



Task-irrelevant emotional faces impact BOLD responses more for prosaccades than antisaccades in a mixed saccade fMRI task

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ABSTRACT

Cognitive control allows individuals to flexibly and efficiently perform tasks by attending to relevant stimuli while inhibiting distraction from irrelevant stimuli. The antisaccade task assesses cognitive control by requiring participants to inhibit a prepotent glance towards a peripheral stimulus and generate an eye movement to the mirror image location. This task can be administered with various contextual manipulations to investigate how factors such as trial timing or emotional content interact with cognitive control. In the current study, 26 healthy adults completed a mixed antisaccade and prosaccade fMRI task that included task irrelevant emotional faces and gap/overlap timing. The results showed typical antisaccade and gap behavioral effects with greater BOLD activation in frontal and parietal brain regions for antisaccade and overlap trials. Conversely, there were no differences in behavior based on the emotion of the task irrelevant face, but trials with neutral faces had greater activation in widespread visual regions than trials with angry faces, particularly for prosaccade and overlap trials. Together, these effects suggest that a high level of cognitive control and inhibition was required throughout the task, minimizing the impact of the face presentation on saccade behavior, but leading to increased attention to the neutral faces on overlap prosaccade trials when both the task cue (look towards) and emotion stimulus (neutral, non-threatening) facilitated disinhibition of visual processing.

1. Introduction

Successful goal-directed behavior is reliant on deploying attention towards relevant stimuli as well as inhibiting distraction from irrelevant stimuli to ensure efficient performance (Bari and Robbins, 2013; Chelazzi et al., 2019; Corbetta and Shulman, 2002; Duque et al., 2017; Gaspelin and Luck, 2018). These behaviors are supported by cognitive control mechanisms, which have been investigated in a multitude of task paradigms and are implemented primarily by frontoparietal brain networks (Braver, 2012; Koechlin et al., 2003; Miller and Cohen, 2001). One paradigm that is particularly effective for exploring how cognitive control deploys attention and selects appropriate responses is the antisaccade task (Hallett, 1978), which contrasts stimulus-driven eye movements towards a target with goal-directed eye movements away from the target (Hutton, 2008; Munoz and Everling, 2004; Pierce et al., 2019). The antisaccade task is a powerful tool for investigating cognitive control and has been adapted across various contexts to explore effects such as manipulation of the symbolic or emotional content of the

saccade cue or target.

When an individual rapidly glances towards a sudden-onset peripheral stimulus (basic prosaccade), this response directs eye movements in a bottom-up, visually-guided manner that relies on ocular motor neural circuitry including the superior colliculus, occipital cortex, posterior parietal cortex, frontal and supplementary eye fields (FEF/SEF), thalamus, and basal ganglia (Leigh and Zee, 2015; McDowell et al., 2008). When one glances away from the stimulus to the mirror image location (complex antisaccade), the eye movement is generated in a more top-down, controlled manner that requires inhibition of the prepotent stimulus-driven response. The added cognitive demands for antisaccade generation increase activation in most regions of the saccade network listed above and recruit additional cognitive control regions including the dorsolateral prefrontal cortex (DLPFC; Dyckman et al., 2007; Ford et al., 2005; McDowell et al., 2008; Munoz and Everling, 2004; Pierce et al., 2019).

While the basic pattern of responses for prosaccades and antisaccades is well known, some studies have further explored the

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underlying cognitive demands of these seemingly simple tasks by modulating the task parameters to examine how cognitive control responds to different contexts. For example, one common manipulation is to change the timing of fixation offset relative to target onset (Hutton, 2008; Reuter-Lorenz et al., 1991; Saslow, 1967), such that the fixation point disappears a short time before the target appears (gap) or stays visible after the target appears (overlap). Typically, the gap condition results in faster reaction times than the overlap condition, due in part to the disengagement of fixation-related neurons that results in greater motor preparation at the time of target onset (Hutton, 2008; Koval et al., 2004; Pierce et al., 2019; Reuter-Lorenz et al., 1991). Another effective manipulation is to change the relative frequency of prosaccade or antisaccade trials within a task (Chiau et al., 2011; Massen, 2004; Pierce et al., 2015; Pierce and McDowell, 2016; Talanow et al., 2016). In two similar functional magnetic resonance imaging (fMRI) studies (Pierce and McDowell, 2016; Talanow et al., 2016), a higher proportion of antisaccade trials relative to prosaccade trials (75% vs. 25%) created a higher demand for control across the entire task, shifting behavior and increasing activation in control regions (i.e., PFC/anterior cingulate cortex), particularly for prosaccade trials. Overall, such manipulations demonstrate that cognitive control can be differentially implemented according to current contextual demands and the saccadic system offers a sensitive measure for tracking these changes.

In addition to adjusting the saccade task parameters as described above, saccadic performance also may be influenced by the emotional context of the task. Emotional stimuli have numerous effects on cognition in general (Inzlicht et al., 2015; Kanske, 2012; Pessoa, 2008; Phelps, 2006), and on cognitive control and attentional processes specifically, which can vary depending on task difficulty and an individual's ability to control their response to salient but irrelevant stimuli (Kanske and Kotz, 2012; Most et al., 2005; O'Toole et al., 2011; Pessoa et al., 2002; Pessoa et al., 2012; Sagaspe et al., 2011; Vuilleumier, 2005). For example, the threat of shock may heighten an individual's stimulus-driven response tendency, favoring prosaccades and increasing directional errors on antisaccade trials (Cornwell et al., 2012). On the other hand, increasing the frequency of antisaccade trials within a block favors slower, more controlled responding (Chiau et al., 2011; Pierce et al., 2015), which might interfere with one's ability to filter irrelevant emotional information or, conversely, might improve performance by minimizing the effect of such distractors.

One type of oft-used emotional stimulus is faces, which constitute a unique stimulus class that is highly familiar and can convey biologically relevant social and affective information (Haxby et al., 2000; Neta et al., 2017; Neta and Whalen, 2011). Emotional faces can elicit strong neural responses in visual regions, including the fusiform gyrus and superior temporal sulcus, as well as in the amygdala (Haxby et al., 2000; Todorov et al., 2011; Vuilleumier et al., 2001). When the face is irrelevant to ongoing goal-directed behavior, however, successful performance relies on inhibition and facilitation processes of cognitive control for maintaining attention on appropriate features and goals of the environment and/or task.

In saccade paradigms, the presentation of emotional faces has been shown to both enhance and interfere with saccade behavior depending on the context (Devue et al., 2012; Malsert and Grandjean, 2016; Mills et al., 2016; Salvia et al., 2020; West et al., 2011). For instance, West et al. (2011) reported that centrally presented fearful faces resulted in faster saccades to a peripheral target than neutral faces, specifically in gap but not overlap trials (i.e., when the face disappeared prior to the saccadic target rather than remaining visible). Furthermore, Mills et al. (2016) found that centrally presented angry faces interfered with antisaccade performance, indicating that the emotional stimulus competed with the cognitive control processes required for inhibiting the prepotent response (Mills et al., 2016). To our knowledge, however, no study has measured the fMRI blood oxygenation level dependent (BOLD) signal during a saccade paradigm in which task-irrelevant emotional faces are presented. Thus, analysis of the BOLD signal in a task with

competing attentional and contextual demands can elucidate how cognitive control and affective neural systems interact with ocular motor circuitry and the extent to which emotional processing occurs for irrelevant stimuli when the task requires frequent inhibition of visual input.

1.1. Current investigation

The current study investigated the effects of task-irrelevant emotion processing on saccade performance and BOLD activation by presenting emotional faces during a mixed saccade task in which antisaccade trials were more frequent than prosaccade trials (66/33%). We expected that the high proportion of antisaccade trials would increase the need for inhibition and cognitive control in the task generally (cf. Pierce and McDowell, 2016; Talanow et al., 2016), making performance of typically low control prosaccade trials more susceptible to the contextual manipulations. Given previous findings suggesting that emotionally salient stimuli can impair task performance (e.g., Devue et al., 2012; Dolcos and McCarthy, 2006) as a function of competing task demands (e.g., Hart et al., 2010), the task, critically, included an irrelevant face that either conveyed emotion (angry expression) or did not (neutral expression) and was presented centrally prior to the onset of the visual target. In half of the trials, the face disappeared before the target appeared (gap trial timing), while in the other half of the trials it remained visible throughout the target/response period (overlap trial timing). We predicted that emotional faces would impair performance compared to neutral faces, capturing attention and increasing BOLD responses in visual and emotion-related brain regions, while interfering with the recruitment of saccadic control resources supported by regions such as DLPFC.

2. Methods

2.1. Participants

Data was collected from 33 participants (20 female; ages 19–44 years, mean (SD) age = 25.79 years (6.24)). All participants reported no history of neurological or psychiatric disorders and no use of psychotropic medications, had normal or corrected-to-normal vision, and were naive to the purpose of the study. One participant was unable to complete the task due to issues with eye tracking equipment, one participant was excluded due to a lack of task compliance, and five participants were excluded from the fMRI data analysis due to technical issues with scan acquisition. The final sample therefore included 26 participants (14 female; ages 19–44 years, mean (SD) age = 26.8(6.5)). This sample size is consistent with recent literature examining similar fMRI effects (Hart et al., 2010 (N = 14); Kühn et al., 2014 (N = 15); Peyrin et al., 2021 (15); Pierce and McDowell, 2016 (N = 35); Rodrigue et al., 2016 (N = 30); Talanow et al., 2016 (N = 16)). All protocols were approved by the University of Nebraska-Lincoln Institutional Review Board. The participants were informed of all procedures prior to participation and gave written informed consent prior to testing in accordance with the Declaration of Helsinki.

2.2. Procedure

Prior to entering the MRI scanner, participants were given verbal task instructions and shown several practice trials to ensure task comprehension. Once in the scanner, participants were positioned on their back and viewed the experimental paradigm via a mirror attached to the head coil. Padding was used to secure the participant's head in a comfortable, static position. Following the task design from Mills et al. (2016), all trials started with the presentation of a central fixation point (a black dot extending 81 × 81 pixels or 2° of visual angle) on a light gray background for 150 ms, which was followed by a centrally presented task cue (a 2° colored dot) for 400 ms. A green dot informed the

participant that the trial was a prosaccade and they should make an eye movement *towards* the upcoming target; a *red* dot informed the participant that the trial was an antisaccade and they should make an eye movement *away from* the upcoming target.

Subsequent to the cue, a task-irrelevant emotion stimulus (240×360 pixels/ $5.5 \times 8^\circ$) was presented centrally. This stimulus consisted of one of four photographs of either a *neutral* or *angry* male/female facial expression selected from the NimStim database (Tottenham et al., 2009). On “overlap” trials, the face remained on screen for 650 ms before the target (a 40×40 pixels/ 1° black dot) was presented on either the left or right side of the screen. On “gap” trials, the face remained on screen for only 400 ms followed by a 250 ms blank screen before the target was presented (Saslow, 1967). Trials were separated by an intertrial interval (ITI) of 1000, 4000 or 7000 ms (mean = 4000 ms) to create a variable interval that minimized anticipation of the initiation of the next trial and to time lock the start of each trial to the start of the MRI volume acquisition; the length of the ITI was balanced across conditions. An example sequence for overlap and gap trials is shown in Fig. 1.

Each of the four experimental runs consisted of a block of 24 gap trials and a block of 24 overlap trials (192 total trials per subject). One third of the trials in each block were prosaccades and two thirds were antisaccades. Angry and neutral faces were presented in equal numbers across all trial types. Trials were pseudo-randomly distributed within each block to balance the order of saccade and emotion conditions and block order (gap/overlap) was counterbalanced across participants.

Eye movements were recorded using an SR Research EyeLink 1000 system (SR Research Ltd., ON, Canada), which has high spatial resolution and a sampling rate of 1000 Hz. Thresholds for detecting the onset of saccadic movements were accelerations of $8000^\circ/s^2$, velocities of $30^\circ/s$, and distances of 0.5° of visual angle. Movement offset was detected when velocity fell below $30^\circ/s$ and remained at that level for 10 consecutive samples. Each participant underwent a nine-point calibration procedure followed by a nine-point calibration accuracy test. Calibration was repeated if any point was in error by more than 1° or if the average error for all points was greater than 0.5° .

2.3. MRI data acquisition parameters

The MRI data were collected at the University of Nebraska-Lincoln Center for Brain, Biology, & Behavior on a Siemens 3 T Skyra scanner

using a 32-channel head coil. Structural images were acquired using a T1-weighted MPRAGE sequence (TR = 2.5 s, TE = 3.37 ms, slices = 192 interleaved, voxel size = $1.0 \times 1.0 \times 1.0$ mm, matrix = 256×256 , FOV = 256 mm, flip angle = 7° , total acquisition time = 5:07). Blood oxygen level-dependent (BOLD) activity was measured using an EPI scanning sequence (TR = 3.0 s, TE = 30 ms, slices = 50 interleaved, voxel size = $2.50 \times 2.50 \times 2.50$ mm, matrix = 88×88 mm, FOV = 220 mm, flip angle = 83° , total acquisition time = 5:48 per block) in which slices were acquired parallel to the AC-PC plane and the volume positioned to cover the entire brain.

2.4. Data analysis

2.4.1. Behavior

Raw eye movement data were analyzed with Data Viewer software (SR Research, Ontario, Canada). A saccade was defined as an eye movement with an amplitude $>3^\circ$. The latency of the first correct saccade was defined as the interval between target presentation and the initiation of a saccade. An error was defined as when the first saccade was directed towards the target in antisaccade trials or away from the target in prosaccade trials. Anticipations (reaction time <100 ms) and late saccades (reaction time >800 ms) were discarded (9.5%). Data were analyzed via a $2 \times 2 \times 2$ within-subject ANOVA with the factors trial timing (gap, overlap), saccade (prosaccade, antisaccade), and emotion (neutral, angry) separately for both dependent factors of reaction time (RT) and directional error rate.

2.4.2. fMRI data

Preprocessing of MR images was conducted using the AFNI program suite (Cox, 1996, 2012). The first four TRs of each run were excluded to allow for scanner stabilization. The time series data were first de-spiked by removing outlying values for each voxel. Then, slice timing correction was accomplished by re-referencing each scan to the first slice. These slice time-corrected volumes next were aligned to each other and aligned to the anatomical image before being warped to the Talairach atlas (Talairach and Tournoux, 1988) provided by AFNI. Functional volumes were then spatially smoothed using a 6 mm^3 full width at half maximum kernel and the time series in each voxel was normalized by dividing each time point by the average across all time points and multiplying by 100. Any images containing movements >0.9 mm, as

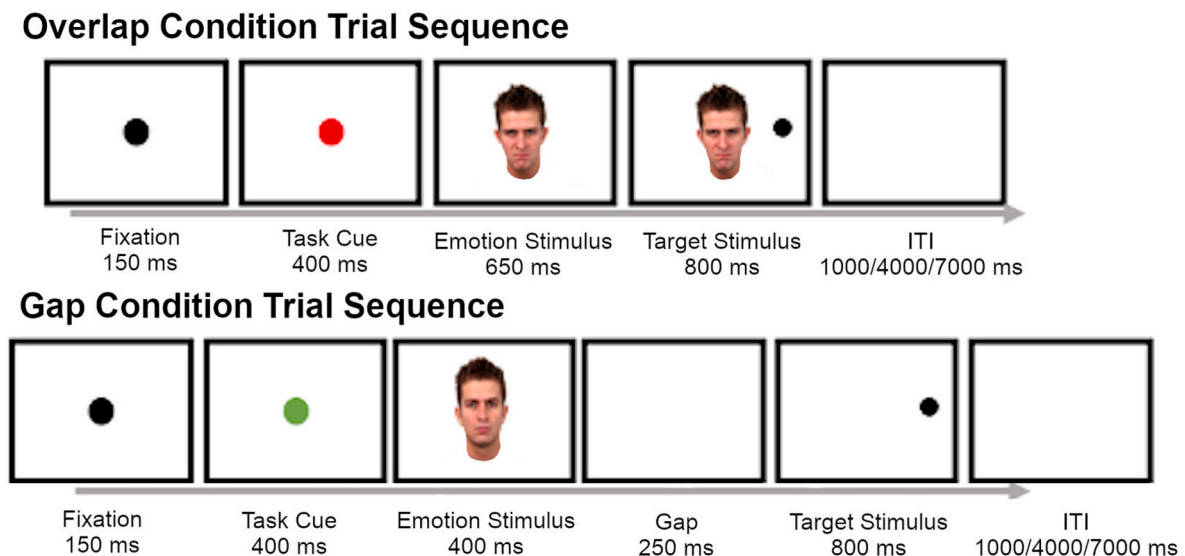


Fig. 1. Example trial sequence for overlap (*top*) and gap (*bottom*) trials. Every trial started with a central fixation point, followed by the task cue (the color of which indicated whether a prosaccade or antisaccade was required), followed immediately by an emotional stimulus (either a neutral or angry face). In the overlap condition the face remained on screen through the presentation of a peripheral target, while in the gap condition the face disappeared 250 ms before the target appeared. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

determined by the motion parameters calculated during spatial realignment, were censored frame-wise from further analysis (only 2 total volumes censored from one participant).

To identify brain regions in which BOLD activity related to each stimulus condition, the BOLD data were submitted to a general linear model (GLM) in which trials were modeled separately in the design matrix according to trial type. Based on behavioral responses, individual subject data from all four runs were submitted to a GLM with 9 stimulus regressors for correct angry overlap antisaccades, angry gap antisaccades, neutral overlap antisaccades, neutral overlap antisaccades, angry overlap prosaccades, angry gap prosaccades, neutral overlap prosaccades, neutral overlap prosaccades, and error/no response trials (stimulus timing was missing for one run from two participants, so their fMRI data was analyzed using only three runs). Regressors of no interest also were included to remove effects from baseline drift (linear, quadratic, cubic) and movement/rotation in the x, y, and z planes.

Individual subject data then were analyzed at the group level via a 2 × 2 × 2 (trial timing (gap, overlap) × saccade (prosaccade, antisaccade) × emotion (neutral, angry)) within-subject ANOVA. To protect against false positives resulting from multiple comparisons across voxels, a clustering method derived from Monte Carlo simulations was applied to the group maps. With a voxelwise $p < .005$, a familywise $\alpha < 0.05$ was preserved by clusters with a minimum of 70 voxels. Post hoc t -tests were performed in JASP (JASP Team (2020), version 0.12.2 [computer software]) to examine significant interaction effects; p -values for post hoc tests were Bonferroni-corrected, with a significance threshold of .05.

3. Results

3.1. Behavioral data

Consistent with prior work, participants were slower and made more errors in their responses on antisaccade trials than on prosaccade trials (Table 1). These control-related costs were significant for both RT ($F(1,25) = 139.12, p < .001, \eta^2 = 0.685$) and error rate ($F(1,25) = 12.36, p = .002, \eta^2 = 0.200$). As predicted, there were also significant effects of trial timing for both RT ($F(1,25) = 17.88, p < .001, \eta^2 = 0.017$) and error rate ($F(1,25) = 4.34, p = .048, \eta^2 = 0.009$), with slower RTs and fewer errors on overlap trials compared to gap trials. There were no significant effects of emotion nor significant interactions.

3.2. fMRI data

3.2.1. Main effects

The ANOVA results yielded four regions of saccadic circuitry that significantly differentiated between saccade type (antisaccade > prosaccade). Details of all clusters are provided in Table 2. Clusters were located in bilateral superior parietal and superior frontal gyri. For the main effect of trial timing, there were five regions with significantly greater activation for overlap trials compared to gap trials. These clusters were located in left superior/medial frontal gyrus, left supplementary motor area, superior medial frontal gyrus, left middle temporal

Table 1
Saccade behavior.

Saccade Type	Trial Timing	Emotion	Error Rate	Reaction Time (ms)
Prosaccade	Gap	Angry	.06 (.10)	207 (39)
		Neutral	.05 (.07)	194 (37)
	Overlap	Angry	.05 (.10)	213 (37)
		Neutral	.05 (.09)	210 (36)
Antisaccade	Gap	Angry	.13 (.11)	274 (53)
		Neutral	.15 (.11)	271 (44)
	Overlap	Angry	.12 (.10)	286 (46)
		Neutral	.10 (.09)	282 (49)

Means and standard deviations for error rate and reaction time for each trial condition.

Table 2
Whole brain analysis fMRI clusters.

# Voxels	Region	Peak F	x	Y	z
Main Effect of Saccade Type					
160	Right Superior Parietal Lobule	27.4	-19	59	51
140	Left Superior Frontal/Precentral Gyrus	19.7	41	9	59
134	Right Superior Frontal Gyrus	25.4	-24	6	56
115	Left Superior Parietal Lobule	20.9	24	54	51
Main Effect of Trial Timing					
484	Left Superior/Medial Frontal Gyrus	29.3	1	-49	24
132	Left Supplementary Motor Area, Superior Medial Frontal Gyrus	30.9	11	-16	56
113	Left Middle Temporal Gyrus	26.3	56	19	-6
81	Right Angular Gyrus	16.3	-46	54	39
Main Effect of Emotion					
2681	Bilateral Superior/Middle Occipital Gyrus	47.2	-21	96	19
204	Left Caudate	39.5	9	-11	9
135	Right Cerebellum (Crus I)	27.3	-39	46	-34
121	Right Thalamus	39.6	-9	16	14
115	Brainstem	23.1	4	24	-31
108	Left Fusiform/Lingual Gyrus	28.7	26	54	-9
102	Left Middle/Superior Temporal Gyrus	21.3	51	19	4
87	Right Putamen/Caudate	31.6	-26	-14	4
80	Left Postcentral Gyrus/Inferior Parietal Lobule	19.4	29	41	44
Timing × Emotion Interaction					
135	Right Middle Occipital Gyrus	29.4	-44	84	1
Timing × Saccade Type × Emotion Interaction					
77	Left Superior Occipital Gyrus	19.8	16	89	36

Note. Peak coordinates are reported in Talairach Atlas space and regions describe the primary anatomical locations encompassed by each cluster as reported in AFNI. Voxel size is 2.5 mm³.

gyrus, and right angular gyrus (Fig. 2). Finally, for the main effect of emotion, there were nine regions with significantly greater activation for trials with a neutral face compared to trials with an angry face. These emotion-sensitive clusters were located in visual and ocular motor regions including a large cluster extending through bilateral superior/middle occipital gyrus, left fusiform/lingual gyrus, left middle/superior temporal gyrus, left postcentral gyrus/inferior parietal lobule, bilateral caudate, right cerebellum (crus I), right thalamus, and the brainstem (Fig. 3).

3.2.2. Interaction effects

The interaction between trial timing (overlap, gap) and emotion (angry, neutral) identified one significant cluster in right middle occipital gyrus, which post-hoc tests showed had significantly greater activation for the overlap neutral condition relative to the gap neutral condition ($t(25) = 4.63, p < .001$), the overlap angry condition ($t(25) = 4.82, p < .001$), and the gap angry condition ($t(25) = 2.85, p = .044$). Additionally, the gap angry condition had greater activation than the gap neutral condition ($t(25) = 3.08, p = .021$). Furthermore, the three-way interaction between trial timing, saccade type, and emotion yielded a significant cluster in left superior occipital gyrus. Post-hoc t -tests demonstrated that for the overlap condition, neutral prosaccades ($t(25) = 5.24, p < .001$) and angry antisaccades ($t(25) = 3.97, p = .004$) had greater activation than angry prosaccades, while no other pairwise comparisons were significant. These results are shown in Fig. 4 and Table 2.

4. Discussion

In this study, participants completed a mixed antisaccade and prosaccade fMRI task that included irrelevant emotional faces at fixation prior to peripheral target onset. Behavioral performance exhibited the predicted pattern of saccade trial type and timing (gap/overlap) effects, yet there were no significant differences in saccadic RT or directional error rate as a function of the emotion condition (i.e., for angry

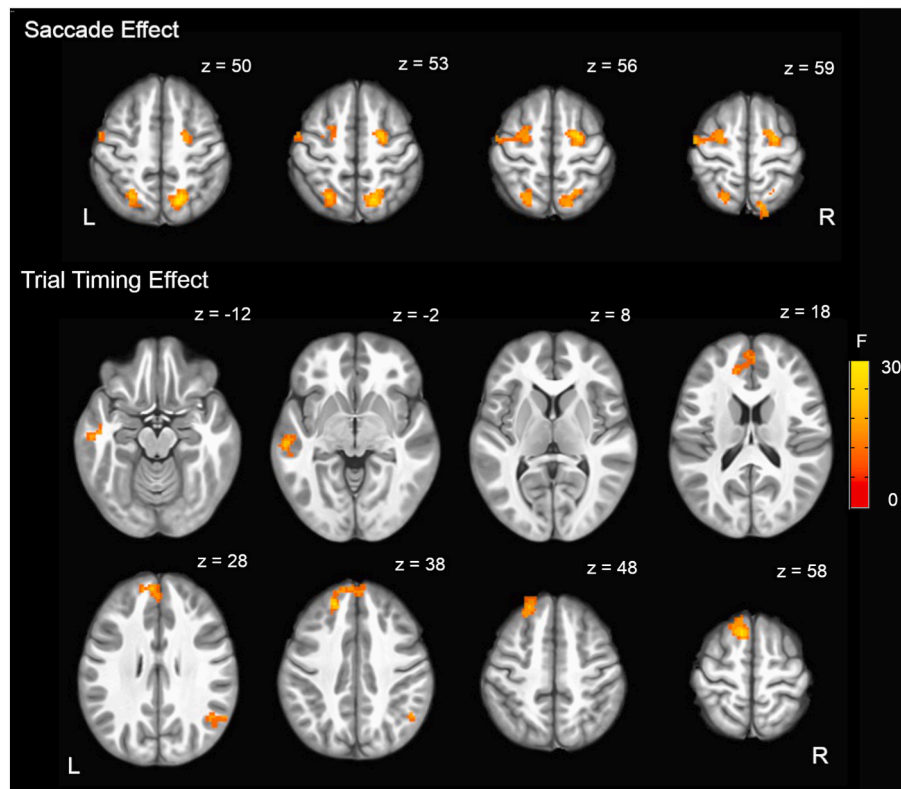


Fig. 2. Main effects of saccade (antisaccade > prosaccade) and trial timing (overlap > gap) overlaid on an anatomical image. No regions showed the opposite pattern for either comparison.

compared to neutral face trials). Although the lack of behavioral emotion effects is difficult to interpret precisely, there were emotion-related effects in the BOLD signal that could shed light on these results. Specifically, several primarily visual regions showed greater BOLD activity for neutral than for angry faces, especially for prosaccade and overlap trials. This brain response may reflect a high level of cognitive control and/or inhibition that was required throughout the task, and that this increased control minimized the impact of the face presentation on saccade behavior. Below we unpack the implications of these findings as they relate to the interaction between emotion and cognitive control.

Emotional stimuli have been shown to elicit a variety of effects on cognitive control across tasks that may be facilitatory if the stimulus is relevant to the task goals or may interfere with performance if the stimulus is irrelevant and distracts from the primary task goal (Hart et al., 2010; O'Toole et al., 2011; Pessoa et al., 2002; Phelps, 2006). Interestingly, the current results revealed no differences in behavior between trials with angry or neutral faces, indicating that any response to the negative emotion was successfully inhibited and did not impede maintenance of the task goals (look towards or look away) nor efficient generation of a saccade to the appropriate location. In the current task, the emotional faces were irrelevant to saccade performance in all conditions, so participants theoretically could completely disregard the emotional content of the faces unless it captured attention automatically (Vuilleumier et al., 2001). Prior studies examining the behavioral effects of emotional stimuli on the antisaccade task have had mixed findings, partly depending on whether the face was positioned at the target location (García-Blanco et al., 2013; Geringswald et al., 2020; Llamas-Alonso et al., 2020; Reinholdt-Dunne et al., 2012; Wieser et al., 2009) or positioned at central fixation (current study; Mills et al., 2016; Malsert and Grandjean, 2016). Using the face as a target increases its relevance to the task and makes it more likely that the emotional content will impact behavior (Kanske, 2012; Pessoa et al., 2002), whereas the current study focused on participants' ability to inhibit irrelevant

emotional information during a concurrent cognitive control task. Furthermore, previous saccade studies with emotional faces have utilized different emotions, such as anger, fear, or happiness, that also may influence how salient the face is to the participant and modulate its impact on task performance (Pessoa et al., 2012).

Despite the lack of behavioral differences in response to the task-irrelevant emotional facial expressions, there were marked differences in BOLD activation between angry and neutral face trials, with overall greater activation for neutral faces in primarily occipital and parietal visual regions as well as in the basal ganglia, thalamus, and cerebellum. Surprisingly, there were no regions with significantly greater activation for trials with angry faces, nor any emotion effects in typical cognitive control frontoparietal regions. This pattern of results is contrary to our expectations and to most previous findings comparing emotional and neutral faces (e.g., Cromheeke and Mueller, 2014; Fusar-Poli et al., 2009). In one previous study of the effects of emotional context on cognitive control (Hart et al., 2010), however, neutral compared to aversive images presented prior to a number Stroop task were associated with increased activity on congruent trials (i.e., when cognitive control demands were low), consistent with our findings for prosaccade trials. As we will discuss below, the unexpected pattern of emotion-based differences in activation may be driven by an interaction with the cognitive control mechanisms engaged by our saccade task, especially by the high relative frequency of antisaccades.

Critically, in addition to this main effect of emotion, the BOLD signal interaction effects indicated that the emotional faces differentially impacted trial timing and saccade type conditions. Specifically, in the right middle occipital gyrus, neutral face trials had a larger overlap – gap activation difference than angry face trials, and, in the left superior occipital gyrus, prosaccade overlap trials exhibited a larger neutral – angry activation difference than antisaccade or gap trials (which showed minimal differences). Speculatively, the fact that antisaccade-related activity did not vary much as a function of the emotion and gap

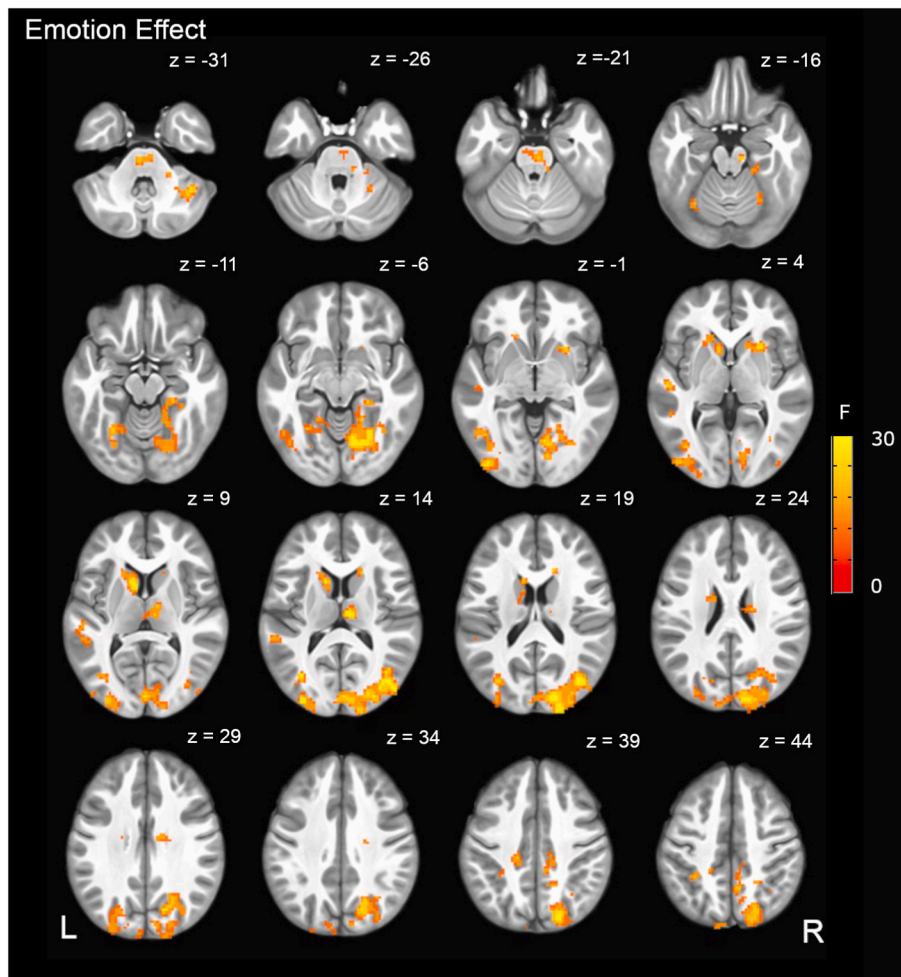


Fig. 3. Main effect of emotion (neutral > angry) overlaid on an anatomical image. No regions showed the opposite pattern.

manipulations may be because the high proportion of antisaccade trials required strong cognitive control throughout the task and favored the activation of inhibitory mechanisms to support efficient antisaccade generation (Pierce and McDowell, 2016). This may also explain the lack of activation differences in frontoparietal control regions during angry face trials, that might be expected if the participants processed the angry faces as a threat that elicited increased stimulus-oriented attention and disrupted antisaccade behavior (Cornwell et al., 2012), which they evidently did not in our task. Instead, the frequent antisaccade trials in the task produced heightened inhibition, which led to minimal processing of the face regardless of its emotion during antisaccade trials.

In contrast, the largest effects of emotion on brain activity occurred during prosaccade trials, with the neutral face trials appearing to recruit more visual processing than the angry face trials. This difference may have arisen due to the inherent bias towards visual stimuli in the prosaccade task (preparing to look at a target) and the non-threatening nature of the neutral face permitting more attention to the face. In contrast, the negative (angry) face perhaps encouraged inhibition (that was already present due to the frequent antisaccade trials) to avoid processing the threatening stimulus (Gupta and Singh, 2021; Marsh et al., 2005; Tipples, 2019). On overlap trials, this effect may have been amplified due to the longer presentation of the emotional face, allowing for further visual processing or requiring increased inhibition. The lower frequency of prosaccades in the task likely resulted in increased control over this normally reflex-like, dominant response. Yet, as indicated by the greater frontal parietal activation for antisaccade trials, prosaccades still elicited weaker cognitive control overall, allowing the

emotion-based differences to emerge in visual regions. Overall, these findings support previous work showing a stronger effect of contextual manipulation on typically low cognitive control prosaccades and demonstrate that the increased inhibition fostered by frequent antisaccade trials can limit behavioral effects from inherently salient, but task-irrelevant, faces.

The emotion effects identified in the current study must be interpreted with respect to certain limitations. First, only neutral or angry expressions were presented and one or the other was presented on every trial (i.e., there was not a condition in which the face was absent entirely). Different negative emotions such as fear or disgust or a positive emotional expression may have led to different emotion-related effects on task performance, perhaps due to differing effects on attention (Davis et al., 2011) or approach/avoidance responses (Marsh et al., 2005). Further, a no-face condition could have provided a baseline for saccade performance without any distractor. Additionally, there were other task design factors that were not considered in our analyses that may also impact performance, such as the length of the ITI and whether a trial required switching saccade task sets (cf. Cornwell et al., 2012; Mueller et al., 2009; Pierce et al., 2015; Pierce and McDowell, 2016). Future work is needed to directly test the impact of these and other design elements on differences in behavior and neural responses.

Finally, the high ratio of antisaccade (66%) to prosaccade (33%) trials means that the individual responses were averaged from a different number of trials for each saccade type. This difference is somewhat mitigated by the higher error rate for antisaccades which resulted in more excluded trials since the analyses were performed only

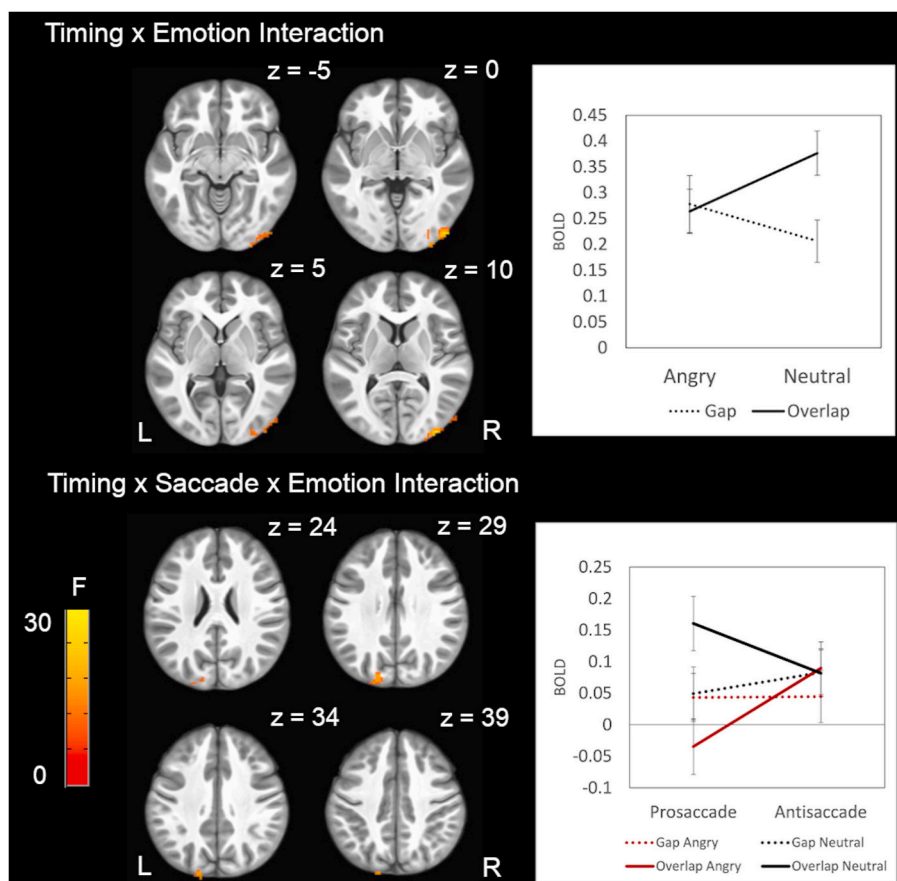


Fig. 4. Interaction effects of trial timing by emotion and trial timing by saccade type by emotion with corresponding BOLD signal graphs. Error bars display ± 1 SE.

on correct trials. Importantly, however, this manipulation of saccade trial type ratio also has been implemented in previous studies with comparable trial numbers (Pierce and McDowell, 2016; Talanow et al., 2016). The high frequency of antisaccades also impacts how cognitive control is implemented in the task, and future work could explore the generalizability of how emotional faces affect performance and BOLD activation in mixed tasks with different saccade frequencies or in separate saccade task blocks.

4.1. Conclusion

When cognitive control demands limit the amount of top-down attentional resources available, bottom-up processing of task-irrelevant stimuli is reduced, even for inherently salient emotional faces. In the current study using a high proportion of antisaccade trials, increased cognitive control demands resulted in greater behavioral costs and BOLD activation for antisaccade than prosaccade trials, but no differences between angry and neutral face antisaccade trials. Conversely, generally lower task demands for prosaccade trials resulted in faster responses and fewer errors than antisaccade trials, coupled with greater BOLD differences between neutral and angry faces, especially for trials when faces were presented for longer durations (i.e., in the overlap condition). With the current task design, high cognitive control and a tonic inhibitory state may have been favored due to the frequent antisaccades and use of negative emotion faces, where neutral prosaccade trials uniquely led to a disinhibition effect with greater visual processing of the non-threatening neutral face. Future work exploring these effects as a function of different emotional expressions and task parameters will be needed to disambiguate these findings. Broadly, the current findings highlight the interplay between cognition, emotion, and action and demonstrate how challenging concurrent task goals can minimize the

behavioral effects of emotional distractors.

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Authors' contributions

Study conception/design was performed and funding was acquired by M.N. and M.D.D. Data collection and preliminary analyses were performed by E.C. and N.M.P. Final data analysis was performed by J.E.P. The first draft of the manuscript was written by E.C. and J.E.P., and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

Data will be made available on request.

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