# ORIGINAL ARTICLE



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# Unexpected sounds induce a rapid inhibition of eye-movement responses

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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 favor of more voluntarily generated ones.

#### **KEYWORDS**

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

# 1 | INTRODUCTION

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

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of expectations is thought to elicit an obligatory orientating response (Sokolov, 1963, 2001) toward 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, 2018a, 2018b). 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 actionstopping. This is thought to occur via a fronto-basal network that includes the right inferior frontal cortex (rIFC), the presupplementary 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 inhibition, that is, 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 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-pitched deviant sound during a scene-viewing task leads to saccadic inhibition some from 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).

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 a 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 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 25 ms 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

<sup>&</sup>lt;sup>1</sup>This effect has also been called "oculomotor freezing" (White & Rolfs, 2016) and "oculomotor inhibition" (Bonneh et al., 2016).

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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 behaviors that are under conscious control. Conversely, involuntary behaviors, 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 behavior 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 toward 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 contrary, 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 antisaccade) 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.

# 1.1 | Present study

We asked participants to perform the pro-saccade and antisaccade 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 antisaccade 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 suggests a similar onset (Iacullo et al., 2020; Wessel & Aron, 2013). 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 behavioral stopping in the Go/No-Go task (Wessel, 2017).

# 2 | 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.

# 2.1 | Participants

Seventy-two members of the Bournemouth community (46 women)<sup>2</sup> 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).

The 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  $\alpha$  level of .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=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.

# 2.2 | 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 recorded.<sup>3</sup> Participants' heads were stabilized 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 inch Alienware 25 LCD monitor (resolution: 1920×1080; refresh rate: 244 Hz). The distance between the eye and the monitor was 62cm. All sound stimuli were played on a Creative Sound Blaster Z soundcard (SB1500) at  $65 \pm 1.5 \,dB(A)$ through QuietComfort 25 noise-canceling 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 8 ms and the sound output latency was 28 ms (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).

# 2.3 Stimuli

# 2.3.1 | 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 150 ms 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 et al., 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).

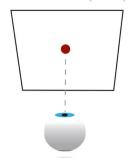
# 2.3.2 | Pro-saccade task

The two tasks, illustrated in Figure 1, followed Antoniades et al.'s (2013) standardized protocol. In the pro-saccade task, participants made horizontal saccades to targets of 10° eccentricity relative to the center 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°, colored dark red (RGB: 149, 0, 0) and presented against a white background. Trials started with a fixation dot (same as the target) at the center 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.

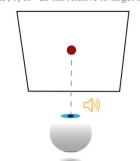
<sup>&</sup>lt;sup>2</sup>A further three participants dropped out after the first session and were replaced.

<sup>&</sup>lt;sup>3</sup>For 7 participants, the left eye was used instead due to tracking issues with glasses/contact lenses.

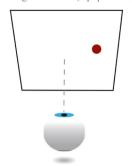




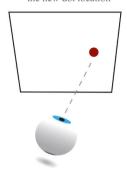
Sound played -150, -125, -100, -75, -50, -25, 0, or +25 ms relative to target step



Fixation dot steps 10° to the left or right of centre (equiprobable)

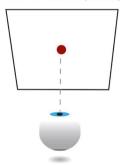


Participant makes a saccade to the new dot location

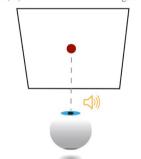


# (b) Anti-saccade trials

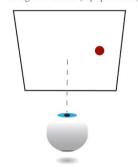
Fixation dot displayed at centre for 1000-2000 ms (random)



Sound played -150, -125, -100, -75, -50, -25, 0, or +25 ms relative to target step



Fixation dot steps 10° to the left or right of centre (equiprobable)



Participant makes a saccade to the opposite side of the new dot location

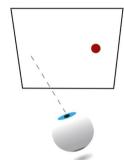


FIGURE 1 An illustration of the pro-saccade (a) and anti-saccade (b) tasks used in the experiment.

#### 2.3.3 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).

#### 2.4 **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 antisaccades and pro-saccades (Zeligman & Zivotofsky, 2017). As such, the blocked presentation allowed us to maximize the differences between the two tasks in order to test how they are affected by unexpected sounds.

Within each task block, the trials were randomized 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 emphasize 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° 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 h.

# 2.5 Data analysis

Saccades were detected with the Eyelink software algorithm. Samples were detected as saccades when they exceeded a velocity threshold of 35°/s and an acceleration threshold of 9500°/s. 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 traveled 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 (Generalized) 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 statistically significant if the p-value was  $\leq$ .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).

# 3 | 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=13,217, 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.

# 3.1 | 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<.001), indicating that novel sounds  $(M=182 \,\mathrm{ms}; \,\mathrm{SD}=70 \,\mathrm{ms})$  led to longer SRTs compared to standard sounds ( $M=165 \,\mathrm{ms}$ ;  $SD=62 \,\mathrm{ms}$ ), d=0.25. Additionally, the results showed a significant main effect of Task (b=0.152, SE=0.008, t=18.717, p<.001), with the anti-saccade task ( $M=197 \,\mathrm{ms}$ ; SD=69 ms) leading to longer SRTs compared to the pro-saccade task  $(M=142 \,\mathrm{ms}; \,\mathrm{SD}=45 \,\mathrm{ms}), \,d=0.90.$  This is in line with previous research (Hallett, 1978). Furthermore, the difference in each sound onset level to the next one was significant (all p-values < .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<.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.

**TABLE 1** Mean saccadic reaction time, saccade amplitude, and error rate for each sound, onset, and task condition (SDs in parentheses).

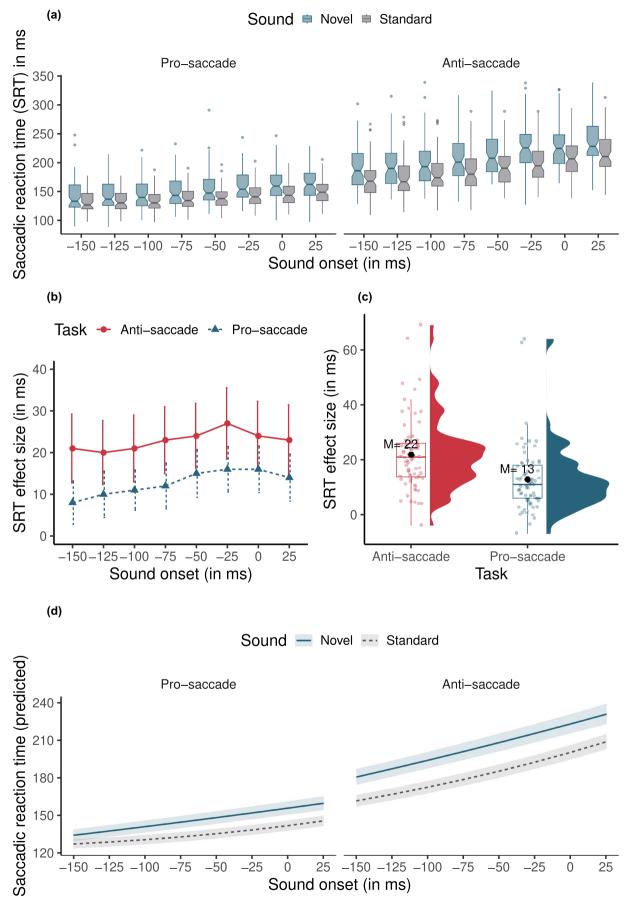
Task	Sound	Sound onset	Saccadic reaction time (ms)	Saccade	Error rate
			` ′	amplitude (°)	(prop. incorrect)
Pro-saccade	Novel	-150 ms	140 (46)	9.98 (1.52)	0.01 (0.08)
Pro-saccade	Standard	-150 ms	132 (42)	9.93 (1.67)	0.01 (0.08)
Pro-saccade	Novel	-125 ms	144 (52)	10.10 (1.41)	<0.01 (0.03)
Pro-saccade	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	$-75\mathrm{ms}$	150 (48)	10.20 (1.43)	<0.01 (0.04)
Pro-saccade	Standard	$-75\mathrm{ms}$	138 (45)	9.97 (1.64)	0.01 (0.07)
Pro-saccade	Novel	$-50\mathrm{ms}$	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)
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)

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 antisaccade and pro-saccade task increased from -125 to  $-100 \, \text{ms}$  (b = 0.009, SE = 0.003, t = 2.768, p = .006), from  $-100 \, \text{to}$   $-75 \, (b = 0.008$ , SE = 0.003, t = 2.428, p = .015), from  $-75 \, \text{to}$   $-50 \, (b = 0.009$ , SE = 0.003, t = 3.010, t = 0.003, and from 0 to t = 0.003, t = 0.003, t = 0.003, t = 0.003.

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 = .005; quadratic term: b = -1.067, SE = 0.343, t = -3.108, p = .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  $-50\,\mathrm{ms}$ . 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<.001), but not the quadratic term (b=0.165, SE=0.343, t=0.480, p=.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.

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FIGURE 2 Saccadic reaction time data in the experiment. (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). (b) shows the novelty distraction effect size (novel—standard) in saccadic reaction times for each sound onset condition. Error bars show ±1 SE. (c) shows the novelty distraction effect size for each task, aggregated over the onset conditions. Dots indicate the by-participant means. (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.

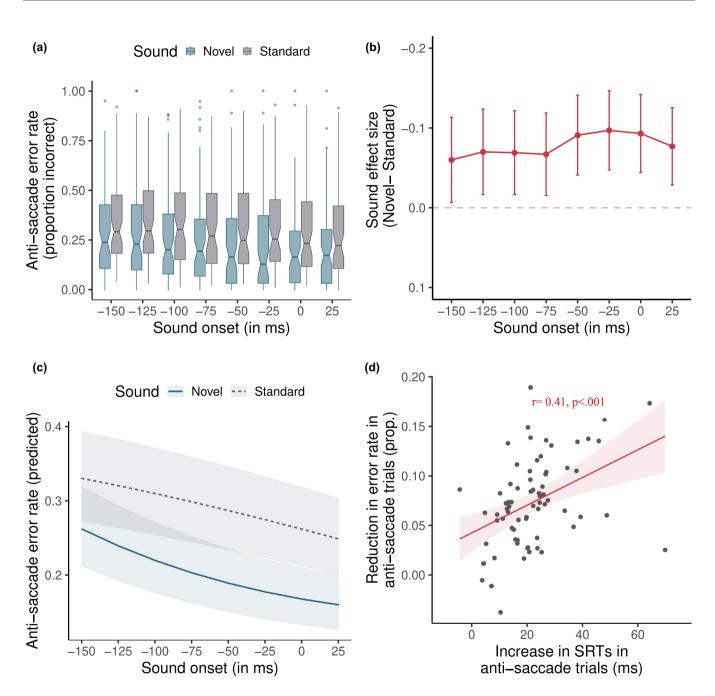


FIGURE 3 Anti-saccade errors in the experiment. (a) shows boxplots of the error rate for each sound and delay condition. (b) shows the sound effect size for anti-saccade error for each delay condition. Error bars show  $\pm 1$  SE. (c) shows the predicted anti-saccade error rate from a GLMM model that treats sound onset as a continuous variable and includes both linear and quadratic terms for it. Shading indicates 95% CIs. (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.

	Log (saccadic reaction time)				Saccade amplitude			
		Std.						
Predictors	Estimate	error	t statistic	p	Estimate	Std. error	t statistic	p
(Intercept)	5.102	0.016	318.483	<.001	9.650	0.156	62.023	<.00
sound	0.048	0.003	16.506	<.001	0.045	0.017	2.688	.007
task	0.152	0.008	18.717	<.001	-0.352	0.009	-39.09	<.00
onset −150 vs. −125	0.020	0.003	6.573	<.001	-0.003	0.035	-0.072	.943
onset −125 vs. −100	0.021	0.003	6.758	<.001	0.025	0.035	0.703	.482
onset -100 vs75	0.033	0.003	10.768	<.001	0.048	0.035	1.357	.175
onset −75 vs. −50	0.035	0.003	11.218	<.001	-0.027	0.036	-0.772	.440
onset -50 vs25	0.033	0.003	10.529	<.001	-0.026	0.036	-0.715	.475
onset −25 vs. 0	0.022	0.003	7.151	<.001	-0.033	0.036	-0.920	.357
onset 0 vs. 25	0.029	0.003	9.256	<.001	-0.063	0.036	-1.759	.079
sound×task	0.007	0.001	9.214	<.001	-0.034	0.009	-3.818	<.00
sound $\times$ onset $-150$ vs. $-125$	0.002	0.003	0.588	.557	-0.012	0.035	-0.334	.739
sound×onset −125 vs. −100	0.001	0.003	0.478	.633	-0.000	0.035	-0.001	.999
sound×onset −100 vs. −75	0.003	0.003	0.918	.358	0.045	0.035	1.272	.203
sound×onset −75 vs. −50	0.003	0.003	1.103	.270	0.018	0.036	0.509	.611
sound×onset −50 vs. −25	0.002	0.003	0.729	.466	-0.010	0.036	-0.286	.775
sound×onset −25 vs. 0	-0.005	0.003	-1.666	.096	0.019	0.036	0.523	.601
sound×onset 0 vs. 25	-0.003	0.003	-1.050	.294	0.017	0.036	0.466	.641
task×onset −150 vs. −125	0.004	0.003	1.199	.231	-0.063	0.035	-1.791	.073
task×onset −125 vs. −100	0.009	0.003	2.768	.006	-0.011	0.035	-0.320	.749
task×onset −100 vs. −75	0.008	0.003	2.428	.015	0.040	0.035	1.135	.256
task×onset −75 vs. −50	0.009	0.003	3.010	.003	0.016	0.036	0.438	.661
task×onset −50 vs. −25	0.006	0.003	2.057	.040	-0.030	0.036	-0.852	.394
task×onset −25 vs. 0	0.002	0.003	0.502	.615	-0.014	0.036	-0.394	.693
task×onset 0 vs. 25	0.009	0.003	2.744	.006	-0.035	0.036	-0.963	.335
sound×task×onset −150 vs. −125	-0.004	0.003	-1.257	.209	-0.039	0.035	-1.103	.270
sound×task×onset −125 vs. −100	-0.005	0.003	-1.461	.144	-0.021	0.035	-0.584	.559
sound×task×onset −100 vs. −75	0.002	0.003	0.557	.578	0.033	0.035	0.933	.351
sound×task×onset −75 vs. −50	-0.003	0.003	-0.864	.388	0.048	0.036	1.346	.178
sound×task×onset −50 vs. −25	0.000	0.003	0.088	.930	-0.055	0.036	-1.538	.124
sound×task×onset −25 vs. 0	-0.004	0.003	-1.427	.154	0.027	0.036	0.750	.453
sound×task×onset 0 vs. 25	-0.001	0.003	-0.374	.708	-0.009	0.036	-0.257	.797
Random effects								
$\sigma^2$	0.061					7.987		
$ au_{00}$	0.018 <sub>sub</sub>					1.737 <sub>sub</sub>		
$ au_{11}$	0.001 <sub>sub.soun</sub>	d				0.014 <sub>sub.sound</sub>		
11	0.005 <sub>sub.task</sub>					Sub.Sound		
$ ho_{01}$	0.450					0.039 <sub>sub</sub>		
F U1	0.253					sub		

	Log (saccadic reaction time)				Saccade amplitude			
Predictors	Estimate	Std. error	t statistic	p	Estimate	Std. error	t statistic	p
ICC	0.260					0.179		
N	72 <sub>sub</sub>					72 <sub>sub</sub>		
Observations	180,818					180,818		
Marginal $R^2$ /conditional $R^2$	0.247/0.443					.012/.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.

To summarize, 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 a little weaker with sound onsets between  $-150\,\mathrm{ms}$  and  $-100\,\mathrm{ms}$  and then increased until reaching a plateau around  $-50\,\mathrm{ms}$ —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  $-75\,\mathrm{ms}$  sound onset conditions in the pro-saccade task, where the effect of the novel sound was no longer significant toward the end of the experiment. This suggests that the inhibition in the first few time intervals (-150 to  $-75\,\mathrm{ms}$ ) was smaller and/or wore off more quickly as participants habituated to the unexpected sounds.

# 3.2 | 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=.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, t<0.001, t=-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<.001): the sound effect was present in the pro-saccade task (b=0.158, SE=0.037, t=4.247, p<.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 sound onsets (see the Supplementary Materials for more details).

## 3.3 Anti-saccade error rate

The statistical results are shown in Table 3. We found a main effect of Sound. As Figure 3a,b show, novel sounds  $(M=0.22; \mathrm{SD}=0.41)$  led to a significantly lower proportion of errors in the anti-saccade task compared to the standard sound  $(M=0.30; \mathrm{SD}=0.46), b=-0.245, \mathrm{SE}=0.012, z=-19.998, p<.001, d=-0.16.$  Additionally, the error rate was significantly lower in the  $-50\,\mathrm{ms}$   $(M=0.27; \mathrm{SD}=0.45)$  compared to the  $-75\,\mathrm{ms}$   $(M=0.29; \mathrm{SD}=0.45)$  sound onset condition  $(b=-0.133, \mathrm{SE}=0.049, z=-2.728, p=.006)$ , 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<.001) and quadratic terms (b=4.985, SE=1.031, z=4.835, p<.001). As Figure 3c shows, the difference in error rates between novel and standard sounds increased with Sound Onset, until reaching a plateau around  $-50 \, \text{ms}$ . This mirrors the pattern in SRTs and suggests that the inhibition of

**TABLE 3** Generalized linear mixed effect results for antisaccade error rate.

	Anti-saccade error rate								
	Std.								
Predictors	Estimate	error	z statistic	p					
(Intercept)	-1.137	0.139	-8.159	<.001					
sound	-0.245	0.012	-19.998	<.001					
onset −150 vs. −125	0.014	0.046	0.306	.759					
onset −125 vs. −100	-0.107	0.046	-2.310	.021					
onset -100 vs. -75	-0.095	0.047	-2.009	.045					
onset -75 vs50	-0.133	0.049	-2.728	.006					
onset -50 vs. -25	-0.030	0.050	-0.606	.544					
onset −25 vs. 0	-0.057	0.051	-1.121	.262					
onset 0 vs. 25	-0.035	0.052	-0.671	.502					
sound×onset −150 vs. −125	-0.028	0.046	-0.612	.541					
sound×onset −125 vs. −100	0.014	0.046	0.295	.768					
sound×onset −100 vs. −75	-0.021	0.047	-0.456	.649					
sound×onset −75 vs. −50	-0.090	0.049	-1.856	.063					
sound×onset −50 vs. −25	-0.015	0.050	-0.290	.772					
sound×onset −25 vs. 0	0.018	0.051	0.356	.722					
sound×onset 0 vs. 25	0.065	0.052	1.240	.215					
Random effects									
$\sigma^2$	3.290								
$ au_{00\mathrm{sub}}$	1.444								
ICC	0.305								
$N_{ m sub}$	72								
Observations	85,699								
Marginal $R^2$ / conditional $R^2$	.012/.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.

incorrect responses was smallest in the earlier Sound Onset conditions.

Therefore, the unexpected novel sounds generally aided response inhibition in the anti-saccade task – they helped subjects suppress the execution of erroneous prosaccades, 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 antisaccades, 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 afterward, 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.

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.

## 4 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 prosaccades. 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 &

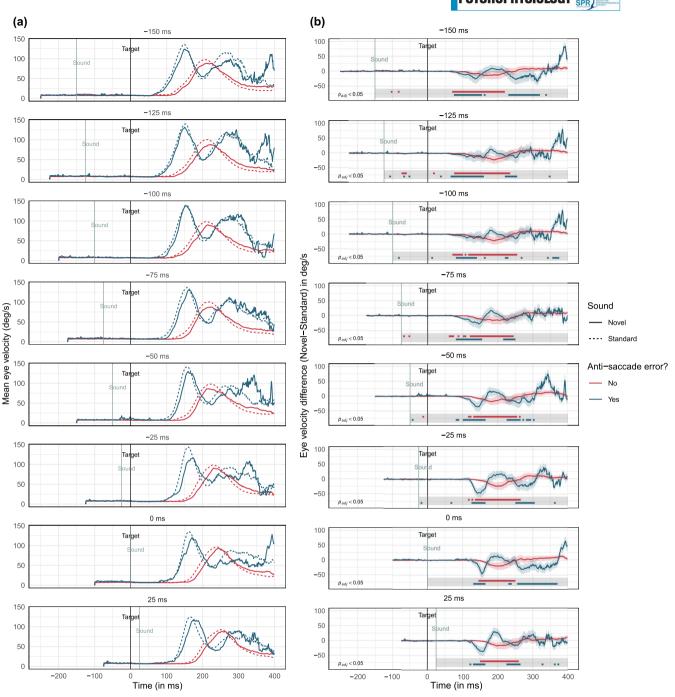


FIGURE 4 Mean eye velocity in the anti-saccade task between novel and standard sounds across all sound onset conditions. Separate lines are plotted for trials on which participants made an anti-saccade error (i.e., executed a pro-saccade) and trials on which they made the correct response. (a) shows the velocity profiles for standard sounds (dashed lines) and novel sounds (solid lines) on correct/incorrect trials (see the main text for more information). (b) shows the difference between the standard and novel curves from (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 400 ms 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 5 ms bins and applying a Bonferroni correction to all p-values.

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 a 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 analyzing 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 and -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 eyemovement responses across all intervals. Even so, there was some evidence that the effect in the pro-saccade task was weaker and started to disappear toward 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 prosaccade 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 175 ms that was identified as most plausible based on previous evidence.

These results may appear to contradict 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 the excitability of the nervous system. SRTs, in contrast, 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 taskrelevant 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 utilizing 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 is 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 anti-saccade error rate.

Indeed, the present data indicates that novel sounds helped suppress this reflexive, stimulus-driven behavior when it is not required by the task, in favor of more voluntary-driven behavior. 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 the 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 &

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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 et al., 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 antisaccade 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 et al., 2006; Goto et al., 2010; Guitton et al., 1985; Ouerfelli-Ethier et al., 2018), thus underscoring the importance of these areas 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 et al., 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 programs 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 contrary, the Cancel process could also affect saccadic programming, for example, by reinstating the oculomotor plans that were put on hold or by canceling 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 to 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 behavioral stopping. While in the present task, the inhibition in SRTs is, to some extent, confounded with the behavioral outcome, future studies could try to disentangle these.

# 5 | 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 behavior. These results raise the possibility that unexpected events may exert a global suppressive effect on the oculomotor system.

# **AUTHOR CONTRIBUTIONS**

Martin R. Vasilev: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. Zeynep G. Ozkan: Data curation; formal analysis; investigation; software; visualization; writing – original draft. Julie A. Kirkby: Conceptualization; writing – original

draft; writing – review and editing. **Antje Nuthmann:** Conceptualization; visualization; writing – original draft; writing – review and editing. **Fabrice B. R. Parmentier:** Conceptualization; funding acquisition; methodology; resources; writing – original draft; writing – review and editing.

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#### DATA AVAILABILITY STATEMENT

All data, analysis code, and materials from this study are available at: https://osf.io/9rb6n/.

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# SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Modulation of novelty distraction by trial order.

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