



Voluntary modulation of mental effort affects the attentional shift induced by angry faces in women

Daniela Ballotta^{a,*}, Riccardo Maramotti^{a,b,c}, Eleonora Borelli^{a,d}, Fausta Lui^a, Giuseppe Pagnoni^a

^a Department of Biomedical, Metabolic and Neural Sciences, University of Modena and Reggio Emilia, Modena 41125, Italy

^b Department of Physics, Informatics and Mathematics, University of Modena and Reggio Emilia, Modena 41125, Italy

^c Department of Mathematics and Computer Sciences, University of Ferrara, Ferrara 44121, Italy

^d Department of Medical and Surgical, Maternal-Infantile and Adult Sciences, University of Modena and Reggio Emilia, Modena 41125, Italy

ARTICLE INFO

Keywords:

Mental effort
Emotion
Facial expression
Spatial attention

ABSTRACT

Facial expressions are biologically and socially relevant stimuli processed in an automatic way. The degree of attentional capture by emotional stimuli varies depending on contextual factors. We used fMRI to investigate whether voluntary modulation of invested effort in a target detection task can offset the automatic attentional shift induced by task-irrelevant angry and happy faces in a female-only sample. Participants had to respond to a target stimulus appearing perceptually closer either to the observer, or to the face stimulus. Crucially, they performed the task “with maximum exertion” (EXR) or “as relaxed as possible” (RLX). We found faster reaction times in the EXR condition, and a significant interaction effect between valence and target position in the RLX condition, suggesting that the engagement of maximum exertion was able to counteract the spatial attentional shifts induced by angry faces. fMRI data showed that brain regions involved in attentional, face, and salience processing were functionally modulated by the interaction of valence and target position. Notably, the fusiform face area was influenced not only by valence and target position, but also by mental effort, suggesting that the deployment of voluntary effort may modulate the activity induced by aversive facial expressions in this region.

1. Introduction

The ability to rapidly detect and recognize emotional stimuli in the environment is crucial for generating adaptive behavioral responses, particularly in the case of negative emotions such as anger and fear, which may signal potential threats (Horstmann and Bauland, 2006). Selective attention reflects this prioritization, treating emotional stimuli as especially relevant objects in our surroundings (Compton, 2003). The interplay between emotion and attention has been widely investigated, with numerous studies showing that the allocation of spatial attention depends on stimulus valence and threat content (Schindler and Bublatzky, 2020). For example, a recent study demonstrated that looming fearful faces appearing in peripersonal space elicited a shift of attention toward the periphery when the face was presented closer to the body (Ellena et al., 2020). Similarly, in work from our group, task-irrelevant angry facial expressions induced a late attentional shift (350 ms after face presentation) away from the face stimulus and toward the observer, a pattern directionally congruent with an aversive

behavioral response (Ballotta et al., 2025). These attentional effects are consistent with behavioral evidence of avoidance (Schmidt et al., 2012; Marsh et al., 2005) or freezing responses (Roelofs et al., 2010) during the detection of angry faces, and with studies showing gaze aversion from angry expressions in both unmasked (Becker and Detweiler-Bedell, 2009; Hunnius et al., 2011) and masked (Vetter et al., 2019) conditions.

It has been proposed that the processing of task-irrelevant or masked threatening facial expressions depends on the availability of attentional resources (Pessoa and Ungerleider, 2004), which are inherently limited (Kahneman, 1973). When these resources may be depleted by a task with high perceptual load, the detection of irrelevant stimuli is reduced or prevented (Lavie et al., 2014). Consistent with this hypothesis, several fMRI studies have shown that task-irrelevant emotional stimuli are processed under low, but not high, perceptual-load conditions. This is evidenced by significant amygdala activation in response to unattended fearful expressions during low versus high perceptual-load conditions (Bishop et al., 2007; Lim et al., 2008; Mitchell et al., 2007; Pessoa et al., 2002, 2005; Silvert et al., 2007). The importance of attentional resource

* Corresponding author at: Via Giardini 1355, 41126, Modena, Italy.

E-mail address: daniela.ballotta@unimore.it (D. Ballotta).

<https://doi.org/10.1016/j.neuroimage.2026.121848>

Received 28 November 2025; Received in revised form 25 February 2026; Accepted 9 March 2026

Available online 10 March 2026

1053-8119/© 2026 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

availability is further supported by a recent event-related potential (ERP) study showing that unconscious detection of fearful faces elicited an ERP fronto-central component (250–700 ms post-stimulus) during a low-, but not during a high-load letter discrimination task (Wang et al., 2016). Thus, according to the perceptual load theory (Lavie et al., 2014), the processing of task-irrelevant threatening faces is therefore constrained by the availability of attentional resources and may be compromised or significantly reduced under high perceptual load.

The studies cited above investigated the effect of high and low perceptual loads — manipulated by altering intrinsic task features — on implicit or unconscious emotion processing. However, humans also appear capable of voluntarily modulating the amount of cognitive resources allocated to a given task (Khachouf et al., 2017). In the present study, we investigated whether the voluntary exertion of high mental effort can attenuate the attentional aversion induced by task-irrelevant angry facial expressions during a low-perceptual-load task, an effect we have previously reported (Ballotta et al., 2025). Specifically, we tested the hypothesis that increased engagement of mental effort — and therefore of attentional resources — in detecting a non-emotional target, reduces the resources available for processing of task-irrelevant threatening faces. If this hypothesis is correct, then when participants perform the task with maximum effort, we would observe a reduction in the spatial attentional shift away from angry faces (as assessed by its effect on reaction times). Conversely, a stronger aversion-driven attentional shift would be expected when the same task is performed under a relaxed attitude, since more cognitive resources would remain available for processing the (task-irrelevant) emotional faces.

Several neural mechanisms are known to enhance the processing of emotional — especially negative — environmental stimuli (Underwood et al., 2021). Bottom-up projections from the amygdala to sensory cortical regions play a critical role in strengthening the sensory-perceptual representations of emotionally salient stimuli (Ballotta et al., 2023; Furl et al., 2013). In parallel, executive prefrontal regions (Underwood et al., 2021) together with ventral and dorsal attentional networks (Viviani, 2013) provide top-down control, selecting emotionally relevant stimuli and guiding adaptive responses while maintaining the locus of attention according to prior information or goals (Corbetta and Shulman, 2002). Voluntary mental effort is associated with widespread increases of activity across attentional, sensory, and executive regions, as well as in the brainstem reticular activating system (Khachouf et al., 2017; Shenhav et al., 2017). Thus, a close interplay between attentional and face-processing regions is expected to support the modulatory effect of voluntary effort on spatial attention shifts induced by threatening facial expressions.

2. Materials and methods

2.1. Participants

Twenty-eight right-handed female volunteers (mean age = 21.4 ± 2.2 years; range: 20–28 years) participated in the fMRI study. Only female participants were recruited, in line with previous evidence of sex differences in emotional processing (McClure, 2000; Olderbak et al., 2018) and emotional responsiveness to negative stimuli (e.g., Fischer et al., 2018), which have been associated with differences in emotion regulation and functional connectivity (Stoica et al., 2021). Exclusion criteria included standard contraindications for MRI, a history of psychiatric or neurological disorders, and current use of psychoactive medications. The study was conducted in accordance with the 2013 Declaration of Helsinki and approved by the local Ethics Committee (protocol number: CE 134/2014/SPER/AOUMO). Written informed consent was obtained from all participants.

2.2. Stimuli

Black-and-white photographs depicting facial expressions of

happiness ($n = 36$, positive stimuli) and anger ($n = 36$, negative stimuli) were used, with 18 expressions per condition performed by female models and 18 by male models (Radke et al., 2017). Hair and non-facial contours were removed, and all images were balanced for brightness, contrast, and arousal ratings across categories. Scrambled versions of the face images served as control stimuli, matched for contrast and luminance but lacking recognizable facial features and emotional content.

2.3. Procedures

An fMRI block design was employed, with the task adapted from a previous study by our group (for details, see Ballotta et al., 2025). Briefly, participants were instructed to respond as quickly as possible to a target stimulus (a small red sphere) appearing 350 ms after the presentation of a face stimulus, for a duration of 100 ms. Crucially, participants were asked to perform the task either “with maximum exertion” (EXR) or “as relaxed as possible” (RLX) in alternating blocks (Khachouf et al., 2017). The target appeared perceptually closer to the face stimulus than to the observer (stimulus-close, SC) in half of the trials (excluding foils, see below) and closer to the observer than to the face stimulus (observer-close, OC) in the other half. Participants were instructed to maintain gaze on the face stimulus throughout (Fig. 1). Responses were made with the right index finger on an MRI-compatible response pad. Each participant completed 4 sessions of 8 blocks each (14 trials per block), for a total of 32 blocks (448 trials: 192 with positive facial expressions, 192 with negative facial expressions, 64 with scrambled stimuli). A small number of foil trials were included, in which either faces (32 positive, 32 negative) or scrambled stimuli (16) were presented without a subsequent target, requiring participants to withhold their response. This manipulation aimed to minimize anticipatory responses to the face stimulus instead of to the target. Each trial lasted 2 s, with an inter-trial interval of 1.4 s. Blocks lasted 50 s, separated by 8 s intervals. Faces were presented on the back wall of a virtual corridor rendered in 3D perspective (Fig. 1, top). Two passive rest periods were included at the beginning and end of each session (12.6 s and 14.6 s, respectively). Stimulus presentation and response collection were managed with E-Prime 3.0 software (Psychology Software Tools, Pittsburgh, PA) connected to fMRI-compatible LCD goggles (<https://www.nordicneurolab.com>) and button-box. From the virtual point of view generated by the 3D-like presentation corresponding to the mid-point of the inferior border of the light blue transparent plane of Fig. 1, red-sphere targets closer to the face (SC condition, 61 pixels wide)

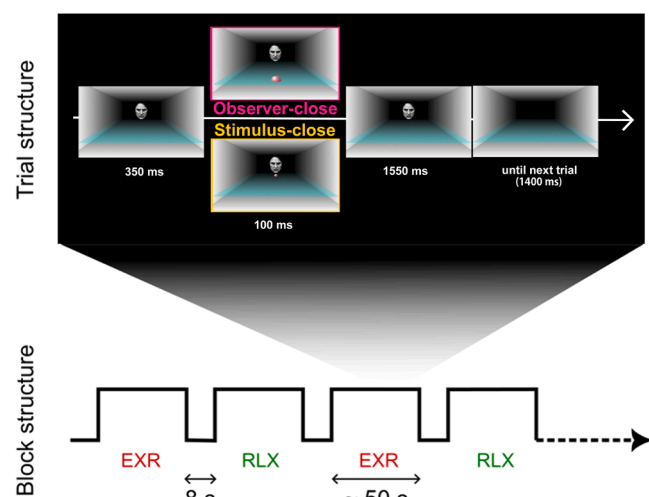


Fig. 1. Block and trial structure of the stimulus presentation sequence. There were 8 blocks per each of the 4 functional sessions. Each block was composed by 14 trials. EXR=exert (maximum effort), RLX=relax (minimum effort).

subtended a visual angle of 10.5° , while targets closer to the observer (OC condition, 167 pixels wide) subtended a visual angle of 72°

At the end of each run, participants evaluated task workload with the NASA-TLX rating instrument (Hart and Staveland, 1988). They verbally rated three dimensions on a 0–10 scale: Performance (“How successful were you in performing the task correctly?”), Effort (“How hard did you have to work to perform the task?”), and Frustration Level (“How insecure, discouraged, irritated, stressed, or annoyed did the task make you feel?”). After scanning, participants rated whether they felt directionally — rather than emotionally — attracted to or repelled by the same positive and negative facial stimuli used in the fMRI experiment. Ratings were provided on a 7-point scale, referred to from here on as ‘Subjective Attraction-Retraction’ (SAR) score. Values from +1 to +3 indicated feeling drawn to the face, values from –1 to –3 indicated feeling repelled, and 0 indicated no directional tendency. Stimuli were presented in randomized order on a laptop using the same 3D corridor layout as during scanning. A 7-step staircase was displayed on the corridor floor, with a stylized human figure at the midpoint, to help participants anchor their judgments. Finally, all faces were also rated for emotional valence on a 7-point scale, with positive values denoting positive valence.

2.4. Behavioral data analysis

Response times (RTs) were recorded for each participant under eight conditions of interest, defined by the combination of effort (EXR vs. RLX blocks), valence (positive vs. negative face stimuli), and target location (OC vs. SC). Error trials, foil trials, and responses occurring within 150 ms of target onset (indicative of anticipatory responses) were excluded. Participants were excluded if their false alarm rates (i.e., key presses during foil trials following face onset) exceeded 10 %, set a priori as an exclusion threshold; no participant met this criterion (see Results).

RT data are known to follow a non-normal, positively skewed distribution, and commonly used parametric statistical tests based on the assumption of normality are generally not appropriate. To overcome this limitation, we modelled RT using a shifted log-normal distribution ($L \sim \text{LogNormal}(\mu, \sigma^2) + c$; Ranger et al., 2020; Rouder, 2005). This approach accommodates the characteristic right-skew of RT data, while explicitly separating different components of response behavior. In our model, the scale parameter (σ , representing the variability of responses) and the shift parameter (c , representing the minimum possible RT) were held constant across conditions, whereas the median RT (μ) was estimated separately for each condition. Coding the predictors as binary variables:

- $s \rightarrow 0$ for negative valence, 1 for positive valence
- $t \rightarrow 0$ for stimulus-close (SC), 1 for observer-close (OC)
- $v \rightarrow 0$ for EXR, 1 for RLX

the condition-specific median RT (in ms) can be expressed as $\mu = c + \exp(b_0 + b_1s + b_2t + b_3v + b_4st + b_5sv + b_6tv + b_7stv)$. In this parameterization, b_0 denotes the expected log-median RT in the reference condition ($s = 0, t = 0, v = 0$; negative valence, SC, EXR). Coefficients b_1 – b_3 index the main effects of valence, target, and effort, i.e., the change in log-median RT associated with a 0→1 shift in each predictor, holding the others constant. Coefficients b_4 – b_6 capture the corresponding two-way interactions, and b_7 the three-way interaction. Parameter estimates for b_0, \dots, b_7 , as well as for σ and c , were obtained in a Bayesian hierarchical model, with random effects at the participant level. Predicted values were then used to calculate RT effects for each combination of factor levels. All analyses were performed in R (R Core Team, 2021) using the brms package (Bürkner, 2017). Five Monte Carlo Markov chains (MCMC) were conducted, each with 3000 burn-in iterations and 5000 sampling iterations.

Then, the hypothesis() function was used to assess credible intervals for each contrast of interest based on the parameter estimates. These contrasts were derived as linear combinations of the Bayesian model’s

posterior parameter estimates:

- $\text{RLX} - \text{EXR}$, which corresponds to $0.25 \cdot (4b_3 + 2b_5 + 2b_6 + b_7)$;
- $(\text{pos} - \text{neg})|_{\text{OC}}$, separately for EXR and RLX. This contrast corresponds to $b_1 + b_4$ in the EXR condition, and $b_1 + b_4 + b_5 + b_7$ in the RLX condition;
- $(\text{OC} - \text{SC})|_{\text{pos}} - (\text{OC} - \text{SC})|_{\text{neg}}$, separately for EXR and RLX. This contrast corresponds to b_4 in the EXR condition, and $b_4 + b_7$ in the RLX condition;
- $(\text{OC} - \text{SC})|_{\text{RLX}} - (\text{OC} - \text{SC})|_{\text{EXR}}$, separately for positive and negative valence. This contrast corresponds to b_6 in the negative condition, and $b_6 + b_7$ in the positive condition;

2.5. Analysis of subjective ratings

To verify the adequacy of the stimulus set, within-subject averages of reported valence and SAR scores for negative and positive faces were computed and compared across participants using a paired-sample t -tests. Mean NASA-TLX scores for Performance, Effort, and Frustration level were calculated for each participant under EXR and RLX conditions. Comparisons between these two conditions were then performed using Wilcoxon signed-rank test, based on the distributional characteristics of the data.

2.6. fMRI data acquisition and preprocessing

fMRI data were acquired on a GE SIGNA Architect 3.0 Tesla MRI scanner. For each participant, data included four functional runs of a gradient-echo echo-planar imaging (EPI) sequence sensitive to blood-oxygen-level-dependent (BOLD) contrast (46 axial slices, thickness = 2.7 mm, gap = 0.3 mm, TR = 1500 ms, in-plane resolution = 3×3 mm), as well as a high-resolution T1-weighted anatomical image (344 sagittal slices, TR = 2184.9 ms, TE = 3.09 ms, voxel size = $1 \times 1 \times 1$ mm). Preprocessing and analysis were performed with AFNI (Cox, 1996; Cox and Hyde, 1997). Preprocessing steps included slice-timing correction, motion correction, spatial normalization to the Montreal Neurological Institute (MNI) template space, Gaussian spatial blurring (6 mm FWHM), and scaling of BOLD signal values to percent signal change.

2.7. fMRI analysis

The effects of interest on BOLD activity were assessed with a subject-level multiple-regression model. Event-related regressors were defined for each block type (EXR and RLX) and included: positive SC, positive OC, negative SC, negative OC, scrambled SC, scrambled OC, positive foil, negative foil, and scrambled foil trials.

Each event was modelled as a 2 s boxcar function, beginning at face stimulus onset, convolved with a gamma function to approximate the hemodynamic response. Confounding covariates included the six motion parameters from motion correction, a 4th-order Legendre polynomial to model slow drifts, the first three principal components of the signal from the lateral ventricle, and a voxelwise regressor of local white-matter signal (Jo et al., 2010, 2013). Models were estimated with 3dREMLfit (AFNI), which implements generalized least squares with voxelwise estimation of temporal autocorrelation. To identify neural correlates of mental effort and spatial attention during emotional face processing, we examined:

- the main effect of mental effort (EXR – RLX);
- the interaction of target location and valence, $(\text{OC} - \text{SC})|_{\text{pos}} - (\text{OC} - \text{SC})|_{\text{neg}}$, pooled across effort conditions.

Group-level analyses were performed with 3dMEMA (AFNI; Chen et al., 2012), a mixed-effect meta-analysis approach that accounts for both within- and between-subject variability. Group maps were thresholded at a combined voxelwise p -value < 0.0001 and cluster size k

> 20 voxels, yielding a conservative family-wise error rate of $\alpha < 0.01$ (Cox et al., 2017a, 2017b), as determined by Monte Carlo simulation of the null cluster distribution with 3dClustSim. This thresholding strategy was intentionally conservative and was chosen to favor spatial specificity, avoiding the formation of overly large clusters that could obscure fine-grained anatomical distinctions and reduce the interpretability of subsequent region-of-interest (ROI) analyses. For the 11 cortical clusters identified in the interaction map, the mean estimated BOLD response (beta coefficients, expressed as percent signal change) was extracted across the eight experimental conditions. Analogously to the reaction times analysis, a Bayesian model was then implemented, this time assuming a Gaussian likelihood for the beta parameters rather than a shifted log-normal distribution. To test whether activity in attention-related regions during emotional face processing was modulated by mental effort, the hypothesis() function of R was used to assess credible intervals for the following contrasts:

- EXR – RLX;
- valence \times target location \times effort;
- $(OC - SC)|_{EXR} - (OC - SC)|_{RLX}$, separately for positive and for negative valence.

3. Results

3.1. Behavioral data

Participants performed the task with high accuracy ($M = 97.5\%$, $SD = 2.4\%$). The mean false-alarm rate (responses to foil trials) was 1.6% ($SD = 2.0\%$), with a maximum of 8.7% , confirming that participants complied with instructions and did not respond in anticipation of the target. Convergence of the MCMC routine was verified using diagnostic tools and visual assessment. For all parameters, the potential scale reduction factor remained below 1.01, indicating satisfactory convergence. Posterior predictive checks further demonstrated good model fit (see Supplementary Figure S1). Parameter estimates for the shifted log-normal distribution are summarized in Supplementary Table S1. The expected values of average reaction times for the eight experimental conditions are reported here in Table 1.

Effect sizes (e.s.) and relative credible intervals (c.i.) reported below refer to the contrasts of parameter estimates and are dimensionless. A main effect of mental effort was observed (e.s. 0.242, 95 % c.i. [0.164, 0.320]), with significantly faster RTs in the EXR condition (expected mean = 231.29 ms) compared to the RLX condition (expected mean = 266.47 ms). The difference in RTs between positive and negative stimuli in the OC condition was significant in the RLX condition (e.s. 0.048, 95 % c.i. [0.017, 0.076]) and weaker but still credible in the EXR condition (e.s. 0.034, 95 % c.i. [0.003, 0.064]). A significant valence \times target position interaction was found in the RLX condition (e.s. 0.075, 95 % c.i. [0.033, 0.118]), but not in the EXR condition (e.s. 0.034, 95 % c.i. [-0.007, 0.077]).

Table 1

Expected mean values and standard errors for reaction time across all different combinations of valence, position, and effort.

valence	target location	effort	expected mean RT	standard error
neg	SC	EXR	231.99 ms	6.52 ms
neg	OC	EXR	223.18 ms	6.09 ms
pos	SC	EXR	232.15 ms	6.56 ms
pos	OC	EXR	226.94 ms	6.31 ms
neg	SC	RLX	267.67 ms	9.20 ms
neg	OC	RLX	249.11 ms	8.25 ms
pos	SC	RLX	263.96 ms	9.19 ms
pos	OC	RLX	255.02 ms	8.99 ms

Abbreviations: EXR=exert (maximum effort), RLX=relax (minimum effort), OC=observer-close, SC=stimulus-close, pos=positive (happy face), neg=negative (angry face).

An effort \times target position interaction also emerged, but only for negative faces (e.s. -0.047 , 95 % c.i. [-0.089, -0.005]); no such effect was observed for positive faces (e.s. -0.007 , 95 % c.i. [-0.049, 0.036]). Specifically, the difference in RTs between OC and SC trials for negative faces was smaller under EXR (expected mean = 9.1 ms, SEM = 8.2 ms) than under RLX (expected mean = 18.2 ms, SEM = 11.8 ms). By contrast, for positive faces the SC–OC difference was comparable across EXR and RLX conditions. (Fig. 2)

3.2. Subjective ratings

Reported valence and SAR scores differed significantly between positive and negative faces. Average valence scores were higher for positive faces ($M = 2.08$) than for negative faces ($M = -1.68$), $t(27) = -15.10$, $p < 0.001$. Similarly, average SAR scores were higher for positive faces ($M = 1.140$) than for negative faces ($M = -1.23$), $t(27) = 9.52$, $p < 0.001$. These results confirm the validity of the original stimulus classification in terms of emotional valence. Wilcoxon signed-rank tests further indicated that subjective evaluations were significantly higher in EXR compared to RLX blocks for Performance ($M = 8.10$ vs. 7.71, $p = 0.007$), Effort ($M = 7.62$ vs. 5.33 for RLX, $p < 0.001$), and Frustration ($M = 4.52$ vs. 3.18, $p < 0.001$). See also Fig. 3 (right side).

3.3. fMRI results

3.3.1. Mental effort

The main effect of mental effort (EXR – RLX) revealed widespread activation across a bilateral cerebral network, including the inferior frontal gyrus/anterior insula (IFG/AI), premotor and motor cortex, intraparietal sulcus (IPS), thalamus, supplementary motor area (SMA), fusiform face area (FFA), putamen and globus pallidus (Fig. 3, Table 2).

3.3.2. Interaction between target location and valence

The contrast $(OC - SC)|_{pos} - (OC - SC)|_{neg}$ yielded significant clusters of activation in the bilateral FFA, parieto-occipital sulcus, and cerebellum, as well as in the left IPS, left sensorimotor area, and right dorsolateral prefrontal cortex (dlPFC). Increased BOLD signal was also found in medial regions, including the anterior and middle cingulate cortex (ACC, MCC) and the precuneus/superior parietal lobule (Fig. 4, Table 3). A main effect of effort (EXR – RLX) was present in 9 of the 11 clusters identified by this interaction contrast, with higher signal in EXR compared to RLX. These included: left and right FFA (e.s. 0.062, 95 % c.i. [0.031, 0.093]; e.s. 0.054, 95 % c.i. [0.027, 0.081]), left IPS (e.s. 0.053, 95 % c.i. [0.030, 0.075]), left sensorimotor area (e.s. 0.050, 95 % c.i. [0.024, 0.076]), right dlPFC (e.s. 0.038, 95 % c.i. [0.013, 0.063]), ACC (e.s. 0.070, 95 % c.i. [0.037, 0.104]), left and right MCC (e.s. 0.029, 95 % c.i. [0.009, 0.048]; e.s. 0.036, 95 % c.i. [0.009, 0.063]), and the precuneus/superior parietal lobule (e.s. 0.099, 95 % c.i. [0.047, 0.151]).

A three-way interaction (valence \times target location \times effort) emerged in the left and right FFA only (e.s. -0.076 , 95 % c.i. [-0.131, -0.021]; e.s. -0.067 , 95 % c.i. [-0.118, -0.017], respectively). In both clusters, the SC–OC difference was smaller in EXR than in RLX for negative faces (left FFA: e.s. 0.097, 95 % c.i. [0.057, 0.138]; right FFA: e.s. 0.072, 95 % c.i. [0.036, 0.108]), while no such difference was found for positive faces (left FFA: e.s. 0.021, 95 % c.i. [-0.020, 0.063]; right FFA: e.s. 0.005, 95 % c.i. [-0.032, 0.044]).

4. Discussion

The aim of this fMRI study was to test whether the voluntary investment of mental effort in detecting a non-emotional target reduces the availability of attentional resources for processing task-irrelevant threatening faces. If so, one would expect a weakening of the automatic tendency of attention to recoil from emotional stimuli. We also predicted faster responses under maximum effort due to increased arousal and premotor readiness. Our behavioral data supported these

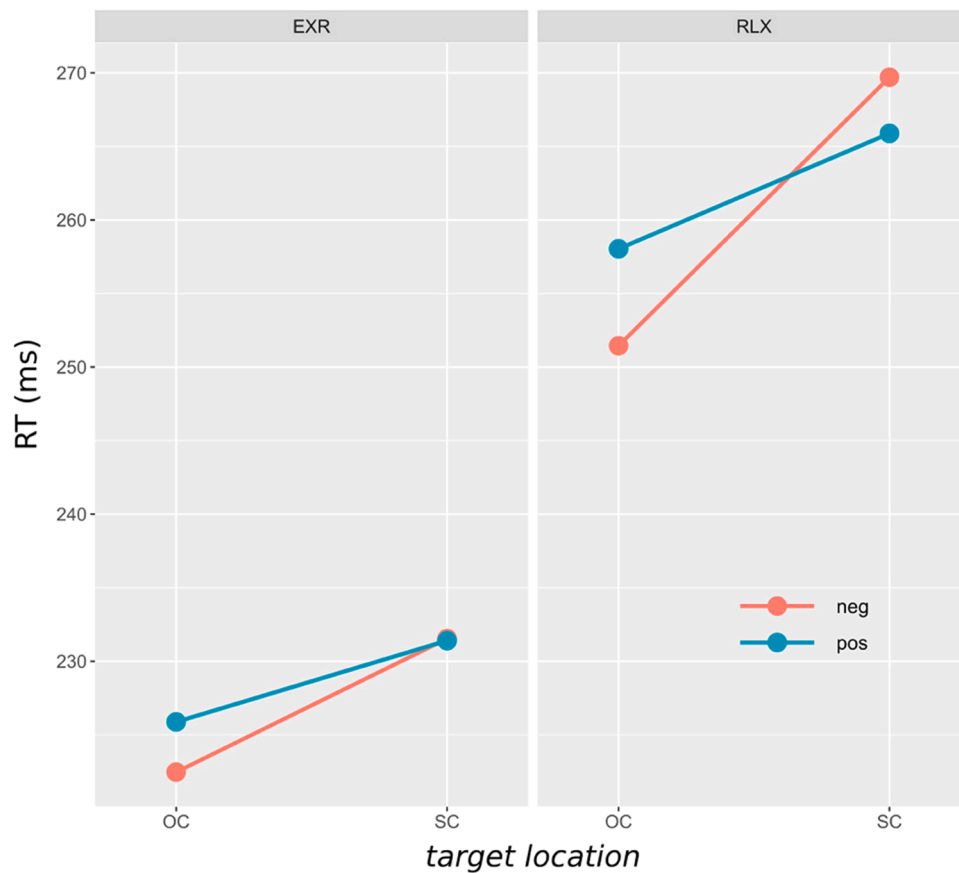


Fig. 2. Interaction plots for the estimated median reaction times. Abbreviations: EXR=exert (maximum effort), RLX=relax (minimum effort), OC=observer-close, SC=stimulus-close, pos=positive (happy face), neg=negative (angry face).

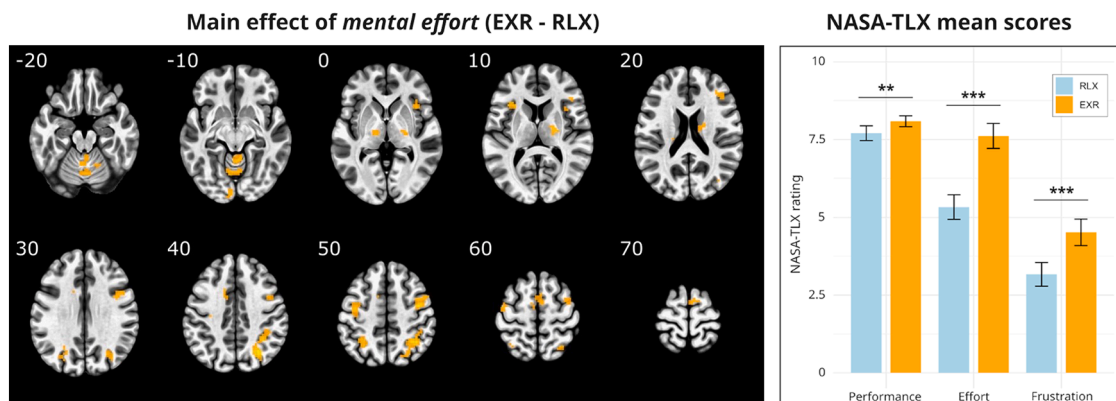


Fig. 3. Left: Brain regions showing a significant main effect of mental effort. The t-maps were corrected $\alpha < 0.01$, and the underlying anatomical image is the MNI template implemented in AFNI. Sections are displayed in neurological convention, with numbers indicating the value of the MNI z-coordinate of the corresponding slice. Right: average scores of NASA-TLX collected at the end of each run.

predictions: (i) smaller reaction time differences between stimulus-close (SC) and observer-close (OC) trials for angry faces when they performed the task “with maximum exertion” (EXR) compared to the “as relaxed as possible” (RLX) block, (ii) an interaction between valence and target position in the RLX condition only, and (iii) overall faster reaction times in EXR relative to RLX blocks.

Previous research has reported attentional (Ballotta et al., in press), behavioral (Marsh et al., 2005; Schmidt et al., 2012), and eye-gaze (Becker and Detweiler-Bedell, 2009; Hunnius et al., 2011; Vetter et al., 2019) avoidance of angry faces. This avoidance response is thought to reflect the direct threat conveyed by anger, associated with

heightened alertness and sensitivity to the peripheral visual field as a potential locus of danger (Davis et al., 2011). Importantly, the processing of task-irrelevant or masked threatening faces has been shown to depend on the availability of attentional resources (Kahneman, 1973; Pessoa and Ungerleider, 2004). In particular, task-irrelevant emotional stimuli are processed under low but not high perceptual load, as evidenced by amygdalar activations in fMRI studies (Bishop et al., 2007; Lim et al., 2008; Mitchell et al., 2007; Pessoa et al., 2002, 2005; Silvert et al., 2007), and by ERP components elicited only under low-load conditions 250–700 ms post-stimulus (Wang et al., 2016).

Consistent with these findings, our participants were overall faster in

Table 2

Significant clusters for the main effect of effort (EXR – RLX). Cluster size (k) is in voxels, and the reported (MNI) coordinates (in mm) refer to each cluster’s statistical peak.

Brain region	k	x	y	z	t-value
R intraparietal sulcus	301	28	-68	44	7.976
L/R cerebellar vermis	185	-8	-65	-11	5.837
L middle cingulate	118	-18	11	47	6.255
R frontal eye fields	107	41	-8	50	6.710
R thalamus	84	20	-11	26	6.799
L primary motor cortex - L frontal eye fields	84	-47	-17	56	5.696
R precentral/inferior frontal gyrus	71	41	5	38	6.578
R anterior insula	49	38	17	2	5.814
L intraparietal sulcus	46	-32	-53	53	6.075
L anterior insula	29	-29	20	14	6.458
L intraparietal sulcus	29	-29	-74	35	5.242
L thalamus	27	-14	-17	5	6.069
R middle frontal gyrus	24	35	35	23	6.766
L primary visual cortex	21	-8	-98	-8	5.933
L thalamus	21	-23	-23	26	5.217

L=left, R=right.

responding to targets following angry compared to happy faces in the OC condition (especially when performing the task in a relaxed manner). The valence × target position interaction observed in RLX but not EXR reflected a reduction of the difference between SC and OC condition for negative faces under maximum effort. These results support the idea that

negative stimuli diffuse attention toward the periphery, but that this effect is attenuated when participants deliberately invest effort in the task, reducing resources available for task-irrelevant emotional processing. A reader may wonder whether the effect of target location is at least partially due to the different size of the red dot in the stimulus-close and observer-close conditions. Although this may very well be true, we

Table 3

Significant clusters for the valence × target location contrast. Cluster size (k) is in voxels, and the reported (MNI) coordinates (in mm) refer to each cluster’s statistical peak.

Brain region	k	x	y	z	t-value
L fusiform face area	1093	-46	-70	-19	8.836
R fusiform face area	1077	1	-85	-10	9.023
L sensori-motor area	548	-46	-16	64	8.000
L/R anterior cingulate cortex	158	-1	4	43	6.905
L/R precuneus - superior parietal lobule	96	-1	-61	67	6.829
R parieto-occipital sulcus	73	10	-82	49	6.096
L parieto-occipital sulcus	71	-4	-79	40	6.235
L intraparietal sulcus	36	-22	-67	46	5.557
L cerebellum (lobule 7a)	34	-7	-82	-43	5.678
R cerebellum (lobule 8a)	31	31	-58	-52	6.076
L cerebellum (lobule 6)	25	-7	-76	-16	6.332
R middle cingulate cortex	25	13	-37	46	6.501
L middle cingulate cortex	24	-13	-31	43	5.648
L cerebellum (lobule 7b)	22	-37	-67	-55	6.613
R dorso-lateral prefrontal cortex	22	31	46	25	5.712

L=left, R=right.

Interaction of valence and target location

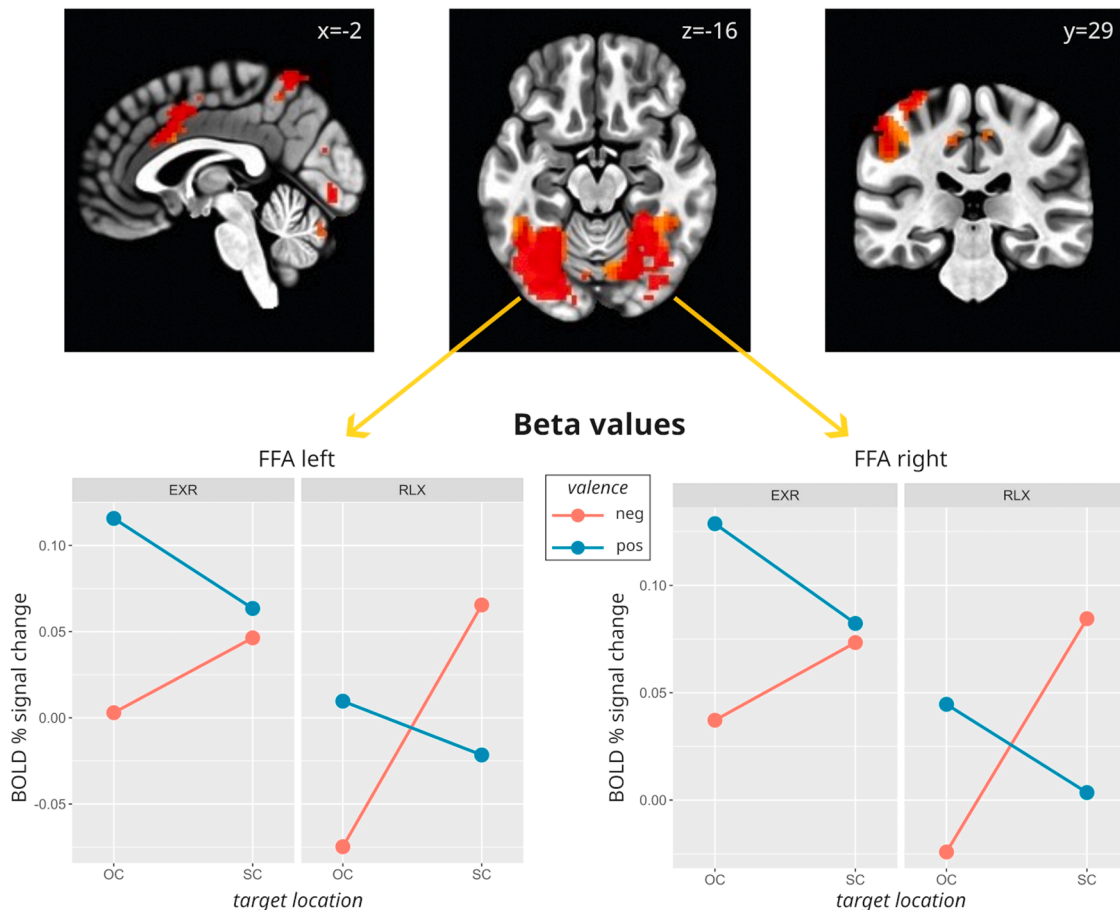


Fig. 4. Top: significant brain activation clusters for the valence × target location effect. Bottom: graphical display of the interaction of the BOLD percent signal change in left and right FFA (fusiform face area).

note that our experiment was planned to test hypotheses about the interaction effect between the target location and the face valence manipulations, and how this interaction effect changes with the intentional application of maximum effort (compared to a relaxed execution of the task). In these contrasts, the potential confound of target size is controlled for, as it is present in both the stimulus-close and the observer-close conditions.

Mental effort has classically been conceptualized as the allocation of limited attentional resources, determined by task difficulty and reward magnitude (Kahneman, 1973; Sarter et al., 2006). These models, however, did not treat effort as something that could itself be modulated voluntarily — despite this notion being central to everyday experience. Our previous work showed that explicitly asking individuals to vary their invested effort yields measurable behavioral differences (Khachouf et al., 2017). The present findings confirm this by showing faster reaction times under EXR relative to RLX.

At the neural level, the intentional engagement of mental effort has been associated with the dorso-medial frontal cortex, ACC, and MCC (Engström et al., 2014; Khachouf et al., 2017; Paus et al., 1998). We previously hypothesized that voluntary effort entails increased neural readiness in fronto-parietal attentional and premotor circuits (Khachouf et al., 2017). The current data confirm this, showing higher recruitment of attentional (IPS), salience (IFG/AI), and premotor regions under EXR compared to RLX.

We also observed a valence \times target position interaction in brain activity, consistent with emotion-related shifts of spatial attention. This effect engaged regions of the dorsal (IPS) and ventral (ACC) attention networks (Corbetta and Shulman, 2002), the executive-control network (Seeley et al., 2007), and the FFA. Notably, a three-way interaction (valence \times target position \times effort) emerged in the FFA only. The observed pattern fits with current models of emotional processing: negative stimuli are prioritized via both bottom-up inputs from the amygdala (Ballotta et al., 2023; Furl et al., 2013) and top-down regulation from prefrontal and attentional networks (Underwood et al., 2021; Viviani, 2013). Suppression of irrelevant emotional information by ACC and dlPFC (Clarke et al., 2014; Ochsner and Gross, 2005) likely supports goal-directed responses (Corbetta and Shulman, 2002). The ACC in particular is implicated in effortful control of threat processing (Pessoa, 2009), with stronger responses linked to impaired performance when distracting threat is present (Lim et al., 2008). Our finding of ACC and dlPFC activation suggests that executive control was recruited to inhibit interference from angry faces, facilitating target detection.

The IPS, part of the dorsal attention network, mediates goal-directed spatial processes (Corbetta and Shulman, 2002) and is modulated by the salience of emotional cues (Armony and Dolan, 2002; Pourtois et al., 2006). Pourtois et al. (2006) showed that IPS activity indexes disengagement costs from threat cues, with stronger activation reflecting greater cost. In our paradigm, OC targets were “spatially incongruent” with the emotional face, while SC targets were congruent. IPS was more active for differences between SC and OC following positive versus negative faces, suggesting a higher disengagement cost for positive stimuli. This supports the view that attention was already disengaged from angry faces — or retracted toward the observer — consistent with our previous behavioral findings (Ballotta et al., in press) replicated here.

The fusiform gyrus, a core region of the face-processing network (Haxby et al., 2002; Kanwisher and Yovel, 2006; Puce et al., 1996), shows greater activity for emotional (particularly negative) faces compared to neutral ones (Vuilleumier et al., 2001), dependent on amygdala input (Morris et al., 1998; Vuilleumier et al., 2004). Our recent work demonstrated that angry faces preferentially enhance FFA activity while happy faces enhance amygdala activity (Ballotta et al., 2023). Here, FFA activation was greater for SC versus OC targets following angry faces, but only in RLX (low-effort) blocks. Under EXR, this difference between SC and OC was reduced, paralleling the reaction time data and suggesting top-down modulation of FFA by attentional

(IPS, ACC) and executive (dlPFC) regions.

In conclusion, our study demonstrates that emotional content modulates spatial attention and that this effect depends critically on the availability of attentional resources, here manipulated via voluntary effort. These findings highlight the close interplay between attentional, executive, and face-processing networks as the neural substrate for the modulation of emotional biases by voluntary mental effort.

5. Limitations and future directions

We acknowledge a number of limitations that should be addressed in further experimental work. First, a limitation of the present study is that the sample included female participants only. This choice was motivated by well-documented sex differences in emotion recognition, emotional reactivity, and regulation, but it limits the generalizability of the findings. Future studies should examine whether sex or gender modulates the interaction between voluntary mental effort and emotion-driven attentional biases. Second, the assessment of effort engagement relied on subjective reports only; future studies should incorporate objective physiological or behavioral markers of effort (e.g., pupillometry or cardiovascular measures). Third, while the modulation of FFA activity is consistent with a top-down influence of attentional control, this interpretation remains indirect; future studies assessing the effective connectivity between FFA and prefrontal region with an optimized experimental design (e.g., with Dynamical Causal Modeling; Friston et al., 2003) will be needed to address this issue. Finally, although our sample size was relatively small, it was within the range typical for studies of this kind; nevertheless, replication using similar paradigms would further strengthen confidence in the findings.

Funding

Funding for this study was awarded by the Ministero dell’Istruzione, dell’Università e della Ricerca (Project title: “The Good and the Bad of Sensory Experience: Understanding the Impact of Emotionally Charged Stimuli on Cognition and Behavior, and the Brain’s Mechanisms to Cope with Them”, Grant number: CUP E94I19000630005).

Data availability

The datasets and code used in this study are not publicly available due to institutional and ethical restrictions, but can be obtained from the corresponding author upon reasonable request.

CRediT authorship contribution statement

Daniela Ballotta: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Riccardo Maramotti:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Eleonora Borelli:** Writing – review & editing, Visualization, Methodology, Investigation, Data curation, Conceptualization. **Fausta Lui:** Writing – review & editing, Visualization, Supervision, Methodology, Funding acquisition, Data curation, Conceptualization. **Giuseppe Pagnoni:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2026.121848](https://doi.org/10.1016/j.neuroimage.2026.121848).

References

- Armony, J.L., Dolan, R.J., 2002. Modulation of spatial attention by fear-conditioned stimuli: an event-related fMRI study. *Neuropsychologia* 40 (7), 817–826. [https://doi.org/10.1016/S0028-3932\(01\)00178-6](https://doi.org/10.1016/S0028-3932(01)00178-6).
- Ballotta, D., Maramotti, R., Borelli, E., Lui, F., Pagnoni, G., 2023. Neural correlates of emotional valence for faces and words. *Front. Psychol.* 14, 1055054. <https://doi.org/10.3389/fpsyg.2023.1055054>.
- Ballotta, D., Maramotti, R., Borelli, E., Lui, F., Pagnoni, G., 2025. Angry facial expressions elicit a late attentional withdrawal. *Sci. Rep.* 15, 41632. <https://doi.org/10.1038/s41598-025-25609-w>.
- Becker, M.W., Detweiler-Bedell, B., 2009. Early detection and avoidance of threatening faces during passive viewing. *Q. J. Exp. Psychol. (Hove)* 62, 1257–1264. <https://doi.org/10.1080/17470210902725753>.
- Bishop, S.J., Jenkins, R., Lawrence, A.D., 2007. Neural processing of fearful faces: effects of anxiety are gated by perceptual capacity limitations. *Cereb. Cortex* 17 (7), 1595–1603. <https://doi.org/10.1093/cercor/bhl070>.
- Bürkner, P.-C., 2017. brms: an r package for bayesian multilevel models using stan. *J. Stat. Softw.* 80, 1–28. <https://doi.org/10.18637/jss.v080.i01>.
- Chen, G., Saad, Z.S., Nath, A.R., Beauchamp, M.S., Cox, R.W., 2012. Fmri group analysis combining effect estimates and their variances. *NeuroImage* 60, 747–765. <https://doi.org/10.1016/j.neuroimage.2011.12.060>.
- Clarke, P.J.F., Browning, M., Hammond, G., Notebaert, L., MacLeod, C., 2014. The causal role of the dorsolateral prefrontal cortex in the modification of attentional bias: evidence from transcranial direct current stimulation. *Biol. Psychiatry* 76 (12), 946–952. <https://doi.org/10.1016/j.biopsych.2014.03.003>.
- Compton, R.J., 2003. The interface between emotion and attention: a review of evidence from psychology and neuroscience. *Behav. Cogn. Neurosci. Rev.* 2, 115–129. <https://doi.org/10.1177/1534582303255278>.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215. <https://doi.org/10.1038/nrn755>.
- Cox, R.W., 1996. Afni: software for analysis and visualization of functional magnetic resonance neuroimages. *Comput. Biomed. Res.* 29, 162–173.
- Cox, R.W., Hyde, J.S., 1997. Software tools for analysis and visualization of fmri data. *NMR Biomed.* 10, 171–178. [10.1002/\(sici\)1099-1492\(199706/08\)10:4/5\(171::aid-nbm453\)3.0.co;2-1](https://doi.org/10.1002/(sici)1099-1492(199706/08)10:4/5(171::aid-nbm453)3.0.co;2-1).
- Cox, R.W., Chen, G., Glen, D.R., Reynolds, R.C., Taylor, P.A., 2017a. fmri clustering and false-positive rates. *Proc. Natl. Acad. Sci. U.S.A.* 114, E3370–E3371. <https://doi.org/10.1073/pnas.1614961114>.
- Cox, R.W., Chen, G., Glen, D.R., Reynolds, R.C., Taylor, P.A., 2017b. Fmri clustering in afni: false-positive rates redux. *Brain Connect* 7, 152–171. <https://doi.org/10.1089/brain.2016.0475>.
- Davis, F.C., Somerville, L.H., Ruberry, E.J., Berry, A.B.L., Shin, L.M., Whalen, P.J., 2011. A tale of two negatives: differential memory modulation by threat-related facial expressions. *Emotion* 11 (3), 647–655. <https://doi.org/10.1037/a0021625>.
- Ellena, G., Starita, F., Haggard, P., Ladavas, E., 2020. The spatial logic of fear. *Cognition* 203, 104336. <https://doi.org/10.1016/j.cognition.2020.104336>.
- Engström, M., Karlsson, T., Landtblom, A.-M., Craig, A.D.B., 2014. Evidence of conjoint activation of the anterior insular and cingulate cortices during effortful tasks. *Front. Hum. Neurosci.* 8, 1071. <https://doi.org/10.3389/fnhum.2014.01071>.
- Fischer, A.H., Kret, M.E., Broekens, J., 2018. Gender differences in emotion perception and self-reported emotional intelligence: a test of the emotion sensitivity hypothesis. *PLoS ONE* 13 (1), e0190712. <https://doi.org/10.1371/journal.pone.0190712>.
- Friston, K.J., Harrison, L., Penny, W., 2003. Dynamic causal modelling. *NeuroImage* 19, 1273–1302. [https://doi.org/10.1016/S1053-8119\(03\)00202-7](https://doi.org/10.1016/S1053-8119(03)00202-7).
- Furl, N., Henson, R.N., Friston, K.J., Calder, A.J., 2013. Top-down control of visual responses to fear by the amygdala. *J. Neurosci.* 33 (44), 17435–17443. <https://doi.org/10.1523/JNEUROSCI.2992-13.2013>.
- Hart, S.G., Staveland, L.E., 1988. Development of NASA-TLX (task load index): results of empirical and theoretical research. *Advances in Psychology*, Advances in Psychology. Elsevier, pp. 139–183 pages.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2002. Human neural systems for face recognition and social communication. *Biol. Psychiatry* 51 (1), 59–67. [https://doi.org/10.1016/S0006-3223\(01\)01330-0](https://doi.org/10.1016/S0006-3223(01)01330-0).
- Horstmann, G., Bauland, A., 2006. Search asymmetries with real faces: testing the anger-superiority effect. *Emotion* 6 (2), 193–207. <https://doi.org/10.1037/1528-3542.6.2.193>.
- Hunnis, S., de Wit, T.C.J., Vrans, S., von Hofsten, C., 2011. Facing threat: infants' and adults' visual scanning of faces with neutral, happy, sad, angry, and fearful emotional expressions. *Cogn. Emot.* 25 (2), 193–205. <https://doi.org/10.1080/15298861003771189>.
- Jo, H.J., Saad, Z.S., Simmons, W.K., Milbury, L.A., Cox, R.W., 2010. Mapping sources of correlation in resting state fmri, with artifact detection and removal. *NeuroImage* 52, 571–582. <https://doi.org/10.1016/j.neuroimage.2010.04.246>.
- Jo, H.J., Gotts, S.J., Reynolds, R.C., Bandettini, P.A., Martin, A., Cox, R.W., Saad, Z.S., 2013. Effective preprocessing procedures virtually eliminate distance-dependent motion artifacts in resting State FMRI. *J. Appl. Math.* <https://doi.org/10.1155/2013/935154>.
- Kahneman, D., 1973. *Attention and Effort*. Prentice-Hall.
- Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical region specialized for the perception of faces. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 361 (1476), 2109–2128. <https://doi.org/10.1098/rstb.2006.1934>.
- Khachouf, O.T., Chen, G., Duzzi, D., Porro, C.A., Pagnoni, G., 2017. Voluntary modulation of mental effort investment: an fmri study. *Sci. Rep.* 7 (1), 17191. <https://doi.org/10.1038/s41598-017-17519-3>.
- Lavie, N., Beck, D.M., Konstantinou, N., 2014. Blinded by the load: attention, awareness and the role of perceptual load. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 369 (1641), 20130205. <https://doi.org/10.1098/rstb.2013.0205>.
- Lim, S.-L., Padmala, S., Pessoa, L., 2008. Affective learning modulates spatial competition during low-load attentional conditions. *Neuropsychologia* 46 (5), 1267–1278. <https://doi.org/10.1016/j.neuropsychologia.2007.12.003>.
- Marsh, A.A., Ambady, N., Kleck, R.E., 2005. The effects of fear and anger facial expressions on approach- and avoidance-related behaviors. *Emotion* 5, 119–124. <https://doi.org/10.1037/1528-3542.5.1.119>.
- McClure, E.B., 2000. A meta-analytic review of sex differences in facial expression processing and their development in infants, children, and adolescents. *Psychol. Bull.* 126, 424–453. <https://doi.org/10.1037/0033-2909.126.3.424>.
- Mitchell, D.G.V., Nakic, M., Fridberg, D., Kamel, N., Pine, D.S., Blair, R.J.R., 2007. The impact of processing load on emotion. *NeuroImage* 34 (3), 1299–1309. <https://doi.org/10.1016/j.neuroimage.2006.10.012>.
- Morris, J.S., Friston, K.J., Büchel, C., Frith, C.D., Young, A.W., Calder, A.J., Dolan, R.J., 1998. A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain* 121 (1), 47–57. <https://doi.org/10.1093/brain/121.1.47>.
- Ochsner, K.N., Gross, J.J., 2005. The cognitive control of emotion. *Trends Cogn. Sci.* 9 (5), 242–249. <https://doi.org/10.1016/j.tics.2005.03.010>.
- Olderbak, S., Wilhelm, O., Hildebrandt, A., Quoidbach, J., 2018. Sex differences in facial emotion perception ability across the lifespan. *Cogn. Emot.* 22, 1–10. <https://doi.org/10.1080/02699931.2018.1454403>.
- Paus, T., Koski, L., Caramanos, Z., Westbury, C., 1998. Regional differences in the effects of task difficulty and motor output on blood flow response in the human anterior cingulate cortex. *Neuroreport* 9 (9), R37–R47. <https://doi.org/10.1097/00001756-199806220-00001>.
- Pessoa, L., 2009. How do emotion and motivation direct executive control? *Trends Cogn. Sci.* 13 (4), 160–166. <https://doi.org/10.1016/j.tics.2009.01.006>.
- Pessoa, L., Ungerleider, L.G., 2004. Neuroimaging studies of attention and the processing of emotion-laden stimuli. *Prog. Brain Res.* 144, 171–182. [https://doi.org/10.1016/S0079-6123\(03\)14412-3](https://doi.org/10.1016/S0079-6123(03)14412-3).
- Pessoa, L., McKenna, M., Gutierrez, E., Ungerleider, L.G., 2002. Neural processing of emotional faces requires attention. *Proc. Natl. Acad. Sci. U. S. A.* 99 (17), 11458–11463. <https://doi.org/10.1073/pnas.172403899>.
- Pessoa, L., Padmala, S., Morland, T., 2005. Fate of unattended fearful faces in the amygdala is determined by both attentional resources and cognitive modulation. *NeuroImage* 28 (1), 249–255. <https://doi.org/10.1016/j.neuroimage.2005.05.048>.
- Pourtois, G., Schwartz, S., Seghier, M.L., Lazeyras, F., Vuilleumier, P., 2006. Neural systems for orienting attention to the location of threat signals: an event-related fMRI study. *NeuroImage* 31 (2), 920–933. <https://doi.org/10.1016/j.neuroimage.2005.12.034>.
- Puce, A., Allison, T., Asgari, M., Gore, J.C., McCarthy, G., 1996. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. *J. Neurosci.* 16 (16), 5205–5215. <https://doi.org/10.1523/JNEUROSCI.16-16-05205.1996>.
- R Core Team, 2021. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Radke, S., Volman, I., Kokal, I., Roelofs, K., de Bruijn, E.R.A., Toni, I., 2017. Oxytocin reduces amygdala responses during threat approach. *Psychoneuroendocrinology* 79, 160–166. <https://doi.org/10.1016/j.psyneuen.2017.02.028>.
- Ranger, J., Kuhn, J.T., Ortner, T.M., 2020. Modeling responses and response times in tests with the hierarchical model and the three-parameter lognormal distribution. *Educ. Psychol. Meas* 80, 1059–1089. <https://doi.org/10.1177/0013164420908916>.
- Roelofs, K., Hagenaaers, M.A., Stins, J., 2010. Facing freeze: social threat induces bodily freeze in humans. *Psychol. Sci.* 21 (11), 1575–1581. <https://doi.org/10.1177/0956797610384746>.
- Rouder, J.N., 2005. Are unshifted distributional models appropriate for response time? *Psychometrika* 70, 377–381. <https://doi.org/10.1007/s11336-005-1297-7>.
- Sarter, M., Gehring, W.J., Kozak, R., 2006. More attention must be paid: the neurobiology of attentional effort. *Brain Res. Rev.* 51 (2), 145–160. <https://doi.org/10.1016/j.brainresrev.2005.11.002>.
- Schindler, S., Bublitzky, F., 2020. Attention and emotion: an integrative review of emotional face processing as a function of attention. *Cortex* 130, 362–386. <https://doi.org/10.1016/j.cortex.2020.06.010>.
- Schmidt, L.J., Belopolsky, A.V., Theeuwes, J., 2012. The presence of threat affects saccade trajectories. *Vis. Cogn.* 20 (3), 284–299. <https://doi.org/10.1080/13506285.2012.658885>.
- Seeley, W.W., Menon, V., Schatzberg, A.F., Keller, J., Glover, G.H., Kenna, H., Reiss, A.L., Greicius, M.D., 2007. Dissociable intrinsic connectivity networks for salience processing and executive control. *J. Neurosci.* 27 (9), 2349–2356. <https://doi.org/10.1523/JNEUROSCI.5587-06.2007>.
- Shenhav, A., Musslick, S., Lieder, F., Kool, W., Griffiths, T.L., Cohen, J.D., Botvinick, M.M., 2017. Toward a rational and mechanistic account of mental effort. *Annu. Rev. Neurosci.* 40 (1), 99–124. <https://doi.org/10.1146/annurev-neuro-072116-031526>.
- Silver, L., Lepstein, J., Fragopanagos, N., Goolsby, B., Kiss, M., Taylor, J.G., Raymond, J.E., Shapiro, K.L., Eimer, M., Nobre, A.C., 2007. Influence of attentional demands on the processing of emotional facial expressions in the amygdala. *NeuroImage* 38 (2), 357–366. <https://doi.org/10.1016/j.neuroimage.2007.07.023>.

- Stoica, T., Knight, L.K., Naaz, F., Patton, S.C., Depue, B.E., 2021. Gender differences in functional connectivity during emotion regulation. *Neuropsychologia* 156, 107829. <https://doi.org/10.1016/j.neuropsychologia.2021.107829>.
- Underwood, R., Tolmeijer, E., Wibroe, J., Peters, E., Mason, L., 2021. Networks underpinning emotion: a systematic review and synthesis of functional and effective connectivity. *Neuroimage* 243 (118486), 118486. <https://doi.org/10.1016/j.neuroimage.2021.118486>.
- Vetter, P., Badde, S., Phelps, E.A., Carrasco, M., 2019. Emotional faces guide the eyes in the absence of awareness. *eLife* 8. <https://doi.org/10.7554/eLife.43467>.
- Viviani, R., 2013. Emotion regulation, attention to emotion, and the ventral attentional network. *Front. Hum. Neurosci.* 7, 746. <https://doi.org/10.3389/fnhum.2013.00746>.
- Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain. *Neuron* 30 (3), 829–841. [https://doi.org/10.1016/s0896-6273\(01\)00328-2](https://doi.org/10.1016/s0896-6273(01)00328-2).
- Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., Dolan, R.J., 2004. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nat. Neurosci.* 7 (11), 1271–1278. <https://doi.org/10.1038/nn1341>.
- Wang, L., Feng, C., Mai, X., Jia, L., Zhu, X., Luo, W., Luo, Y.-J., 2016. The impact of perceptual load on the non-conscious processing of fearful faces. *PLoS One* 11, e0154914. <https://doi.org/10.1371/journal.pone.0154914>.