitude, and Error Rate for each Sound, Onset, and Task Condition (SDs in parentheses)

Task	Sound	Sound onset	Saccadic reaction time (ms)	Saccade amplitude ($^\circ$)	Error rate (prop. incorrect)
Pro-saccade	Novel	-150 ms	140 (46)	9.98 (1.52)	0.01 (0.08)
Pro-saccade	Standard	-150 ms	132 (42)	9.93 (1.67)	0.01 (0.08)
Pro-saccade	Novel	-125 ms	144 (52)	10.10 (1.41)	<0.01 (0.03)
Pro-saccade	Standard	-125 ms	134 (42)	9.95 (1.64)	0.01 (0.08)
Pro-saccade	Novel	-100 ms	145 (43)	10.10 (1.40)	<0.01 (0.06)
Pro-saccade	Standard	-100 ms	134 (39)	9.97 (1.58)	0.01 (0.08)
Pro-saccade	Novel	-75 ms	150 (48)	10.20 (1.43)	<0.01 (0.04)
Pro-saccade	Standard	-75 ms	138 (45)	9.97 (1.64)	0.01 (0.07)
Pro-saccade	Novel	-50 ms	155 (54)	10.10 (1.44)	<0.01 (0.04)
Pro-saccade	Standard	-50 ms	140 (43)	9.96 (1.60)	<0.01 (0.07)
Pro-saccade	Novel	-25 ms	159 (51)	10.10 (1.58)	<0.01 (0.06)
Pro-saccade	Standard	-25 ms	143 (42)	9.92 (1.64)	0.01 (0.08)
Pro-saccade	Novel	0 ms	163 (51)	10.10 (1.37)	<0.01 (0.02)
Pro-saccade	Standard	0 ms	147 (43)	9.91 (1.63)	0.01 (0.07)
Pro-saccade	Novel	25 ms	165 (50)	10.10 (1.52)	<0.01 (0.06)
Pro-saccade	Standard	25 ms	151 (46)	9.85 (1.73)	0.01 (0.08)

Table 1 (continued)

Task	Sound	Sound onset	Saccadic reaction time (ms)	Saccade amplitude (°)	Error rate (prop. incorrect)
Anti-saccade	Novel	-150 ms	195 (75)	9.23 (4.14)	0.26 (0.44)
Anti-saccade	Standard	-150 ms	174 (65)	9.23 (4.15)	0.32 (0.47)
Anti-saccade	Novel	-125 ms	197 (66)	9.12 (4.17)	0.26 (0.44)
Anti-saccade	Standard	-125 ms	177 (64)	9.23 (4.15)	0.33 (0.47)
Anti-saccade	Novel	-100 ms	203 (71)	9.11 (4.24)	0.24 (0.43)
Anti-saccade	Standard	-100 ms	182 (65)	9.27 (4.18)	0.31 (0.46)
Anti-saccade	Novel	-75 ms	211 (71)	9.30 (4.27)	0.23 (0.42)
Anti-saccade	Standard	-75 ms	188 (65)	9.28 (4.19)	0.30 (0.46)
Anti-saccade	Novel	-50 ms	220 (68)	9.34 (4.27)	0.20 (0.40)
Anti-saccade	Standard	-50 ms	196 (65)	9.20 (4.20)	0.29 (0.45)
Anti-saccade	Novel	-25 ms	230 (78)	9.21 (4.28)	0.19 (0.39)
Anti-saccade	Standard	-25 ms	203 (67)	9.22 (4.21)	0.29 (0.45)
Anti-saccade	Novel	0 ms	234 (72)	9.21 (4.28)	0.18 (0.38)
Anti-saccade	Standard	0 ms	210 (69)	9.13 (4.20)	0.27 (0.45)
Anti-saccade	Novel	25 ms	242 (74)	9.14 (4.19)	0.18 (0.39)
Anti-saccade	Standard	25 ms	219 (70)	9.02 (4.26)	0.26 (0.44)

Saccadic Reaction Time (SRT). The statistical results are shown in Table 2. We found a significant main effect of Sound ($b= 0.048$, $SE= 0.003$, $t= 16.506$, $p < 0.001$), indicating that novel sounds ($M= 182$ ms; $SD= 70$ ms) led to longer SRTs compared to standard sounds ($M= 165$ ms; $SD= 62$ ms), $d= 0.25$. Additionally, the results showed a significant main effect of Task ($b= 0.152$, $SE= 0.008$, $t= 18.717$, $p < 0.001$), with the anti-saccade task ($M= 197$ ms; $SD= 69$ ms) leading to longer SRTs compared to the pro-saccade task ($M= 142$ ms; $SD= 45$ ms), $d= 0.90$. This is in line with previous research (Hallett, 1978). Furthermore, the difference of each sound onset level to the next one was significant (all p -values < 0.001 ; see Table 2 for the full results). As

Figure 2a shows, SRTs increased slightly, in a linear fashion, as the sound was played closer in time to the onset of the saccade target.

Crucially, we found a significant Sound by Task interaction ($b= 0.007$, $SE= 0.001$, $t= 9.214$, $p < 0.001$). As Figure 2c shows, novel sounds were more distracting in the anti-saccade task ($d= 0.31$) than in the pro-saccade task ($d= 0.26$), $b= 0.029$, $SE= 0.00315$, $z= 9.21$, $p < .001$. Finally, the results showed a significant Task by Sound Onset interaction in a few of the sound onset windows. Specifically, the difference in SRTs between the anti-saccade and pro-saccade task increased from -125 to -100 ms ($b= 0.009$, $SE= 0.003$, $t= 2.768$, $p= 0.006$), from -100 to -75 ($b= 0.008$, $SE= 0.003$, $t= 2.428$, $p= 0.015$), from -75 to -50 ($b= 0.009$, $SE= 0.003$, $t= 3.010$, $p= 0.003$), and from 0 to +25 ms ($b= 0.009$, $SE= 0.003$, $t= 2.744$, $p= 0.006$).

When Sound Onset was treated as a continuous predictor, it exhibited a significant interaction with Sound (linear term: $b= 0.969$, $SE= 0.343$, $t= 2.823$, $p= 0.005$; quadratic term: $b= -1.067$, $SE= 0.343$, $t= -3.108$, $p= 0.002$; see Supplementary Materials for full details). As Figure 2d shows, the difference between novel and standard sounds increased slightly as the sound was played closer in time to the target, before reaching a plateau around -50 ms. There was also a significant three-way interaction between Sound, Task, and Sound Onset in the linear ($b= -1.724$, $SE= 0.343$, $t= -5.023$, $p < 0.001$), but not the quadratic term ($b= 0.165$, $SE= 0.343$, $t= 0.480$, $p= 0.631$) for Sound Onset. As Figure 2d illustrates, there was a trend for the novelty distraction effect to be weaker in the pro-saccade task compared to the anti-saccade task and increase more strongly with Sound Onset.

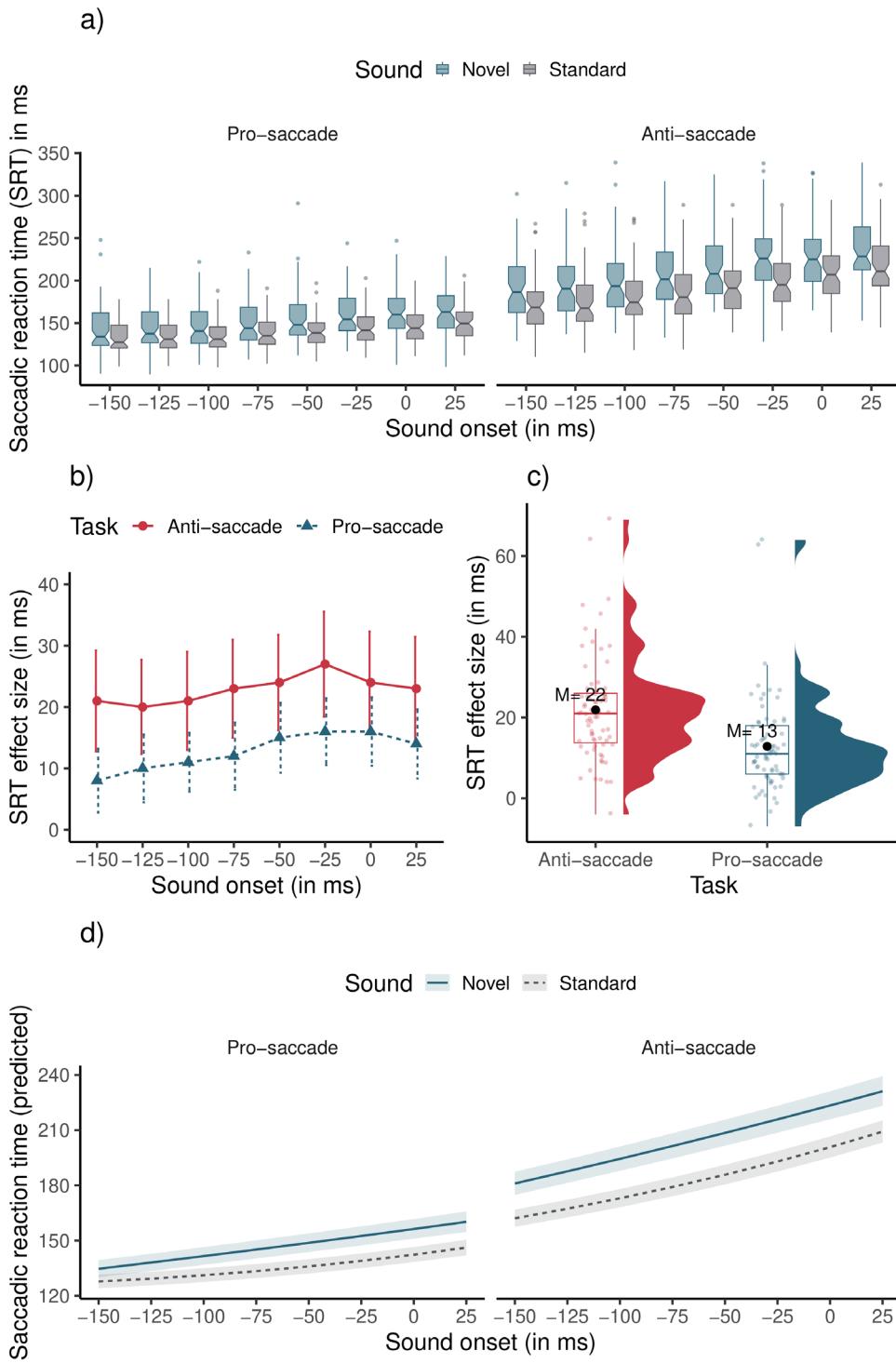


Figure 2. Saccadic reaction time data in the experiment. Panel a) boxplots show the data for each sound, onset condition, and task. Sound onsets are relative to the appearance of the target stimulus on the screen (at 0 ms). Panel b) shows the novelty distraction effect size (novel - standard) in saccadic reaction times for each sound onset condition. Error bars show ± 1 SE. Panel c) shows the novelty distraction effect size for each task, aggregated over the onset

conditions. Dots indicate the by-participant means. Panel d) shows the predicted saccadic reaction times from a LMM model that treats sound onset as a continuous variable and includes both linear and quadratic terms for it. Shading indicates 95% CIs.

To summarise, novel sounds led to longer SRTs compared to standard sounds and this effect was stronger in the anti-saccade task compared to the pro-saccade task. However, the novelty distraction effect was present across all sound onset delay conditions. It started off a little weaker with sound onsets between -150 ms to -100 ms and then increased until reaching a plateau around -50 ms- a trend that was more apparent in the pro-saccade task than the anti-saccade task (see Figure 2b). Therefore, novel sounds led to a general increase in SRTs across all time intervals and there was only a small gradual increase with greater sound onsets.

Furthermore, a post-hoc analysis (see Figure S1 in the Supplementary Materials) showed that the novelty distraction effect decreased, and then plateaued, as the experiment progressed, but generally remained significant by the end of the experiment. The only exception to this were the -150, -125, and -75 ms sound onset conditions in the pro-saccade task, where the effect of the novel sound was no longer significant towards the end of the experiment. This suggests that the inhibition in the first few time intervals (-150 to -75 ms) was smaller and/or wore off more quickly as participants habituated to the unexpected sounds.

Saccade amplitude. The statistical results are shown in Table 2. Saccade amplitudes, measured in degrees of visual angle, were significantly longer in the novel ($M= 9.66$; $SD= 3.05$) compared to the standard sound condition ($M= 9.58$; $SD= 3.06$), $b= 0.045$, $SE= 0.017$, $t= 2.688$, $p= 0.007$, though the effect size was marginal ($d= 0.03$). Additionally, saccade amplitudes were significantly longer in the pro-saccade ($M= 9.97$; $SD= 1.57$) compared to the anti-saccade task ($M= 9.17$; $SD= 4.10$), $b= -0.352$, $SE= 0.009$, $t= -39.09$, $p < 0.001$, $d= -0.25$. With the target

consistently occurring at a 10° eccentricity, the data suggest that while mean saccade accuracy was very high for pro-saccades (Nuthmann et al., 2016), it was considerably reduced for anti-saccades, in line with previous research (Krappmann, 1998).

The interaction between Sound and Task was also significant ($b = -0.034$, $SE = 0.009$, $t = -3.818$, $p < 0.001$): the sound effect was present in the pro-saccade task ($b = 0.158$, $SE = 0.037$, $t = 4.247$, $p < 0.001$, $d = 0.09$), but not in the anti-saccade task ($b = 0.021$, $SE = 0.038$, $t = 0.537$, $p = 1$, $d = 0$). One possible explanation for this finding is that the more frequent standard sounds may have induced adaptation or repetition enhancement with successive saccades (Kadosh & Bonneh, 2022a), leading to slightly shorter saccades compared to novel sounds. Finally, the Supplementary model treating Sound Onset as a continuous predictor showed that the difference between novel and standard sounds in saccade amplitudes increased with greater sounds onsets (see the Supplementary Materials for more details).

Anti-saccade error rate. The statistical results are shown in Table 3. We found a main effect of Sound. As Figures 3a and 3b show, novel sounds ($M = 0.22$; $SD = 0.41$) led to significantly lower proportion of errors in the anti-saccade task compared to the standard sound ($M = 0.30$; $SD = 0.46$), $b = -0.245$, $SE = 0.012$, $z = -19.998$, $p < 0.001$, $d = -0.16$. Additionally, error rate was significantly lower in the -50 ms ($M = 0.27$; $SD = 0.45$) compared to the -75 ms ($M = 0.29$; $SD = 0.45$) sound onset condition ($b = -0.133$, $SE = 0.049$, $z = -2.728$, $p = 0.006$), though the effect size was marginal ($d = -0.03$). There were no other significant differences.

In the Supplementary model treating Sound Onset as a continuous predictor, there was a significant interaction between Sound and Sound Onset in both the linear ($b = -10.754$, $SE = 0.890$, $z = -12.086$, $p < 0.001$) and quadratic terms ($b = 4.985$, $SE = 1.031$, $z = 4.835$, $p < 0.001$). As Figure 3c shows, the difference in error rates between novel and standard sounds increased with Sound

Onset, until reaching a plateau around -50 ms. This mirrors the pattern in SRTs and suggests that the inhibition of incorrect responses was smallest in the earlier Sound Onset conditions.

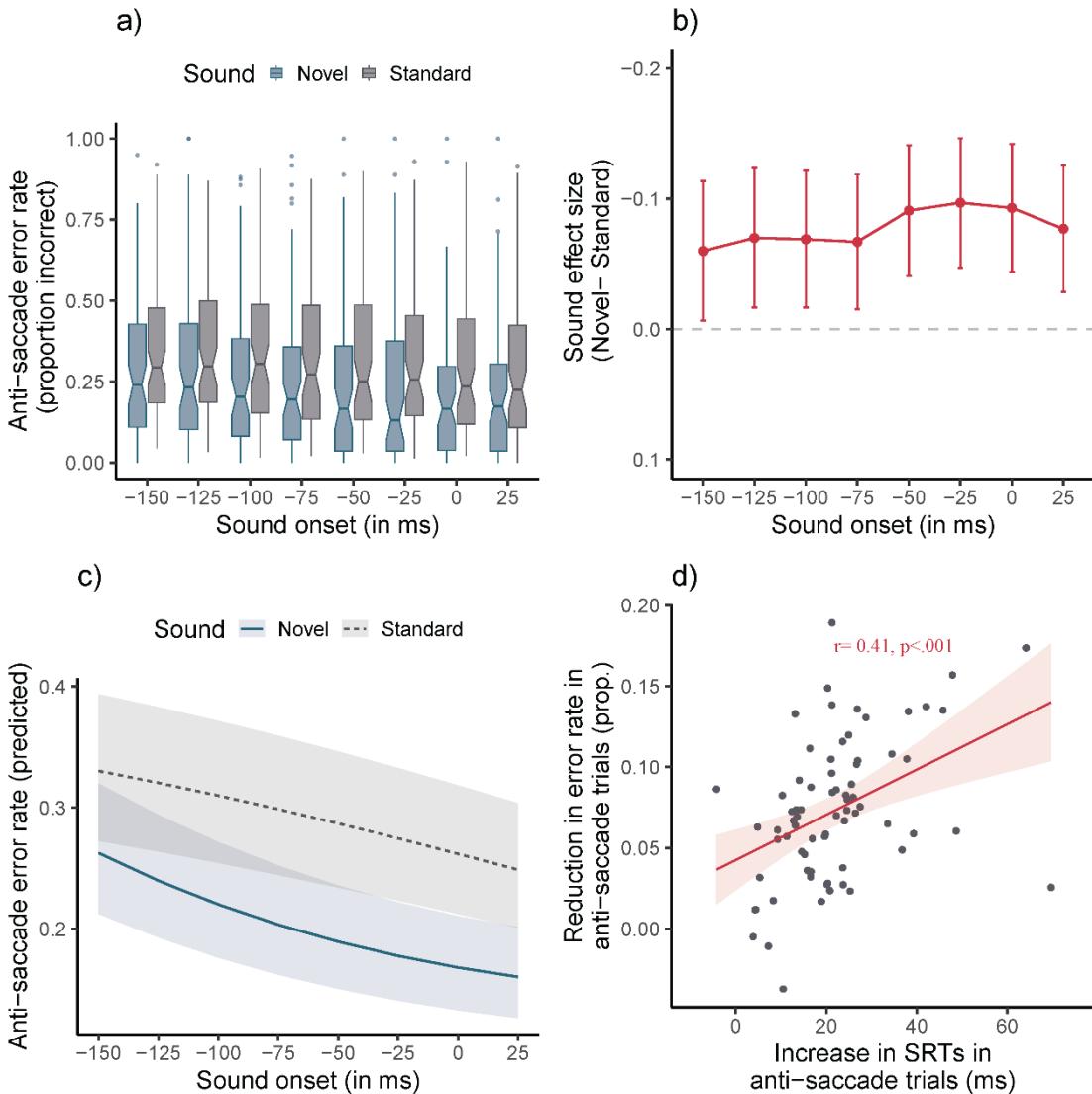


Figure 3. Anti-saccade errors in the experiment. Panel a) shows boxplots of the error rate for each sound and delay condition. Panel b) shows the sound effect size for anti-saccade error for each delay condition. Error bars show ± 1 SE. Panel c) shows the predicted anti-saccade error rate from a GLMM model that treats sound onset as a continuous variable and includes both linear and quadratic terms for it. Shading indicates 95% CIs. Panel d) shows a positive correlation between the reduction in error rate and the size of the novelty distraction effect in SRTs in the anti-saccade task. In other words, participants with greater saccadic inhibition in SRTs also show a greater reduction in anti-saccade errors. Dots show the individual effect size for each participant.

Table 2

Linear Mixed Effect Results for Saccadic Reaction Time and Saccade Amplitude

Predictors	log(Saccadic reaction time)				Saccade amplitude			
	Estimate	Std. Error	t statistic	p	Estimate	Std. Error	t statistic	p
(Intercept)	5.102	0.016	318.483	<0.001	9.650	0.156	62.023	<0.001
sound	0.048	0.003	16.506	<0.001	0.045	0.017	2.688	0.007
task	0.152	0.008	18.717	<0.001	-0.352	0.009	-39.09	<0.001
onset -150 vs -125	0.020	0.003	6.573	<0.001	-0.003	0.035	-0.072	0.943
onset -125 vs -100	0.021	0.003	6.758	<0.001	0.025	0.035	0.703	0.482
onset -100 vs -75	0.033	0.003	10.768	<0.001	0.048	0.035	1.357	0.175
onset -75 vs -50	0.035	0.003	11.218	<0.001	-0.027	0.036	-0.772	0.440
onset -50 vs -25	0.033	0.003	10.529	<0.001	-0.026	0.036	-0.715	0.475
onset -25 vs 0	0.022	0.003	7.151	<0.001	-0.033	0.036	-0.920	0.357
onset 0 vs 25	0.029	0.003	9.256	<0.001	-0.063	0.036	-1.759	0.079
sound × task	0.007	0.001	9.214	<0.001	-0.034	0.009	-3.818	<0.001
sound × onset -150 vs -125	0.002	0.003	0.588	0.557	-0.012	0.035	-0.334	0.739
sound × onset -125 vs -100	0.001	0.003	0.478	0.633	-0.000	0.035	-0.001	0.999
sound × onset -100 vs -75	0.003	0.003	0.918	0.358	0.045	0.035	1.272	0.203
sound × onset -75 vs -50	0.003	0.003	1.103	0.270	0.018	0.036	0.509	0.611
sound × onset -50 vs -25	0.002	0.003	0.729	0.466	-0.010	0.036	-0.286	0.775
sound × onset -25 vs 0	-0.005	0.003	-1.666	0.096	0.019	0.036	0.523	0.601
sound × onset 0 vs 25	-0.003	0.003	-1.050	0.294	0.017	0.036	0.466	0.641

Note: Statistically significant p-values are formatted in **bold**. A Bonferroni correction was applied and the significance threshold was $0.05/3= 0.016$.

Table 2 (continued)

<i>Predictors</i>	log(Saccadic reaction time)				Saccade amplitude			
	<i>Estimate</i>	<i>Std. Error</i>	<i>t statistic</i>	<i>p</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>t statistic</i>	<i>p</i>
task × onset -150 vs -125	0.004	0.003	1.199	0.231	-0.063	0.035	-1.791	0.073
task × onset -125 vs -100	0.009	0.003	2.768	0.006	-0.011	0.035	-0.320	0.749
task × onset -100 vs -75	0.008	0.003	2.428	0.015	0.040	0.035	1.135	0.256
task × onset -75 vs -50	0.009	0.003	3.010	0.003	0.016	0.036	0.438	0.661
task × onset -50 vs -25	0.006	0.003	2.057	0.040	-0.030	0.036	-0.852	0.394
task × onset -25 vs 0	0.002	0.003	0.502	0.615	-0.014	0.036	-0.394	0.693
task × onset 0 vs 25	0.009	0.003	2.744	0.006	-0.035	0.036	-0.963	0.335
sound × task × onset -150 vs -125	-0.004	0.003	-1.257	0.209	-0.039	0.035	-1.103	0.270
sound × task × onset -125 vs -100	-0.005	0.003	-1.461	0.144	-0.021	0.035	-0.584	0.559
sound × task × onset -100 vs -75	0.002	0.003	0.557	0.578	0.033	0.035	0.933	0.351
sound × task × onset -75 vs -50	-0.003	0.003	-0.864	0.388	0.048	0.036	1.346	0.178
sound × task × onset -50 vs -25	0.000	0.003	0.088	0.930	-0.055	0.036	-1.538	0.124
sound × task × onset -25 vs 0	-0.004	0.003	-1.427	0.154	0.027	0.036	0.750	0.453
sound × task × onset 0 vs 25	-0.001	0.003	-0.374	0.708	-0.009	0.036	-0.257	0.797
Random Effects								
σ^2	0.061				7.987			
τ_{00}	0.018	sub			1.737	sub		
τ_{11}	0.001	sub.sound			0.014	sub.sound		
	0.005	sub.task						
ρ_{01}	0.450				0.039	sub		
	0.253							
ICC	0.260				0.179			
N	72	sub			72	sub		
Observations	180818				180818			
Marginal R ² / Conditional R ²	0.247 / 0.443				0.012 / 0.189			

Note: Statistically significant p-values are formatted in **bold**. A Bonferroni correction was applied and the significance threshold was $0.05/3= 0.016$.

Table 3

Generalised Linear Mixed Effect Results for Anti-saccade Error Rate

Predictors	Anti-saccade error rate			
	Estimate	std. Error	z statistic	p
(Intercept)	-1.137	0.139	-8.159	<0.001
sound	-0.245	0.012	-19.998	<0.001
onset -150 vs -125	0.014	0.046	0.306	0.759
onset -125 vs -100	-0.107	0.046	-2.310	0.021
onset -100 vs -75	-0.095	0.047	-2.009	0.045
onset -75 vs -50	-0.133	0.049	-2.728	0.006
onset -50 vs -25	-0.030	0.050	-0.606	0.544
onset -25 vs 0	-0.057	0.051	-1.121	0.262
onset 0 vs 25	-0.035	0.052	-0.671	0.502
sound × onset -150 vs -125	-0.028	0.046	-0.612	0.541
sound × onset -125 vs -100	0.014	0.046	0.295	0.768
sound × onset -100 vs -75	-0.021	0.047	-0.456	0.649
sound × onset -75 vs -50	-0.090	0.049	-1.856	0.063
sound × onset -50 vs -25	-0.015	0.050	-0.290	0.772
sound × onset -25 vs 0	0.018	0.051	0.356	0.722
sound × onset 0 vs 25	0.065	0.052	1.240	0.215

Random Effects

σ^2	3.290
$\tau_{00 \text{ sub}}$	1.444
ICC	0.305
N _{sub}	72

Observations	85699
Marginal R ² / Conditional R ²	0.012 / 0.313

Note: Statistically significant p-values are formatted in **bold**. A Bonferroni correction was applied and the significance threshold was 0.05/3= 0.016.

Therefore, the unexpected novel sounds generally aided response inhibition in the anti-saccade task – they helped subjects suppress the execution of erroneous pro-saccades, thereby increasing the number of correct responses. Additionally, as Figure 3d shows, the reduction in error rate in the anti-saccade task was moderately correlated with the increase in SRTs by novel sounds. In other words, participants who showed greater oculomotor inhibition in SRTs in the anti-saccade task were also more likely to have a lower error rate.

To test for more subtle evidence of inhibition in anti-saccades, we performed a post-hoc analysis of the eye velocity for trials that contained an error and trials that did not contain an error. The velocities averaged across trials and subjects (see Figure 4a) showed the typical acceleration/deacceleration curve around 150-350 ms for correct anti-saccade trials. Incorrect trials showed an average velocity curve that occurred earlier (75-250 ms), replicating the typical finding that errors are executed faster than correct responses (Coe & Munoz, 2017). There were also bimodal/trimodal velocity peaks afterwards, due to participants performing a corrective saccade to the correct area of the screen on some trials (~ 14% of the time). Of interest, the difference between standard sounds (dashed line) and novel sounds (solid line) showed that eye velocity was generally lower following novel sounds, particularly during the start of the saccade.

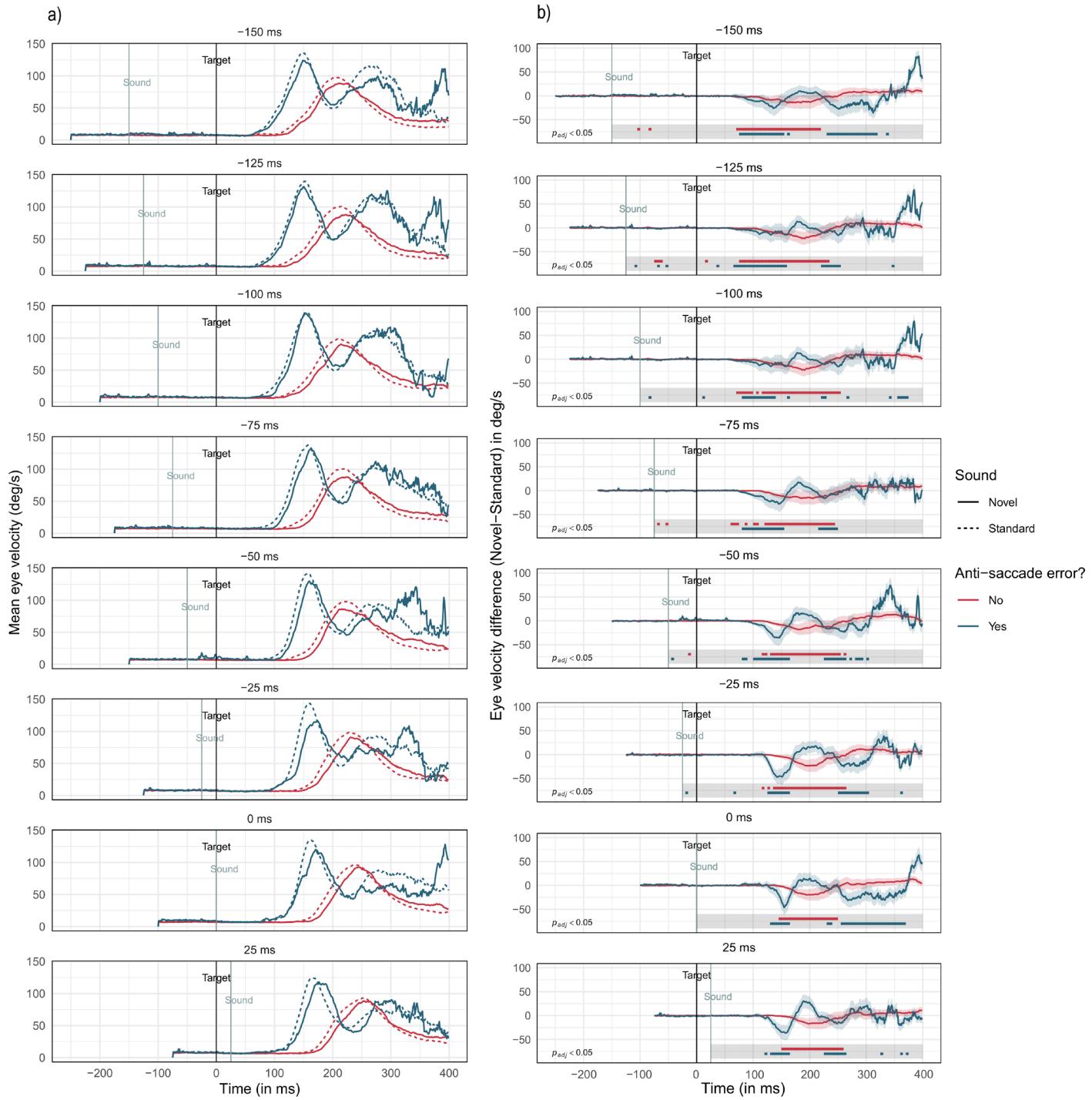


Figure 4. Mean eye velocity in the anti-saccade task between novel and standard sounds across all sound onset conditions. Separate lines are plotted for trials on which participants made an anti-saccade error (i.e., executed a pro-saccade) and trials on which they made the correct response. Panel a) shows the velocity profiles for standard sounds (dashed lines) and novel sounds (solid lines) on correct/ incorrect trials (see the main text for more information). Panel b) shows the difference between the standard and novel curves from panel a). Negative differences indicate

slower eye-velocity following novel sounds. Eye-velocities were extracted from 100 ms before the sound onset to 400 ms following the visual target onset (velocities after 400ms are not included as there were too few samples for reliable estimation across the different cells). The bottom of each plot shows the time intervals (solid horizontal lines) during which the decrease in velocity was statistically significant. This was estimated using 5ms bins and applying a Bonferroni correction to all p values.

A closer examination of the difference between the two velocity curves (see Figure 4b) suggested that novel sounds led to a more sustained reduction in eye velocity on correct trials compared to incorrect trials. This was especially the case in the critical time window of about 100-250 ms when most anti-saccades would have been executed. Therefore, while these results need to be interpreted with caution, they suggest that, on correct trials, novel sounds were more successful at inhibiting eye velocities. Whether this is related to the improvement in anti-saccade performance remains to be tested.

Discussion

The present study tested how quickly novel sounds begin to affect eye-movement responses and whether this differs between voluntary anti-saccades and reflexive pro-saccades. For both types of saccades, novel sounds led to significantly longer SRTs compared to standard sounds. This finding is consistent with previous work using reading and scene viewing as well as fixation tasks (Graupner et al., 2007; Kadosh & Bonneh, 2022b; Valsecchi & Turatto, 2009; Vasilev et al., 2019, 2021, 2023; Widmann et al., 2014). Thus, unexpected sounds appear to have a general inhibitory effect on eye-movement responses, supporting the notion that unexpected events cause global inhibition of motor actions (Wessel & Aron, 2013, 2017).

The present study builds upon previous work on microsaccades (Kadosh & Bonneh, 2022b; Valsecchi & Turatto, 2009; Widmann et al., 2014) by showing that oculomotor inhibition also extends to larger saccadic eye-movements, such as pro-saccades and anti-saccades. Interestingly, the inhibition effect of novel sounds was stronger (albeit also more variable) in anti-saccades compared to pro-saccades, suggesting that voluntarily generated saccades are inhibited to a greater extent. Despite the increase in SRTs, novel sounds had limited effect on saccade amplitudes, confirming previous reports that they don't inhibit saccade execution (Vasilev et al., 2021). This result was further confirmed by analysing saccade velocities as a function of the time between playing the sound and the saccade onset (see the Supplementary Materials for more information).

The key manipulation of sound onset timing revealed an interesting, if surprising, pattern of results. The novelty distraction effect was present in all time intervals. The effect was weaker in the earlier sound onset conditions (between -150 to -100 ms), particularly in the pro-saccade task, and gradually increased until reaching a plateau around -50 ms before the saccade target. Therefore, contrary to expectations, the effect was not transient for the time intervals that were tested. Rather, novel sounds led to a general inhibition of eye-movement responses across all intervals. Even so, there was some evidence that the effect in the pro-saccade task was weaker and started to disappear towards the end of the experiment when the sound was presented from 150 to 75 ms before the saccade target (see the Supplemental Materials). This further suggests that some of the earlier onset conditions led to weaker inhibition in the pro-saccade task. Because we did not include sound onsets before -150 ms or after 25 ms, we cannot clearly state when the inhibition starts or stops. However, our data shows that the oculomotor system is inhibited during a window of 175ms that was identified as most plausible based on previous evidence.

These results may appear to contradict to data from MEPs, which suggests that global motor inhibition occurs at 150 ms following the sound onset but already disappears 25 ms later (Iacullo et al., 2020; Wessel & Aron, 2013). However, the present study only measured motor output latency in task-relevant muscles (controlling the eye), whereas previous studies have mostly examined excitability in task-irrelevant muscles. MEPs are thought to measure cortico-spinal tract excitability following TMS stimulation (Duque et al., 2017) and usually occur within 10-50 ms of the TMS pulse (Rossini et al., 2015; Wilson et al., 2021). Therefore, they only give a small window of information about excitability of the nervous system. SRTs, on the other hand, typically have a latency of 100-250 ms (Edelman et al., 2006; Fischer & Weber, 1992) and reflect the more variable nature of eye-movement programming. Therefore, both methods provide different information about motor inhibition and their timelines may not match up precisely. Additionally, the time course for global motor inhibition may be more flexible, with some studies suggesting it can start as early as 100 ms after sound onset (Novembre et al., 2018; Tatz et al., 2023). In this sense, the present data only suggests that the planning of task-relevant eye movements is disrupted within the 175 ms window that we tested. However, it does not tell us how task-irrelevant muscle activity may be affected.

This pattern of results may not be surprising given that previous eye movement studies have found the effect at different times, approximately along the time window that we tested (Graupner et al., 2007; Kadosh & Bonneh, 2022b; Vasilev et al., 2019, 2021; Widmann et al., 2014). However, it is worth noting that saccadic inhibition by visual distractors typically requires a close temporal overlap between the processing of the distractor and saccade programming (e.g., Bompas & Sumner, 2009; Reingold & Stampe, 2004). This suggests that unexpected sounds may have a broader inhibitory effect by influencing a sufficient proportion of SRTs at each time window. It is also interesting that the inhibition was slightly stronger than previous studies

utilising more “natural” tasks such as reading (Vasilev et al., 2019, 2021, 2023). We speculate that this may be because the sounds overlap more strongly with the saccadic programming stages, which is harder to achieve in active vision tasks where the decision of when to make an eye movement is also affected by other cognitive and perceptual processes. Additionally, it is possible that the use of novel sounds (as compared to pitch deviants) creates greater acoustical deviance, which further increases oculomotor inhibition (Kadosh & Bonneh, 2022a).

Interestingly, novel sounds also *reduced* errors in the anti-saccade task across all sound onset intervals, suggesting that they aided inhibitory control. This provides further evidence that the effect of novel sounds is truly inhibitory in nature. While this result may appear counter-intuitive at first, it’s important to keep in mind that correct performance in the anti-saccade task requires two separate processes: 1) suppressing the execution of the reflexive response (pro-saccade) and 2) voluntary programming of a saccade in the opposite direction (anti-saccade). It is only the first process that is captured by the antisaccade error rate.

Indeed, the present data indicates that novel sounds helped suppress this reflexive, stimulus-driven behaviour when it is not required by the task, in favour of more voluntary-driven behaviour. Suppression of pro-saccades in the anti-saccade task depends on top-down inhibition of neurons in areas such as the frontal eye fields and the intermediate layer of the superior colliculus (Everling et al., 1998; Everling & Munoz, 2000; Munoz & Everling, 2004). We speculate that the activation of the fronto-basal action stopping network (Diesburg & Wessel, 2021; Wessel & Aron, 2013) by unexpected sounds may facilitate this inhibition, both through activation of frontal areas and the STN.

The STN is thought to play a key role in mediating the global motor inhibition response and receives direct cortical projections via the hyperdirect pathway (Diesburg & Wessel, 2021;

Wessel & Aron, 2013). The STN also receives similar projections from key areas involved in saccadic control (such as the frontal eye fields; Nambu, Tokuno, & Takada, 2002) and can enhance the inhibition of superior colliculus neurons, thus suppressing the generation of saccades (Bakhtiari et al., 2020; Hikosaka et al., 2000; Watanabe & Munoz, 2011). Such inhibition may be stronger in the anti-saccade task as it involves greater frontal/parietal activation than the pro-saccade task (DeSouza & Everling, 2002; Furlan et al., 2016). Additionally, patients with frontal/BG disorders show a distinct reduction in anti-saccade accuracy (e.g., Amador, Hood, Schiess, Izor, & Sereno, 2006; Goto et al., 2010; Guitton, Buchtel, & Douglas, 1985; Ouerfelli-Ethier et al., 2018), thus underscoring their importance for task performance.

Not many factors are known to reduce anti-saccade errors, especially in healthy adults. Some studies suggest that practice on the task (Dyckman & McDowell, 2005; Montenegro & Edelman, 2019), as well as certain chemicals such as nicotine (Larrison et al., 2004; Petrovsky et al., 2013) and antipsychotic drugs (Burke & Reveley, 2002), which potentially affect pre-frontal cortex neurons, lead to reduced errors. However, some attentional influences have been noted as well. For example, the presentation of an auditory or visual cue at the target location (Karatekin, 2006) and dual-task paradigms where participants also have to judge luminance changes (Evens & Ludwig, 2010; but cf. Kristjánsson, Chen, & Nakayama, 2001) both lead to a reduction in anti-saccade errors. These latter results suggest that increased task demands, and the cuing of attention may modulate successful anti-saccade performance. In fact, novel sounds may have a similar effect by briefly diverting attention away from the target, which could potentially make the execution of the erroneous pro-saccade less likely in the first place. This would be consistent with Wessel's (2018a) proposal that the motor inhibition and attention orienting responses are part of the same cascade and may be inseparable from each other.

In the Pause-then-Cancel model (Diesburg & Wessel, 2021), a Pause process is generated every time an unexpected event occurs, resulting in global motor inhibition and the orientation of attention. A Cancel process is then also programmed in parallel, which aims to readjust (or completely cancel) motor programmes via activation of the pre-SMA (Diesburg & Wessel, 2021). While we cannot distinguish between these two processes, it is possible that both may be at play here. The Pause process may be responsible for the general inhibition of oculomotor plans, which manifests itself as slower SRTs. On the other hand, the Cancel process could also affect saccadic programming, for example, by reinstating the oculomotor plans that were put on hold or by cancelling those that are task-inappropriate (such as executing a pro-saccade instead of the required anti-saccade). Future neuroimaging work could potentially shed light on this, for example by looking for pre-SMA activation as evidence for the Cancel process.

It may be surprising that unexpected sounds affected *both* error rates and SRTs in the anti-saccade task. However, the two effects are complementary with each other, as they both indicate that the oculomotor system was inhibited. In fact, as Figure 3d shows, the two effects are moderately correlated and share some variance. Further research is needed to understand if they are both caused by similar processes. However, it is worth noting that Dutra et al. (2018) also observed a similar correlation between inhibition of MEPs and successful stopping in the Go/No-Go task- suggesting that the degree of inhibition is related to actual behavioural stopping. While in the present task the inhibition in SRTs is, to some extent, confounded with the behavioural outcome, future studies could try to disentangle these.

Conclusion

Previous research has established that unexpected sounds yield inhibition of microsaccades (Kadosh & Bonneh, 2022b; Valsecchi & Turatto, 2009; Widmann et al., 2014)

and saccadic eye-movements during reading and scene viewing (Graupner et al., 2007; Rettie et al., 2024; Vasilev et al., 2019, 2021, 2023). The present study showed that unexpected sounds have a general inhibitory effect on reflexive pro-saccade responses and the more voluntary anti-saccade responses. This inhibition was found to emerge quickly and to be relatively constant for sounds presented between 150 ms before the target to 25 ms after the target. However, the effect was weaker for sounds presented between 150 ms to 100 ms before the target, particularly for pro-saccades. Additionally, unexpected sounds reduced error rates on the anti-saccade task, suggesting that they aided inhibitory control and helped participants reduce their reliance on reflexive, stimulus-driven behaviour. These results raise the possibility that unexpected events may exert a global suppressive effect on the oculomotor system.

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Credit Contribution**Vasilev, Martin R.**

Conceptualization
Data curation
Formal analysis
Funding acquisition
Investigation
Methodology
Project administration
Resources
Software
Supervision
Validation
Visualization
Writing - original draft
Writing - review & editing

Visualization

Writing - original draft

Kirkby, Julie A.

Conceptualization
Writing - original draft
Writing - review & editing

Nuthmann, Antje

Conceptualization
Visualization
Writing - original draft
Writing - review & editing

Parmentier, Fabrice

Conceptualization
Funding acquisition
Methodology
Resources
Writing - original draft
Writing - review & editing

Ozkan, Zeynep G.

Data curation
Formal analysis
Investigation
Software

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Supplemental Materials

Modulation of Novelty Distraction by Trial Order

There is some evidence suggesting that distraction by unexpected sounds decreases throughout the experiment (e.g., Parmentier, 2008; Wessel & Aron, 2013; Wetzel et al., 2021), presumably as the acoustic novelty of sounds wears off and participants gradually learn to expect novel sounds with a certain probability. To find out if this was the case in the present study, we conducted a post-hoc analysis, testing if the novelty distraction effect changed throughout the experiment. The trials for each task were grouped into small “blocks” of 30, which were used for the purpose of sound randomisation in the study. Each block consisted of 48 trials (8 novel and 40 standard- corresponding to one full run of all the conditions within a task) and the order of blocks corresponded to the order in which they appeared in the study.

The statistical analysis was done with Generalised Additive Mixed Models (GAMMs) using the “mgcv” R package v.1.9-1 (Wood, 2011, 2017). GAMMs are especially useful for modelling temporally correlated data (such as groups of trials that occur one after another), especially if the data exhibits potentially non-linear patterns. In GAMMs, some of the predictors are specified as “smooths”, which represent the weighted sum of cubic spline functions (Baayen et al., 2017; Sóskuthy, 2017). In this analysis, smooths were included for the random intercept of subjects, the random slope of sound for subjects, the effect of block order, the interactions between subject and block order, and the interaction between sound and block order. The remaining fixed effects were the same as LMM model in the main text (Table 2). The results from the analysis are visualised in Figure S1.

There was a significant interaction between block order and novel sounds ($edf= 3.94$, $F(4.85)= 32.896$, $p < 0.001$). As Figure S1 shows, SRTs in the novel sound condition generally tended to decrease as the experiment progressed, before reaching a plateau towards the end of the experiment. Standard sounds did not exhibit an interaction with block order ($edf= 0.0009$, $F(0.001)= 0.026$, $p= 0.99$), suggesting that they remained relatively constant during the experiment. In the anti-saccade task, the regression line for standard sounds was mostly flat; in the pro-saccade task, there was a small trend for SRTs to *increase* towards the end of the experiment. However, overall, the interaction between standard sounds and block order was not significant.

Looking at the difference between Novel and Standard sounds (see the right-hand plots in Figure S1), the novelty distraction effect size decreased throughout the experiment. However, the effect generally remained significant until the end of the study. A few small exceptions to this were the -150ms, -125ms, and -75 ms sound onset conditions in the pro-saccade task, where the effect was no longer significant in the last several blocks. Therefore, the present data generally supports previous studies (e.g., Parmentier, 2008; Wetzel et al., 2021) and suggests that novelty distraction tends to decrease and plateau towards the end of the experiment. Interestingly, the effect was no longer significant in some of the earliest delay conditions in the pro-saccade task towards the end of the study. This suggests that the inhibition there was weaker and/or wore off more quickly. Of course, the present study presented only a limited number of novel sounds per task (240 in total). Therefore, it is possible that the effect may also wear off in some of the remaining conditions if more testing had been done.

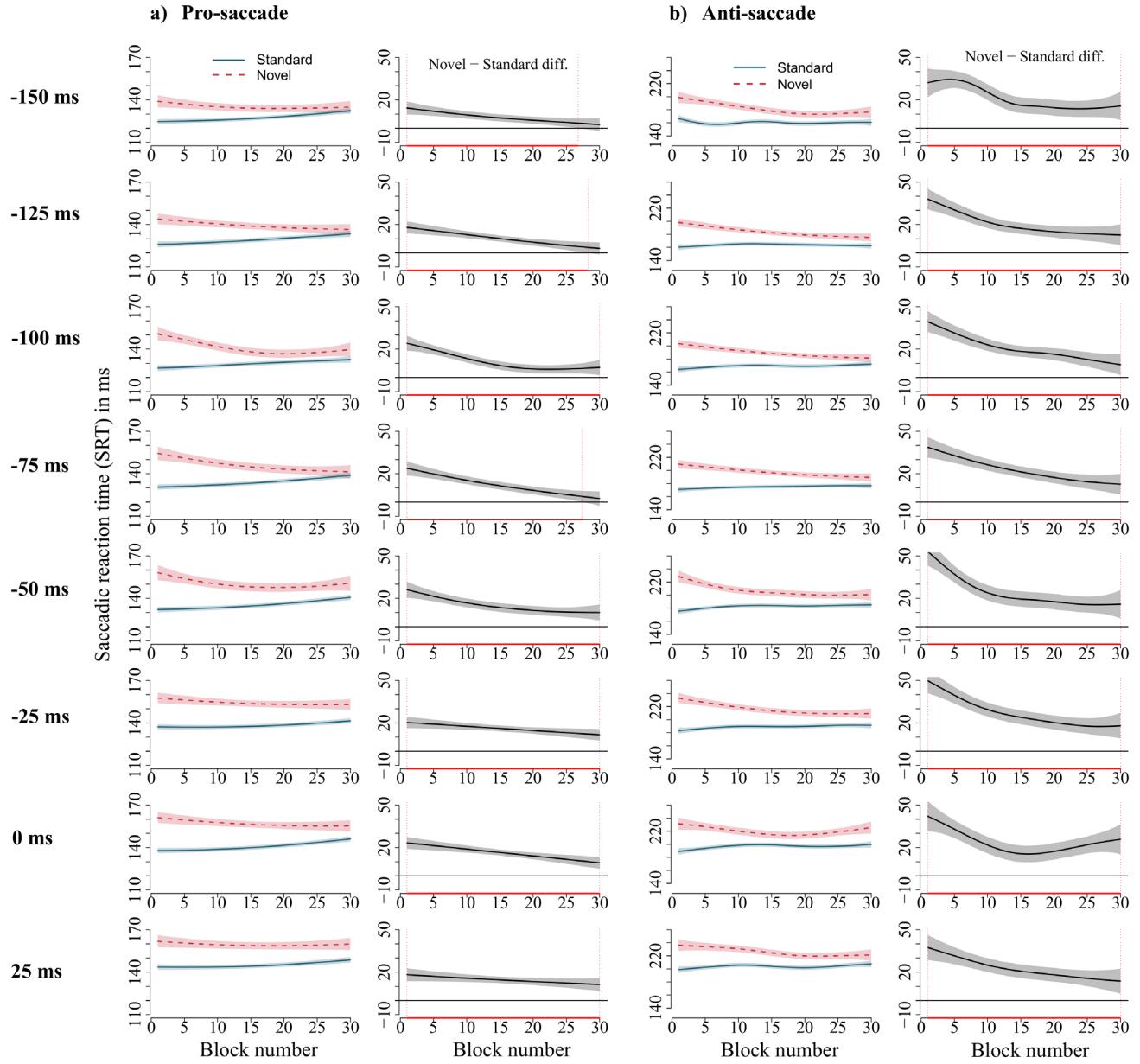


Figure S1. Modulation of the novelty distraction effect in the pro-saccade (panel **a**) and the anti-saccade (panel **b**) task. In each panel, the plots on the left show the saccadic reaction times (SRTs) for each sound type as a function of block number. The plots on the right in each panel show the novelty distraction effect size in SRTs (Novel- Standard difference) as a function of block number. Shading indicates 95% CIs. Note that the effect is significant if the regression line CI limits are above 0. For convenience, red colour on the x-axis indicates the block numbers during which the novelty distraction effect was significant.

Analysis of the data with Linear and Quadratic Terms for Sound Onset

The analyses in the main paper treated Sound Onset as a discrete predictor and compared each time interval to the next. The results indicated that the magnitude of the novelty distraction effect did not change with Sound Onset, as there were no significant two-way or three-way interactions. However, there could still be small changes that occur between the different levels that are not detected by this analysis. For this reason, we conducted post-hoc supplementary analyses where Sound Onset was treated as a continuous variable. We included both linear and quadratic terms for Sound Onset. Adding the quadratic term significantly improved the model fit for SRTs ($\chi^2(4)= 52.60$, $p < .001$) and saccade amplitude ($\chi^2(4)= 38210$, $p < .001$). For anti-saccade error rate, the model failed to converge with just a linear term for Sound Onset. Therefore, for this measure, we also report the model with both linear and quadratic terms (which did converge). The results are presented in Tables S1 and S2.

Saccadic reaction times. The results were generally consistent with the model reported in the main paper (see Table 2). For SRTs, novel sounds were more distracting than standard sounds ($b= 0.048$, $SE= 0.003$, $t= 16.439$, $p < 0.001$), and the significant Sound by Task interaction ($b= 0.008$, $SE= 0.001$, $t= 9.464$, $p < 0.001$) shows that this effect was stronger in the anti-saccade task than the pro-saccade task. Sound Onset had a significant positive effect in both the linear ($b= 28.039$, $SE= 0.343$, $t= 81.676$, $p < 0.001$) and quadratic terms ($b= 0.895$, $SE= 0.343$, $t= 2.610$, $p= 0.009$), with SRTs increasing as the sound was played closer in time to the target. This is again consistent with the main model in the paper. However, there was a significant Sound by Sound Onset interaction in both linear ($b= 0.969$, $SE= 0.343$, $t= 2.823$, $p= 0.005$) and quadratic terms ($b= -1.067$, $SE= 0.343$, $t= -3.108$, $p= 0.002$). As Figure S2 shows, the difference between novel and standard sounds increased slightly as the sound was played closer in time to the target, before

reaching a plateau around -50 ms. The three-way interaction between Sound, Task and Sound Onset was significant in the linear ($b = -1.724$, $SE = 0.343$, $t = -5.023$, $p < 0.001$), but not the quadratic term ($b = 0.165$, $SE = 0.343$, $t = 0.480$, $p = 0.631$). As Figure S2 shows, there was a trend for the difference between novel and standard sounds to increase more strongly with sound onset in the pro-saccade compared to the anti-saccade task. In summary, the results confirm the main model in the paper, but also suggest that inhibition of SRTs by novel sounds was slightly weaker in the first few onset conditions. This trend was more pronounced in the pro-saccade task.

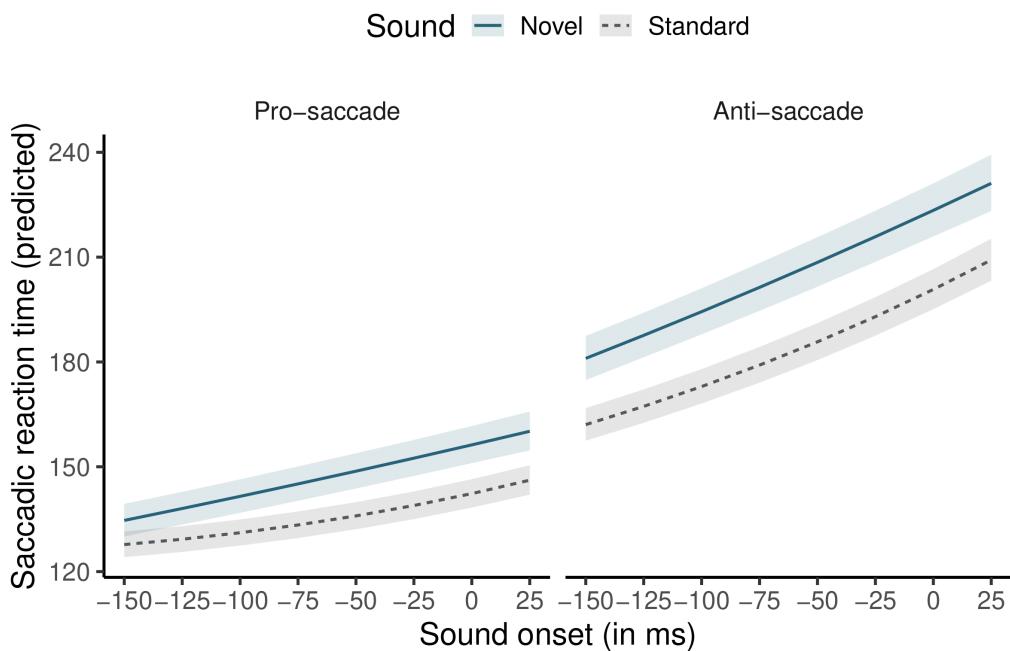


Figure S2. Predicted saccadic reaction times from an LMM model that treats sound onset as a continuous variable and includes both linear and quadratic terms for it. Shading indicates 95% CIs.

Table S1

Linear Mixed Effect Results for Saccadic Reaction Time and Saccade Amplitude, Treating Sound Onset as a Continuous Variable (using Linear and Quadratic Terms)

Predictors	log(Saccadic reaction time)				Saccade amplitude			
	Estimate	std. Error	Statistic	p	Estimate	std. Error	Statistic	p
(Intercept)	5.107	0.016	327.772	<0.001	9.722	0.164	59.324	<0.001
Sound	0.048	0.003	16.439	<0.001	0.045	0.008	5.651	<0.001
Task	0.158	0.001	194.209	<0.001	-0.271	0.148	-1.836	0.066
Onset [Linear]	28.039	0.343	81.676	<0.001	-8.502	3.410	-2.494	0.013
Onset [Quadratic]	0.895	0.343	2.610	0.009	-13.335	3.408	-3.912	<0.001
Sound × Task	0.008	0.001	9.464	<0.001	-0.031	0.008	-3.813	<0.001
Sound × Onset [Linear]	0.969	0.343	2.823	0.005	12.577	3.410	3.689	<0.001
Sound × Onset [Quadratic]	-1.067	0.343	-3.108	0.002	1.138	3.408	0.334	0.738
Task × Onset [Linear]	6.642	0.343	19.350	<0.001	-7.502	3.410	-2.200	0.028
Task × Onset [Quadratic]	-0.271	0.343	-0.791	0.429	-1.547	3.408	-0.454	0.650
Sound × Task × Onset [Linear]	-1.724	0.343	-5.023	<0.001	2.705	3.410	0.793	0.428
Sound × Task × Onset [Quadratic]	0.165	0.343	0.480	0.631	1.759	3.408	0.516	0.606
Random Effects								
σ^2	0.065				6.457			
τ_{00}	0.017	sub			1.929	sub		
τ_{11}	0.001	sub.sound			1.568	sub.task		
ρ_{01}	0.454	sub			0.906	sub		
ICC	0.197				0.340			
N	72	sub			72	sub		
Observations	180818				180818			
Marginal R ² / Conditional R ²	0.262 / 0.408				0.007 / 0.345			

Note: Statistically significant p-values are formatted in **bold**. A Bonferroni correction was applied and the significance threshold was $0.05/3= 0.016$.

Saccade amplitude. Similar to the main model in the paper, novel sounds led to significantly longer saccades compared to standard sounds ($b= 0.045$, $SE= 0.008$, $t= 5.651$, $p <0.001$). Additionally, the effect of Sound Onset was significant in both the linear ($b= -8.502$, $SE= 3.410$, $t= -2.494$, $p= 0.013$) and quadratic ($b= -13.335$, $SE= 3.408$, $t= -3.912$, $p <0.001$) terms. As Figure S3 shows, there was a small decrease in saccade amplitudes in the last few sound onset conditions. The interaction between Sound and Task was also significant ($b= -0.031$, $SE= 0.008$, $t= -3.813$ $p <0.001$). This was again due to the difference between novel and standard sounds being significant in the pro-saccade, but not in the anti-saccade task. Finally, the interaction between Sound and Sound Onset was significant for the linear ($b= 12.577$, $SE= 3.410$, $t= 3.689$, $p <0.001$), but not for the quadratic term ($b= 1.138$, $SE= 3.408$, $t= 0.334$, $p= 0.738$). There was a trend for the difference between standard and novel sounds to increase in size in the pro-saccade, but not in the anti-saccade task. Therefore, the results were consistent with the model reported in the main paper, but further suggest that the difference in saccade length between the sounds in the pro-saccade task increased with sound onset.

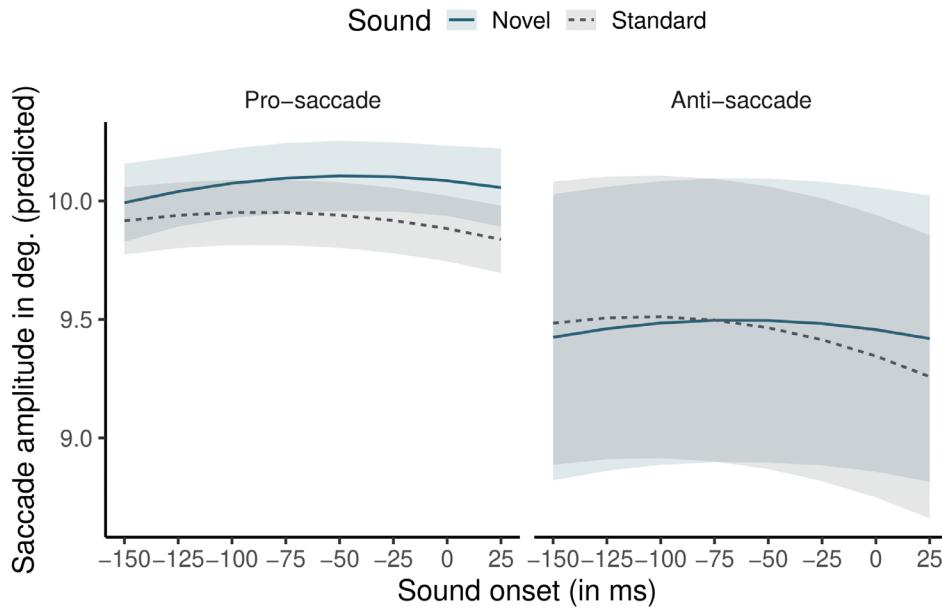


Figure S3. Predicted saccade amplitudes from an LMM model that treats sound onset as a continuous variable and includes both linear and quadratic terms for it. Shading indicates 95% CIs.

Anti-saccade error rate. The GLMM results are shown in Table S2. Consistent with the main model in the paper, novel sounds led to significantly lower error rates in the anti-saccade task compared to standard sounds ($b = -0.245$, $SE = 0.012$, $z = -20.086$, $p < 0.001$). Sound Onset also had a significant effect on error rates in both the linear ($b = -48.776$, $SE = 0.904$, $z = -53.943$, $p < 0.001$) and quadratic terms ($b = 2.288$, $SE = 0.836$, $z = 2.736$, $p = 0.006$). As Figure S4 shows, error rates decreased as the sound was played closer to the target. Therefore, while some of the successive Sound Onset differences were not significant in the main model in the paper, this analysis shows that there was an overall trend for error rates to decrease with Sound Onset. Finally, the interaction between Sound and Sound Onset was also significant in both the linear ($b = -10.754$, $SE = 0.890$, $z = -12.086$, $p < 0.001$) and quadratic terms ($b = 4.985$, $SE = 1.031$, $z = 4.835$, $p < 0.001$). As Figure 4 shows, this was due the difference between novel and standard sounds increasing with Sound Onset, until reaching a plateau around -50 ms. In summary, the results confirm the main paper model, but also suggest that the decrease in error rates by novel

sounds was smallest in the first few onset conditions and generally increased when the sound was played closer to the target. Interestingly, this trend closely resembles the pattern observed in the SRT data.

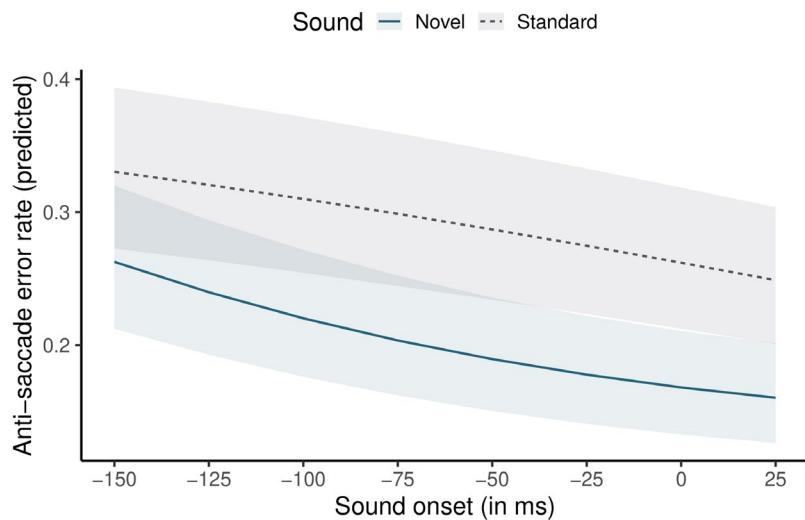


Figure S4. Predicted anti-saccade error rates from a GLMM model that treats sound onset as a continuous variable and includes both linear and quadratic terms for it. Shading indicates 95% CIs.

Table S2

Linear Mixed Effect Results for Anti-saccade Error Rate, Treating Sound Onset as a Continuous Variable (using Linear and Quadratic Terms)

<i>Predictors</i>	Anti-saccade error rate			
	<i>Estimate</i>	<i>std. Error</i>	<i>z statistic</i>	<i>p</i>
(Intercept)	-1.136	0.140	-8.090	<0.001
Sound	-0.245	0.012	-20.086	<0.001
Onset [Linear]	-48.776	0.904	-53.943	<0.001
Onset [Quadratic]	2.288	0.836	2.736	0.006
Sound × Onset [Linear]	-10.754	0.890	-12.086	<0.001
Sound × Onset [Quadratic]	4.985	1.031	4.835	<0.001
Random Effects				
σ^2	3.290			
$\tau_{00\ sub}$	1.444			
ICC	0.305			
N _{sub}	72			
Observations	85699			
Marginal R ² / Conditional R ²	0.011 / 0.313			

Note: Statistically significant p-values are formatted in **bold**. A Bonferroni correction was applied and the significance threshold was 0.05/3= 0.016.

Effect of Sound on Eye Velocity in Subsequent Saccade

The analysis of saccade amplitudes in the main paper suggested that novel sounds have a limited effect on saccade execution. To further explore this, we analysed average saccade

velocity as a function of the time between playing the sound and the onset of the next saccade (rather than the onset of the visual target). This may give more sensitive information about the timeline of potential effects compared to the experimental sound onset condition. The results are visualised in Figure S5 and the LMM results are presented in Table S3.

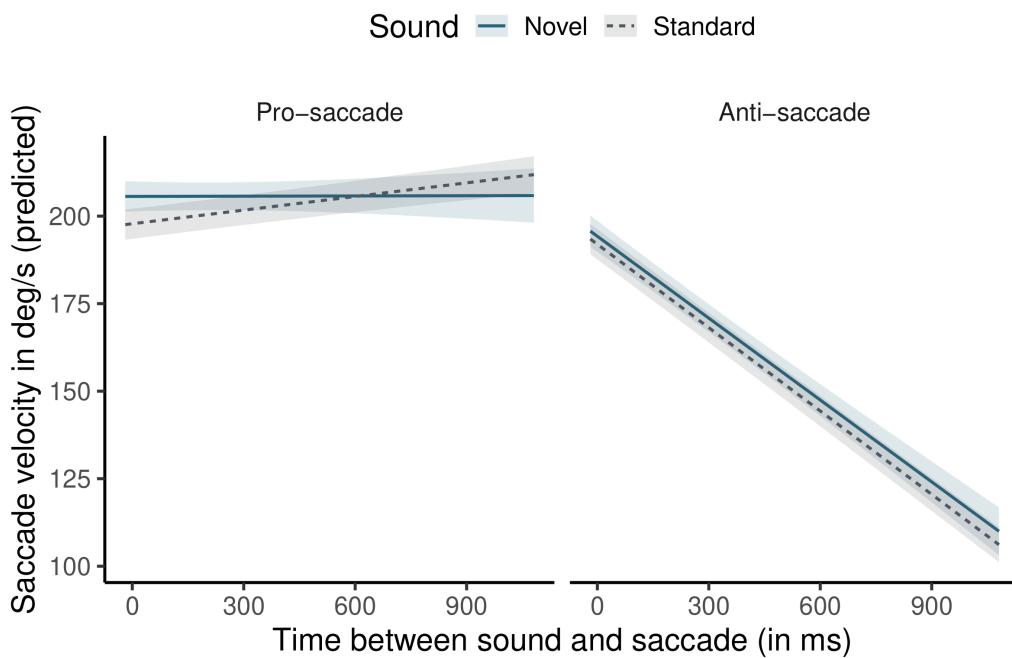


Figure S5. Average saccade velocity in the two tasks and sound conditions as a function of the time duration between playing the sound and the onset of the saccade. Estimates are derived from the LMM model predictions. Note that the duration was centred at 0 in the analysis and back-transformed here for visualisation purposes. Shading indicates 95% CIs.

The results followed the saccade amplitude data closely. Novel sounds led to significantly higher average velocity compared to standard sounds ($b = 1.868$, $SE = 0.327$, $t = 5.715$, $p < 0.001$). Additionally, the pro-saccade task led to higher velocities compared to the anti-saccade task ($b = -14.163$, $SE = 0.117$, $t = -120.745$, $p < 0.001$). There was also a significant interaction between Sound and Task ($b = -0.561$, $SE = 0.117$, $t = -4.790$, $p < 0.001$). Similar to the saccade amplitude data, this was again due to a bigger Sound effect in the pro-saccade task compared to the anti-

saccade task. Therefore, these results indicate a close correspondence between saccade amplitudes and saccade velocity. This is not surprising as the two measures are highly correlated with each other (Bahill et al., 1975).

Furthermore, longer durations between sound onset and saccade onset were associated with lower saccade velocities. However, there was a significant Time to saccade by Task interaction ($b = -0.043$, $SE = 0.001$, $t = -29.851$, $p < 0.001$). As Figure S5 shows, velocities decreased more strongly with greater Time to saccade in the anti-saccade task compared to the pro-saccade task. Finally, the three-way interaction between Sound, Task, and Time to saccade was also significant ($b = 0.004$, $SE = 0.001$, $t = 2.484$, $p = 0.013$). This is again illustrated in Figure S5, as velocities following standard sounds tended to increase in the pro-saccade task while velocities following novel sounds remained constant. This was in contrast to the anti-saccade task, where no such modulation was evident. Therefore, these results confirm the main analysis with saccade amplitudes. They also illustrate that the modulation of saccade execution in the pro-saccade task is mostly driven by changes following the standard sound. In summary, these results confirm previous reports that unexpected sounds have no notable effect on saccade execution (Vasilev et al., 2021).

Table S3

LMM Results for Average Saccade Velocity, as Predicted by Sound, Task, and Time from Sound Onset until Saccade Onset

<i>Predictors</i>	Average saccade velocity			
	<i>Estimate</i>	<i>std. Error</i>	<i>Statistic</i>	<i>p</i>
(Intercept)	189.083	2.060	91.780	<0.001
Sound	1.868	0.327	5.715	<0.001
Task	-14.163	0.117	-120.745	<0.001
Time to saccade	-0.036	0.001	-24.037	<0.001
Sound × Task	-0.561	0.117	-4.790	<0.001
Sound × Time to saccade	-0.003	0.001	-1.895	0.058
Task × Time to saccade	-0.043	0.001	-29.851	<0.001
Sound × Task × Time to saccade	0.004	0.001	2.484	0.013
Random Effects				
σ^2	1120.283			
τ_{00} sub	304.613			
τ_{11} sub.sound	6.711			
ρ_{01} sub	-0.262			
ICC	0.226			
N sub	72			
Observations	180813			
Marginal R ² / Conditional R ²	0.142 / 0.336			

Note

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