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The Amygdala and Appraised Concern-Relevance: Initial Evidence That Intrinsic Motivation Modulates Amygdala Response to Otherwise Neutral Stimuli

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Based on an affective neuroscience approach to appraisal theories of emotion, the present study tested the hypothesis that the amygdala is involved in the processing of *concern-relevance*. Thirty-five students with varying intrinsic academic motivation performed three target-detection tasks using affectively neutral letter stimuli as targets. In one task, participants were given a cover story that their task performance was indicative of future academic success. This *intrinsic motivation* condition was controlled with two other conditions: an *extrinsic motivation* condition allowing participants to earn money for themselves based on their task performance, and a *baseline* condition where participants were simply requested to perform the task while they were told that we were calibrating the scanner. Participants reported their intrinsic academic motivation using a standardized academic motivation scale. Results illustrated an interaction effect both at the whole-brain and region of interest levels. When accounting for all three conditions, only during the *intrinsic motivation* condition did bilateral amygdala activation significantly increase with increasing academic motivation scores when responding to targets (vs. nontargets). Findings suggest that intrinsic academic motivation modulates amygdala response to otherwise neutral stimuli when they are relevant to academic success, consistent with the proposal that the amygdala is sensitive to the degree to which stimuli are relevant to the individual's concerns. This stresses the need for more personalized analyses of brain responses to stimuli and tasks that are typically considered "neutral" and hold important implications for psychiatric populations suffering from deficiencies in affective processing, particularly anxiety disorders.

Keywords: motivation, appraisal, emotion theory, neuroimaging, self-relevance

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The 21st century has witnessed a significant increase in the affective sciences (Dukes et al., 2021), and research investigating the neural substrates of emotion processing may be the clearest example of this development (see, e.g., Adolphs & Anderson, 2018; Armony & Vuilleumier, 2013), highlighting, in particular, the amygdala's central role (Whalen & Phelps, 2009). This has allowed scientists to exploit neuroimaging research in order to comparatively test psychological theories of emotion (see, e.g., Kragel et al., in press; Sander, 2013). Notably, evidence from experimental and meta-analytic neuroimaging studies present the amygdala as fear-specific (e.g., Bertini et al., 2020; Öhman & Mineka, 2001; Vytal & Hamann, 2010), which could argue for a brain topography reflective of basic emotions theory. Although neuroimaging studies have reported amygdala response to various positive and negative emotional stimuli (Cunningham & Brosch, 2012; O'Neill et al., 2018; Sander et al., 2003), presenting the amygdala as central to the "fear module" hub (Öhman & Mineka, 2001), the "fear circuit" (Panksepp et al., 2011), or the "defensive survival circuit" (LeDoux & Brown, 2017) remains prominent in the literature (cf. Hamann, 2012; Kragel & LaBar, 2016; Tiwari et al., 2019). The fact that the amygdala is critical for some components of fear is

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The authors declare no conflicting interests.

This study was not preregistered. Due to ongoing supplemental analyses of these data, which will compose part of a future manuscript, we are unable to openly share our data publicly at this time. We are, however, happy to honor requests for data sharing from interested parties and subsequent approval from our institutional ethics committee.

Ryan J. Murray contributed toward formal analysis and writing–original draft. Hana H. Kutlikova contributed toward data curation and writing–review and editing. Tobias Brosch contributed toward conceptualization and writing–review and editing. David Sander contributed toward conceptualization and writing–review and editing.

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unquestionable but, more than a decade ago, LeDoux already concluded that "Especially important for the future will be studies that attempt to understand whether the importance of the amygdala in fear reflects the importance of fear to the amygdala or whether fear is just the function that has been studied most" (LeDoux, 2008). In fact, other interpretations of the available data have already suggested that the reason why the amygdala is so important for fear may come from a confound: threatening stimuli would be processed by the amygdala because they are appraised as relevant for the concerns of the organism and not *specifically* because they are fear-inducing (see Sander et al., 2003). According to this alternative approach, the amygdala's key role in affective processing thus lies in detecting relevant information, which includes, but is not limited to, threat-related information (Sander et al., 2003; see also Brosch & Sander, 2013b; Cunningham & Brosch, 2012; Sander et al., 2018). Once appraised as relevant, stimuli are further appraised, and not only elicit an emotional response (De Leersnyder et al., 2018; Olteanu et al., 2019), but also facilitate mechanisms such as attention (Pool et al., 2016) and learning (Stussi et al., 2018).

Here, we wished to test the degree to which the human amygdala is involved in appraised concern-relevance, using a functional magnetic resonance imaging (fMRI) experiment. Neuroimaging studies suggest amygdala activation is flexibly sensitive to participants' current processing goals (see Cunningham et al., 2008), and may not be restricted to "canonically" emotional stimuli, such as fear-relevant or arousing images, but may occur upon detecting any stimuli deemed relevant to the individual (see Cunningham & Brosch, 2012; Sander, 2009). For instance, the amygdala responds to stimuli without any particular valence (e.g., letters/numbers) that have become behaviorally relevant (Ousdal et al., 2008), especially when extrinsic reinforcements are involved (Ousdal et al., 2012). These findings allude to a more personalized processing mechanism modulating amygdala response. To our knowledge, however, no neuroimaging study has thus far directly tested the claim that the amygdala plays a role in detecting and processing information relevant to long-term personal motivations regarding important goals (e.g., self-esteem maintenance and enhancement) and values (general guiding principles in life). Here, we manipulated motivational relevance, or concern-relevance, by presenting participants with stimuli that were intrinsically neutral (e.g., letters) but could be relevant to the achievement goals of the participants depending only on the way the task was presented to participants. In our design, stimuli were not only relevant for correct task performance, but also related to intrinsic achievement motivation, rendering them concern-relevant. We administered three target-detection tasks: targets (Ts) and nontargets (NTs) were affectively neutral, for example, letters or lines. According to our cover stories, and counterbalanced across participants, one task was rendered intrinsically motivationally relevant (i.e. *intrinsic motivation* condition), where stimuli therein were imbued with concern-relevance. In order to create a condition in which stimuli were relevant to intrinsic motivation, we first administered an fMRI task claiming to measure participants' personal academic potential, thereby targeting the self-enhancing goal of academic achievement. We subsequently measured self-reported intrinsic academic motivation of participants using the standardized academic motivation scale (Vallerand et al., 1992). In addition to this *intrinsic motivation* condition, we also included two control fMRI conditions. One was an *extrinsic motivation* condition, where participants could earn money for themselves given their performance. The other control condition was a *baseline condition*, where participants believed their completion of the task was to be used for technical purposes only, with no regard toward their performance.

Based on our hypothesis that the amygdala is involved in concern-relevance, we predicted significantly increased amygdala responses to Ts (vs. NTs) as a function of intrinsic academic motivation (hereafter, Academic Motivation) when participants believed their task performance was indicative of academic potential (*intrinsic motivation* experimental condition), and that such increase would be higher than when participants believed their task- performance would increase remuneration (*extrinsic motivation* control condition) or would not be evaluated (*baseline* control condition).

Method

Participants

Thirty-six student volunteers (18 female, M_{age}: 24.4 years) from various departments of the University of Geneva participated in the study. This number allowed for optimal counterbalancing of the three target-detection task types used in this study, the three experimental conditions in which they occurred, and their ordering. The rationale behind the sample size is explained in further detail in the "Experimental Procedure" section. All participants were right-handed, had normal or corrected-to-normal vision, and had no history of neurological or psychiatric disease. All participants provided informed consent via a signed consent form. This study was approved by the University of Geneva research ethics committee.

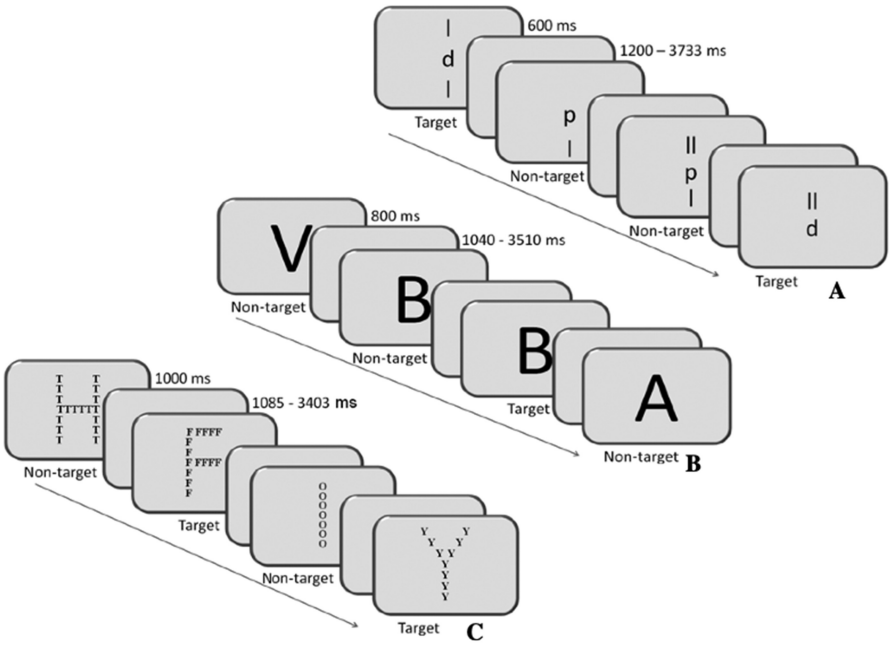
Experimental Tasks

Three different target-detection tasks were chosen for the experiment, a d2, one-back, and global–local task (Figure 1). In the d2 Concentration Endurance test (Brickenkamp, 1981), participants were presented with individual stimuli consisting of a letter (d or p) surrounded by one to four apostrophes, arranged individually or in pairs, above or below the letter. Participants were instructed to detect target stimuli defined as the letter d surrounded by two apostrophes. In the one-back task, participants were presented with a sequence of individual letters and were instructed to detect target stimuli defined as a letter that was identical to the previously presented one. In the global–local task (Navon, 1977), participants were presented with individual stimuli consisting of large letters composed of smaller-sized letters. Participants were instructed to detect target stimuli defined as a large letter that is composed of identical small letters. A behavioral pretest ($n = 20$) assured that the three tasks did not differ significantly in terms of accuracy rate, $F(2, 38) = 1.09$, $p = .35$, reaction times, $F(2, 38) = 2.38$, $p = .11$, or subjective difficulty ratings, $F(2, 38) = .58$, $p = .57$.

Experimental Procedure

Participants were informed that the aim of the study was to validate an fMRI-based measure of cognitive competence whose results were highly predictive of academic and professional success. In addition to this competence task (i.e., *intrinsic motivation* condition), participants were told that they would perform two further tasks, one determining the monetary amount they would receive for their participation (which could range from CHF 25 to CHF 40; *extrinsic motivation* condition), and another one serving as a technical scanner calibration task whose performance would not

Figure 1
Experimental Procedure



Note. The figure shows three target-detection tasks. Task A is a d2 target-detection task. Task B is a 1-back target-detection task, and task C is a global–local target detection. All tasks were counterbalanced across participants and conditions.

be evaluated (*baseline* condition). The three different tasks (d2 task, global–local task, and one-back task) were alternatingly assigned to the three different experimental conditions so that their role was counterbalanced across participants. Furthermore, the order of the three tasks during the experiment was pseudorandomized across participants so that one-third of the participants would begin with the *intrinsic motivation* task, one-third with the *extrinsic motivation* task, and one-third with the *baseline* task. The complete counterbalancing of the different tasks and sequences assures that any observed differences are not attributable to the different task types, but solely to the motivational condition they were presented in. This resulted in a sample size of 36 participants. All participants followed a 15-min training in front of a desktop computer to be familiarized with the functionality and rules of each task.

Participants thus performed three functional scanning runs, each corresponding to one experimental condition, with 200 trials (120 NTs, 40 Ts, 40 null events) each. Stimulus presentation time in the d2 task was 600 ms, in the global–local task 1,000 ms, and in the one-back task 800 ms (these parameters were determined during pilot studies to obtain the same level of subjective difficulty for each task). Following the offset of each stimulus, a blank screen was presented for a duration that resulted for each task in an average stimulus-onset asynchrony of 3,000 ms (d2 task: 1,200–3,733 ms; mean: 2,400 ms; global–local task: 1,085–3,403 ms; mean: 2,000 ms; one-back task: 1,040–3,510 ms; mean: 2,200 ms). Stimuli were back-projected on a screen that participants viewed through a mirror system attached to the head coil. Each task began with an instruction display informing the participant about the motivational condition. Participants were instructed to respond to the target (T) by pressing the "YES" key of a magnetic resonance imaging (MRI)-compatible response box with their right index finger. They were also required to press the "NO" key with their right middle finger whenever an NT was presented.

Psychological Measures

After the fMRI session, participants indicated, using 9-point Likert scales, how difficult and how important they found each one of the tasks. Specifically, they were asked to indicate on a scale from 1 to 9, to what extent they found each task difficult and to what extent it was important for them to succeed in each task. They then completed the academic motivation scale (Vallerand et al., 1992), which comprises 28 items subdivided into seven subscales measuring three types of Academic Motivation (intrinsic motivation for knowledge, to accomplish tasks, and for stimulation) and three types of extrinsic motivation (external, introjected, and regulated). Questions measuring academic motivation include items such as "I go to university for the pleasure that I experience while I am surpassing myself in one of my personal accomplishments" or "University allows me to experience a personal satisfaction in my quest for excellence." Participants were also administered a sociodemographic questionnaire, were debriefed, and then thanked for their participation. We measured the variation of blood-oxygen-level dependent (BOLD) response as a function of total Academic Motivation. Academic Motivation thus consists of a composite score of the following three subscales: (a) Intrinsic Knowledge Motivation, (b) Intrinsic Accomplishment Motivation, and (c) Intrinsic Stimulation motivation (Vallerand et al., 1992). We also report findings from the same analyses but using the subscale measuring intrinsic motivation to accomplish tasks (Intrinsic Accomplishment Motivation) in order

to determine if a subscale specifically targeting accomplishment-focused motivation can explain BOLD variation to concern-relevant tasks.

fMRI Acquisition and Analysis

A 3-T Siemens TIM TRIO scanner with a 12-channel head coil was used for whole-brain data acquisition. Anatomical images were acquired using a T1-weighted protocol (256 × 256 matrix, 256 1-mm sagittal slices). Whole-brain functional images were acquired using a single-shot gradient-echo echo-planar-imaging (EPI) sequence (repetition time = 2.1 s; echo time = 30 ms; field of view = 205 mm; flip angle = 80°). We obtained 36 contiguous oblique-axial slices (3.2 × 3.2 × 3.2 mm voxels) parallel to the anterior commissure–posterior commissure line. Data were preprocessed using SPM12 (Wellcome Trust Center for Neuroimaging, http://www.fil.ion.ucl.ac.uk/spm/). All images were realigned, corrected for slice timing, normalized to an EPI template (resampled voxel size of 3 mm), spatially smoothed (5 mm full-width/half-maximum Gaussian kernel), and high-pass-filtered (cutoff = 128 s). MRI data were collected at the Brain and Behaviour Laboratory at the University of Geneva.

Experimental epochs were modeled by a standard synthetic hemodynamic response function. For the main experiment, six event types were defined at the first (individual) level: *intrinsic motivation* task Ts, *intrinsic motivation* task NTs, *extrinsic motivation* task Ts, *extrinsic motivation* task NTs, *baseline* task Ts, and *baseline* task NTs. At the second (group) level, we first conducted a 2 × 3 flexible factorial design investigating whole-brain BOLD dynamics across all three conditions, using Stimulus (T, NT) and Condition (*intrinsic motivation*, *extrinsic motivation*, *baseline*) as within-subjects factors and Subject as a random-effects factor. We investigated any main effect of Stimulus or Condition as well as a Stimulus × Condition interaction. To measure BOLD variation as a function of intrinsic motivation traits, we additionally conducted two individual two-sample *t*-test correlations between whole-brain BOLD reactivity to Ts, relative to NTs, and both scales (Academic Motivation composite scale and Intrinsic Accomplishment Motivation subscale) for the three separate conditions. In the main text, we report findings for correlations with Academic Motivation whereas, in the online supplemental materials, we provide results using the subscale, Intrinsic Accomplishment Motivation. Specifically, we included Academic Motivation (and the subscale Intrinsic Accomplishment Motivation, provided in the online supplemental materials) as a parametric modulator for each of the three conditions (*intrinsic motivation*, *extrinsic motivation*, and *baseline*) separately using participants' BOLD response specific to T (i.e., participants' beta values resulting from the specific contrast T> NT). This approach allowed us to control for any confounding effects of stimulus exposure. We thus investigated the covariation of BOLD response with Academic Motivation individually in three separate regressions in order to determine the influence of concern-relevance on neural responding in each of the three conditions.

Second-level analyses and multiple comparison corrections were implemented on whole-brain analyses using threshold-free cluster enhancement (TFCE) nonparametric permutation testing via the FMRIB Software Library randomize algorithm (Winkler et al., 2014). Contrary to cluster-based thresholding, which requires an initial and often arbitrary cluster-forming threshold, the TFCE method allows for a data-driven thresholding approach, yielding outputs in which voxel-wise values represent "the amount of cluster-like local spatial support" (Smith & Nichols, 2009). The TFCE method has been shown to exhibit greater sensitivity, yielding increased signal-to-noise values (Smith & Nichols, 2009). We, therefore, constructed the null distribution, generating 10,000 permutations of the input data, of the maximum (across voxels) TFCE score, and then tested the resulting TFCE image against it. The TFCE image is then thresholded once the 95th percentile in the null distribution is located, thus allowing for an inference at the $p < .05$ (corrected) level (Smith & Nichols, 2009). In cases where this level yielded clusters too large to extract meaningful data (i.e., the clusters were too large to yield precise coordinates), we decreased our *p*-corrected level even further (i.e., $p < .025$, $p < .01$, $p < .005$, $p < .0025$, $p < .001$, etc.).

T-test correlation results were also verified using Bonferroni-correction, defining a cluster-forming threshold at $p = .01$, in order to correct for separate multiple correlation testing across three conditions. A mean of the gray matter of the resulting participants was used as a base for an inclusive gray matter mask. Peak cluster locations of all analyses are reported using the Montreal Neurological Imaging coordinates.

Region of Interest Analyses

In order to conduct our amygdala region of interest (ROI) analysis, participants performed a functional face localizer, a behavioral task validated to independently localize bilateral amygdala activation (Kanwisher et al., 1997). During this localizer task, participants performed a one-back task during a blocked presentation of neutral faces, fearful faces, houses, and scrambled images. The localizer task consisted of 16 blocks, each containing 20 pictures presented for 550 ms followed by a fixation cross presented for 1,000 ms. Participants were required to press the response button whenever the same stimulus was presented twice in a row. For the face localizer experiment, three conditions were defined: faces, houses, and scrambled images. To localize amygdala activity, we captured BOLD response when viewing faces, relative to scrambled images. This provided robust effects within the bilateral amygdalae (see Figure 2).

Results

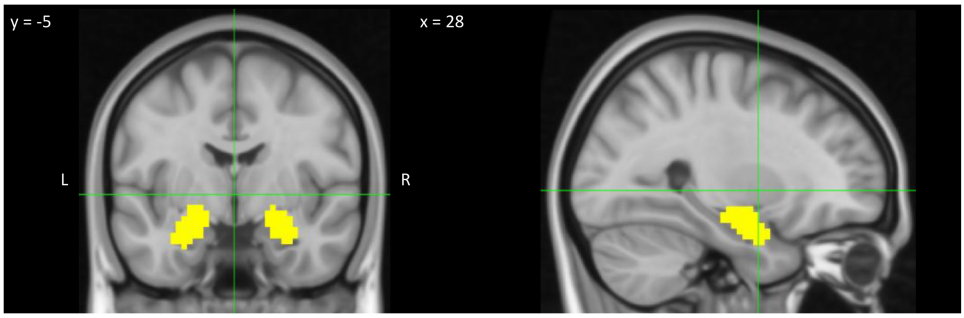
Participants

One participant was removed due to excessive right amygdala activity, which was more than 3 *SD* above the mean of the entire sample. We therefore analyzed our data using 35 participants (18 female; mean 24.5 years).

Behavioral Results

As a manipulation check, we first assessed the objective difficulty of each target-detection task type, irrespective of the experimental condition. To this aim, we conducted a repeated-measures analysis of variance (ANOVA) using within-subjects factor Task (d2, *n*-back, and global–local) and performance errors (missed hits and false alarms) as the dependent variable. This yielded no significant differences in mean errors between target-detection tasks, $F(2, 68) = .127$, $p = .88$. This indicates that the three target-detection tasks (d2, n-back, and global–local) were not statistically different in objective difficulty and suggests that task difficulty did not bias performance in any particular experimental condition (i.e., *intrinsic motivation*, *extrinsic motivation*, and *baseline*).

Figure 2
Amygdala Regions of Interest (ROIs)



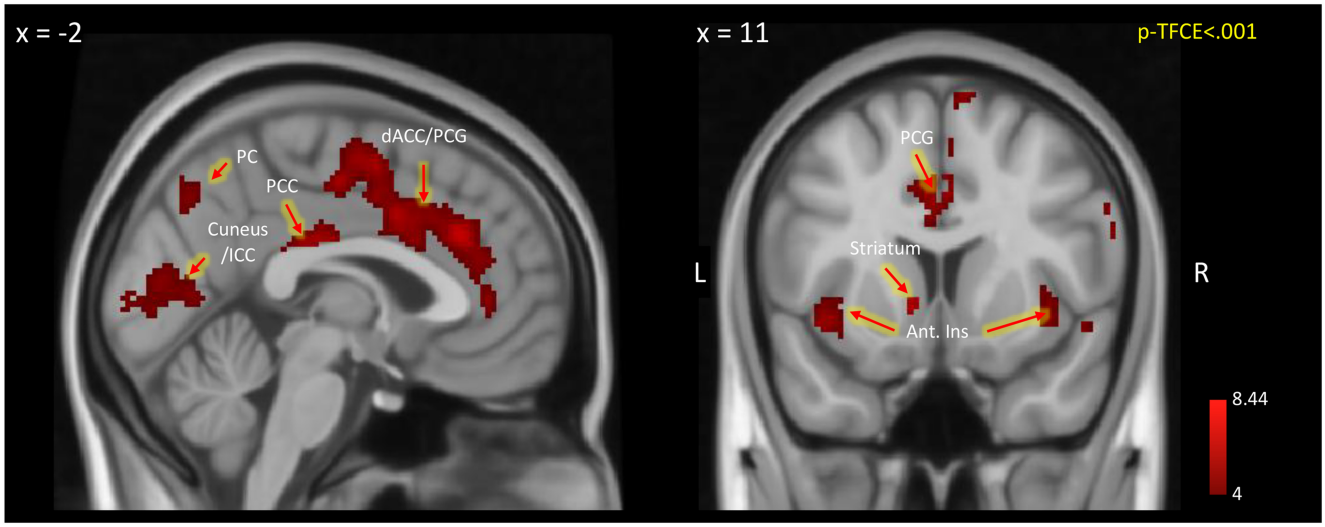
Note. The figure shows bilateral amygdala activations, as elicited by the functional face localizer task (Kanwisher et al., 1997). See the online article for the color version of this figure.

We next measured performance errors as a function of motivational conditions. A repeated-measures ANOVA was thus conducted on performance errors using Condition (*intrinsic motivation*, *extrinsic motivation*, and *baseline*) as a within-subjects factor. This analysis revealed a main effect of Condition, $F(2, 68) = 4.34$, $p = .017$, partial $\eta^2 = .11$. Planned pairwise comparisons indicated that participants committed significantly fewer errors in tasks performed in the *extrinsic motivation* condition ($M = 5.4$) than in tasks performed in the *baseline* condition ($M = 14.9$, difference extrinsic motivation—baseline significant at $p = .023$, two-tailed). Mean errors in the *intrinsic motivation* condition ($M = 10.9$) did not differ significantly from those in the *extrinsic motivation* or *baseline* conditions ($ps > .10$). Academic Motivation composite scores were then added as a covariate. Consequently, the main effect of the Condition was no longer significant, $F(2, 66) = .535$, $p = .588$, suggesting that intrinsic motivation likely influences performance across all conditions.

We next measured subjective difficulty (i.e., self-report ratings) for each motivational condition. A repeated-measures ANOVA was thus conducted on subjective task difficulty ratings using within-subjects factor Condition (*intrinsic motivation*, *extrinsic motivation*, and *baseline*) and yielded no significant effect. This suggests that tasks did not differ significantly in terms of perceived difficulty as a function of the motivational condition they were presented in, $F(2, 68) = .68$, $p = .51$.

Finally, we wished to determine if participants attributed importance differently across the three motivational conditions. A repeated-measures ANOVA was thus conducted on subjective importance ratings, with Condition again as a within-subjects factor. Results revealed only a trend for the effect of Condition, $F(2, 68) = 2.817$, $p = .07$. Although the *baseline* condition was rated as significantly less important than both the *intrinsic motivation* ($t = 2.115$, $p = .042$) and the *extrinsic motivation* ($t = 2.283$,

Figure 3
Main Effect of Stimulus (T > NT)



Note. The figure shows voxel-wise (i.e., whole-brain) BOLD activations in response to Stimulus (T>NT) across all three conditions (*intrinsic motivation*, *extrinsic motivation*, and *baseline;* $p < .001$). Color bars represent *t*-values. Abbreviations: T = target; NT = nontarget; Ant. Ins = anterior insula; dACC = dorsal anterior cingulate cortex; ICC = intracalcarine cortex; PCC = posterior cingulate cortex; PC = precuneus; PCG = paracingulate gyrus; BOLD = blood-oxygen-level dependent. See the online article for the color version of this figure.

$p = .029$) conditions, these statistical differences did not survive multiple comparisons correction.

Neuroimaging Results

Whole-Brain Analyses

For our fMRI analyses, we observed an effect of Stimulus (p-TFCE $< .001$), with T > NT yielding significantly increased activity in the supramarginal gyrus extending into the dorsal anterior cingulate (dACC), orbitofrontal cortex/anterior insula, dorsolateral prefrontal cortex (dLPFC), precentral gyrus, anterior insula, striatum (caudate), posterior insula, precuneus, and cerebellum (Figure 3 and Table 1). Inversely, the NT > T yielded no significantly increased activity.

We observed a main effect of Condition for both *extrinsic motivation* and *baseline* conditions, irrespective of stimulus type ($ps < .05$). Relative to *intrinsic motivation* and *baseline* conditions, the *extrinsic motivation* condition yielded significant BOLD activity within the parahippocampal gyrus, fusiform cortex, lingual gyrus and cerebellum (Figure 4A and Table S1A in the online supplemental materials). The *baseline* condition, relative to the *intrinsic motivation* and *extrinsic motivation* conditions, yielded significantly greater activity within the striatum (putamen), posterior insula, angular gyrus, and precuneus (Figure 4B and Table S1B in the online supplemental materials). The *intrinsic motivation* condition, relative to *extrinsic motivation* and *baseline* conditions and when considering together T and NT stimuli, however, did not yield significantly elevated BOLD activation.

We observed no effect from a Stimulus × Condition interaction.

Finally, we included Academic Motivation as a regressor for each individual condition for the contrast T > NT in order to determine the influence of concern-relevance on neural responding. This yielded significant positive correlations in the *intrinsic motivation* (p-TFCE $< .01$) and *baseline* (p-TFCE $< .01$) conditions only, both of which survived multiple comparison corrections. In the *intrinsic motivation* condition, we observed robust effects, with a significant positive correlation between academic motivation and BOLD response in the bilateral frontal pole, striatum (putamen), bilateral amygdala, hippocampus, insular cortex, planum polare, precentral gyrus, superior and mid temporal gyrus, postcentral gyrus, superior parietal lobe, supramarginal gyrus, angular gyrus, and cerebellum (see Figure 5A and Table 2A). In the *baseline* condition, we observed a significant positive correlation within posterior regions only, that is, the precuneus, intracalcarine gyrus, lingual gyrus, and occipital pole (Figure 5B and Table 2C). When correlating with Intrinsic Accomplishment Motivation, we observed a significant positive correlation in the *intrinsic motivation* condition only within the dLPFC, fusiform, cerebellum, and lateral occipital cortex (p-TFCE $< .05$, Table S2 in the online supplemental materials).

Table 1
Main Effect of Stimulus (T > NT)

Region/subregion	Voxels	*T*-score	*x*	*y*	*z*
Supramarginal gyrus	6,029	7.81	58	−14	40
Postcentral gyrus		6.75	56	−14	30
		6.74	58	−12	26
		6.67	50	−26	52
Paracingulate gyrus		6.72	−2	30	30
Posterior cingulate		6.52	4	−30	26
Supramarginal gyrus	2,550	7.47	−52	−22	50
Postcentral gyrus		7.13	−38	−32	48
		7.07	−50	−32	52
		6.96	−38	−16	64
		6.47	−54	−18	36
		6.31	−58	−18	40
Precuneus	1,854	6.73	10	−66	42
Lingual gyrus		5.23	6	−68	−6
Precuneus		5.17	6	−78	38
Cuneus		5.13	6	−74	24
Intracalcarine cortex		5.04	10	−80	14
		5.02	14	−76	8
Orbitofrontal cortex/anterior insula	912	8.44	32	22	−10
Anterior insula		7.34	40	18	−6
Temporal pole		6.18	50	16	−10
Anterior insula		5.06	38	8	−6
Anterior insula	510	7.58	−36	14	−4
Orbitofrontal cortex		7.13	−30	22	−10
		4.77	−44	20	−10
Posterior insula	99	4.98	−42	−2	6
Posterior insula		4.77	−42	−4	10
Cerebellum	23	5.63	−26	−54	−22
Striatum (caudate)	9	6.17	−10	8	2
Striatum (caudate)		5.9	−10	12	−2
dLPFC	7	4.89	58	8	32
Precentral gyrus	5	4.72	60	10	22

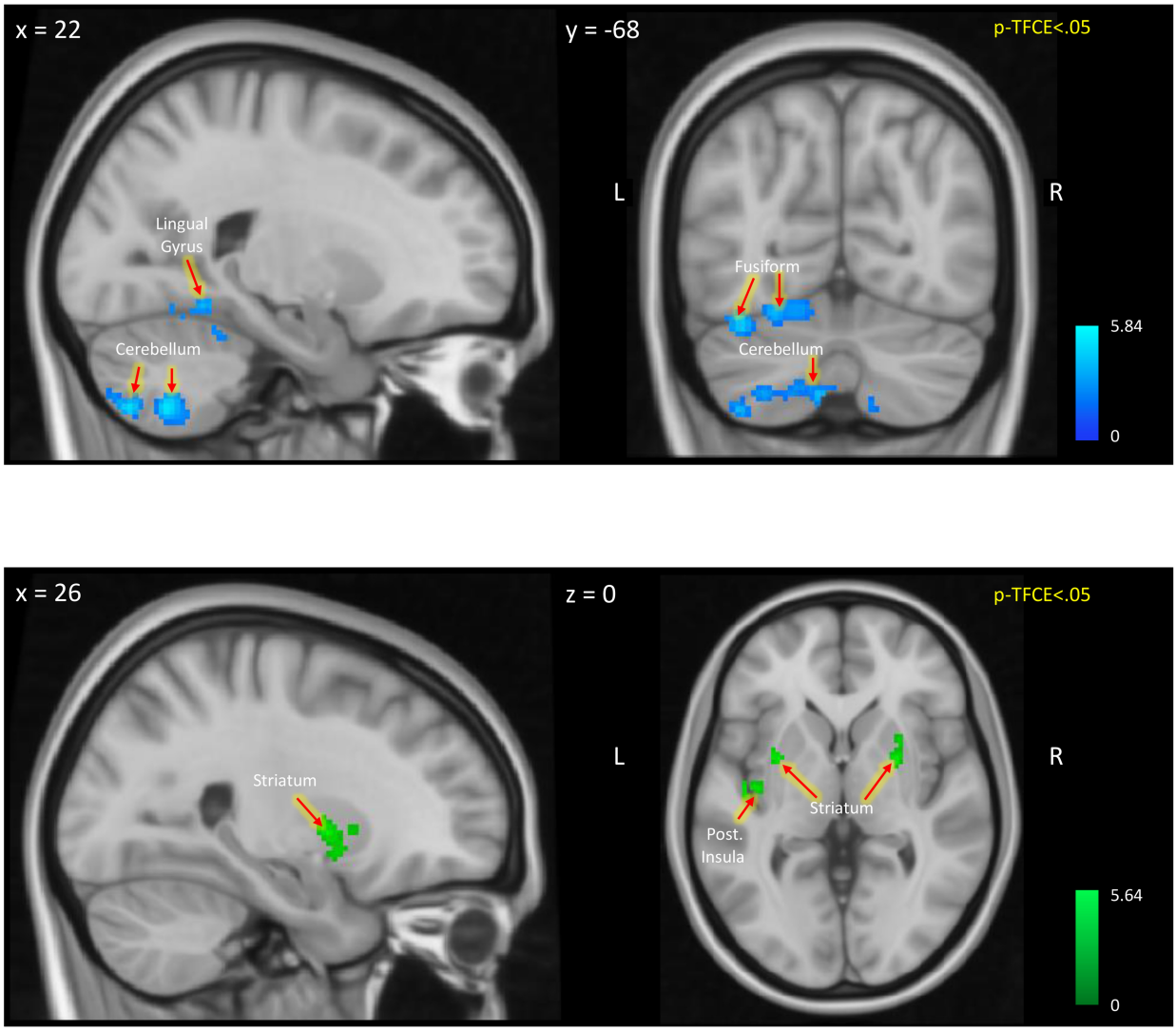
Note. Whole-brain effects of T (>NT) on BOLD response across all three conditions (p-TFCE $< .001$). BOLD = bold oxygen-level dependent; p-TFCE = probability threshold-free cluster enhancement; T = target; NT = nontarget; dLPFC = dorsolateral prefrontal cortex.

ROI Analyses

To further investigate the specificity of the effect of concern-relevance on amygdala response, we conducted an ROI analysis, selecting the bilateral amygdala clusters resulting from the face localizer task (Figure 2). We analyzed individual activation parameters (i.e., beta values) extracted from the bilateral amygdala ROIs, employing a 2 × 3 × 2 repeated-measures ANOVA using within-subject factors Hemisphere (left/right), Condition (*intrinsic motivation*, *extrinsic motivation*, and *baseline*), and Stimulus (T and NT). Scores from the Academic Motivation composite scale as well as the Intrinsic Accomplishment motivation subscale were included as covariates in two separate analyses. Findings including the Intrinsic Accomplishment Motivation subscale are provided in the online supplemental materials. When including Academic Motivation as a covariate, we observed no main effect of Hemisphere, $F(1, 33) = .417$, $p = .523$, with no interaction effect of Academic Motivation ($p = .806$). We observed no main effect of Condition, $F(2, 66) = .567$, $p = .570$), with no interaction effect of Academic Motivation ($p = .595$). We also observed no main effect of Stimulus, $F(1, 66) = 1.819$, $p = .187$, with a marginal interaction effect of Academic Motivation, $F(2, 66) = 3.946$, $p = .055$.

When examining our specific analysis of interest, that is, Condition × Stimulus interaction, we observed a significant effect, $F(2, 66) = 8.49$, $p = .001$, partial $\eta^2 = .205$, modulated by the influence of the covariate Academic Motivation, $F(2, 66) = 9.732$, $p < .001$, partial $\eta^2 = .228$. Posthoc linear regressions showed that only when comparing Ts to NTs in the *intrinsic motivation* condition

Figure 4
Main Effect of Condition



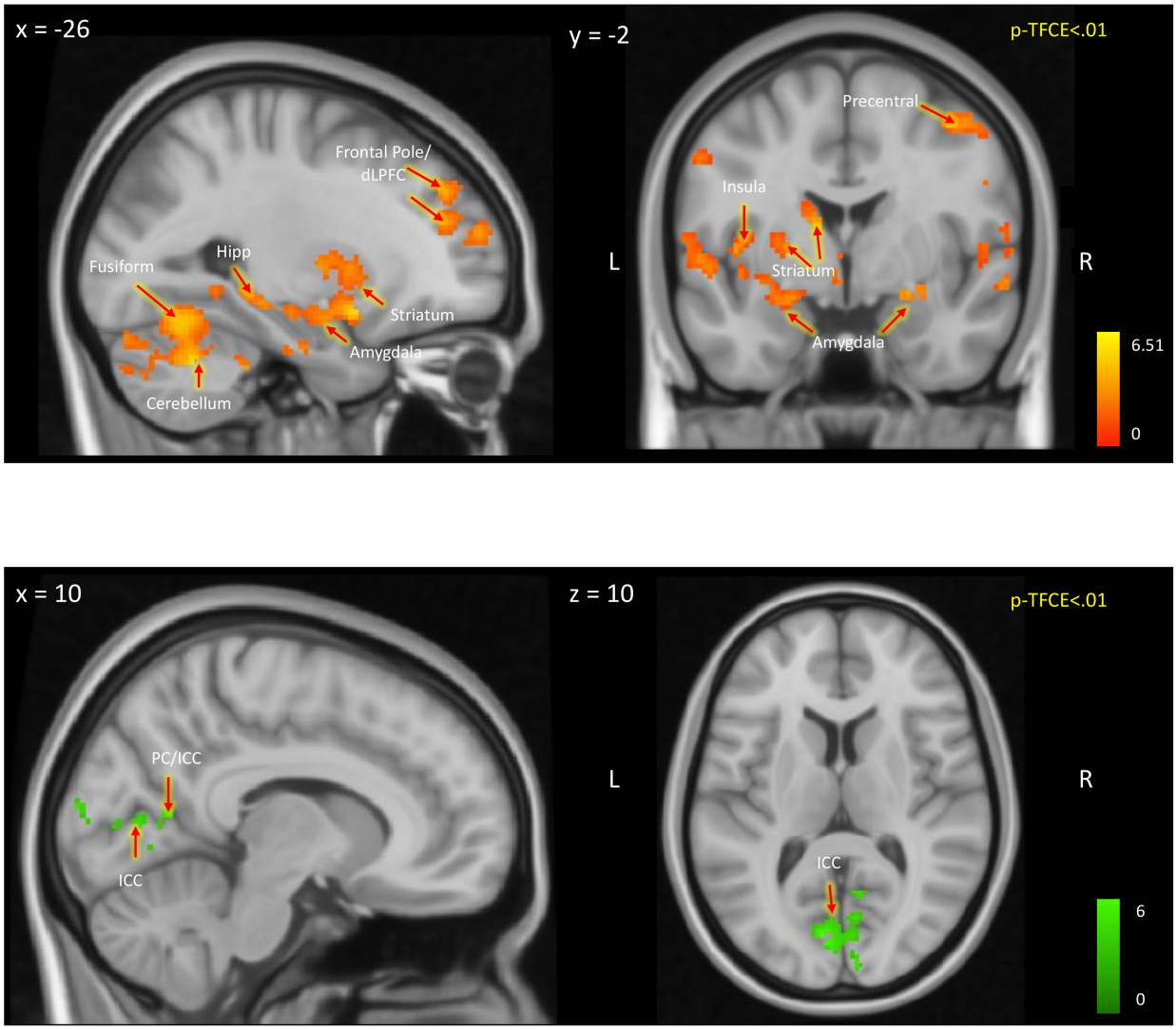
Note. (A) *Extrinsic motivation condition* > (*intrinsic motivation condition* + *baseline condition*). (B) *Baseline condition* > (*intrinsic motivation condition* + *extrinsic motivation condition*). Color bars represent *t*-values. Post. Insula = posterior insula; p-TFCE = probability threshold-free cluster enhancement. See the online article for the color version of this figure.

did the Academic Motivation covariate correlate with both left and right amygdala response ($\beta = .633$, $t = 4.694$, $p < .001$ and $\beta = .614$, $t = 4.463$, $p < .001$, respectively; Figure 6). In the *extrinsic motivation* condition, we observed a significant correlation in neither the left ($\beta = -0.191$, $p = .271$) nor the right ($\beta = -1.669$, $p = .105$) amygdala, and no significant association in the *baseline* condition (left: $\beta = 0.167$, $p = .339$; right: $\beta = 0.218$, $p = .208$; see Figure 6). We found similar findings when using the covariate Intrinsic Accomplishment Motivation subscale (see Figure S3 in the online supplemental materials), suggesting that intrinsic academic motivation, and in particular accomplishment motivation, correlates with bilateral amygdala reactivity to goal-based stimuli (i.e., targets), uniquely when the individual is made to believe performance implicates academic potential (i.e., *intrinsic motivation* condition).

Discussion

In a task that they believed to measure academic potential, participants with higher intrinsic academic motivation exhibited stronger bilateral amygdala activation during the detection of otherwise effectively neutral targets, suggesting the amygdala may subserve the detection of concern-relevance. This increased activation of the amygdala as a function of academic motivation was stronger in this condition than in the two control conditions in which participants performed exactly the same task but without the cover story rendering the task relevant to their intrinsic motivation. These results occurred despite participants objectively displaying fewer errors in the condition offering the chance at receiving financial remuneration (i.e., *extrinsic motivation*

Figure 5
Effect of Concern-Relevance



Note. (A) *Intrinsic motivation* condition (T > NT) correlating with academic motivation composite score (academic motivation scale; Vallerand et al., 1992). (B) *Baseline* condition (T > NT) correlating with academic motivation composite score. Color bars represent *t*-values. T = target; NT = nontarget; dLPFC = dorsolateral prefrontal cortex; Hipp = hippocampus; ICC = intracalcarine cortex; PCC = posterior cingulate cortex; PC = precuneus; p-TFCE = probability threshold-free cluster enhancement. See the online article for the color version of this figure.

condition). Furthermore, performance differences were no longer significant when accounting for academic motivation. Taken together, our findings suggest that variation in amygdala response to task-related stimuli is influenced by their personal concern-relevance.

In addition to typical studies showing the role of the amygdala in processing threat-related stimuli, rewards (Lieberman & Eisenberger, 2009; Sander & Nummenmaa, 2021), and arousing pleasant and unpleasant stimuli (Costa et al., 2010), previous work also showed the importance of participants' current goals in modulating amygdala activity: amygdala response was found to be modulated by the perception of famous people as a function of the current evaluative goals of the participants (Cunningham et al., 2008) or by the detection of neutral stimuli as a function of their behavioral task-relevance (Ousdal et al., 2008) or as a function of their task-relevance in facilitating the potential obtention of rewards (Ousdal et al., 2012). To our knowledge, we provide the first explicit demonstration that otherwise neutral stimuli elicit amygdala activation as a function of individuals' personal intrinsic motivation. Our results therefore present additional evidence concerning the specificity of the role of the amygdala in emotion processing, the topic of an active debate in affective neuroscience. The data presented here bolster the view that the computational profile of the amygdala is restricted neither to basic emotions (e.g., fear) nor to arousal; rather, as a structure, it would be involved in the appraisal of concern-relevance. The view proposed by LeDoux

Table 2
Effect of Concern-Relevance

Region/subregion	Hem	*K*	*T*	*x*	*y*	*z*
(A) Intrinsic motivation condition–academic motivation						
Cerebellum	L	12,181	6.51	−28	−38	−38
Fusiform	L		5.93	−40	−60	−22
Lingual gyrus	R		5.77	14	−54	0
	L		5.76	−10	−60	2
Cerebellum	L		5.58	−32	−54	−36
	L		5.57	−28	−56	−34
Superior parietal lobe	R	2,327	5.78	40	−42	56
Precentral gyrus	R		5.22	44	−8	58
Postcentral gyrus	R		5.12	56	−12	44
	R		4.94	42	−34	62
	R		4.87	54	−22	52
Inferior frontal gyrus	R		4.8	56	12	2
Frontal pole/dLPFC	L	593	5.83	−48	40	18
	L		4.92	−36	42	22
	L		4.85	−40	48	20
	L		4.49	−38	52	20
	L		4.38	−28	44	22
	L		4.37	−34	54	22
Frontal pole/dLPFC	R	173	5.19	32	56	18
	R		4.59	40	42	32
	R		4.3	38	48	28
	R		4.24	42	46	28
	R		4.07	28	62	18
	R		3.89	26	56	6
Striatum (putamen)	R	148	4.98	24	8	−10
	R		4.75	22	14	−10
Amygdala	R		4.69	24	−4	−12
	R		4.5	30	−8	−14
Striatum (putamen)	R		3.95	18	10	−2
Amygdala	R		3.79	28	−2	−10
Planum polare	R	28	4.84	50	4	−14
Mid temporal gyrus	R	16	4.1	44	−32	−2
Supramarginal gyrus	L	14	3.61	−56	−48	22
Angular gyrus	L		3.57	−60	−54	20
Postcentral gyrus	L	14	4.88	−44	−32	62
Postcentral gyrus	L		4.55	−48	−28	58
Superior temporal gyrus	R	9	3.33	68	−30	4
Postcentral gyrus	L	9	3.28	−64	−12	24
Precentral gyrus	L	8	3.18	−40	2	40
Cerebellum	R	3	5.37	32	−46	−46
Striatum (putamen)	L	3	3.26	−30	−18	6
Precentral gyrus	R	3	2.95	54	−2	30
(B) Extrinsic motivation condition–academic motivation n.s.						
(C) Baseline condition–academic motivation						
Intracalcarine gyrus	L	345	5.17	−8	−80	10
	L/R		4.79	0	−84	4
Lingual gyrus	R		4.55	4	−70	0
	R		4.42	2	−70	6
Occipital pole	R		4.38	8	−94	10
	R		4.2	10	−96	14
Precuneus/intracalcarine gyrus	R	18	4	10	−60	10
Lingual gyrus	R		3.51	10	−64	6
Lingual gyrus	L	8	4.42	−10	−66	2

Note. (A) *Intrinsic motivation* condition (T > NT) correlating with academic motivation composite score (p-TFCE < .01). (B) *Extrinsic motivation* condition (T > NT) correlating with academic motivation composite score. (C) *Baseline* condition (T > NT) correlating with academic motivation composite score (p-TFCE < .01). Academic motivation composite score taken from the academic motivation scale (Vallerand et al., 1992). T = target; NT = nontarget; dLPFC = dorsolateral prefrontal cortex; p-TFCE = probability threshold-free cluster enhancement.

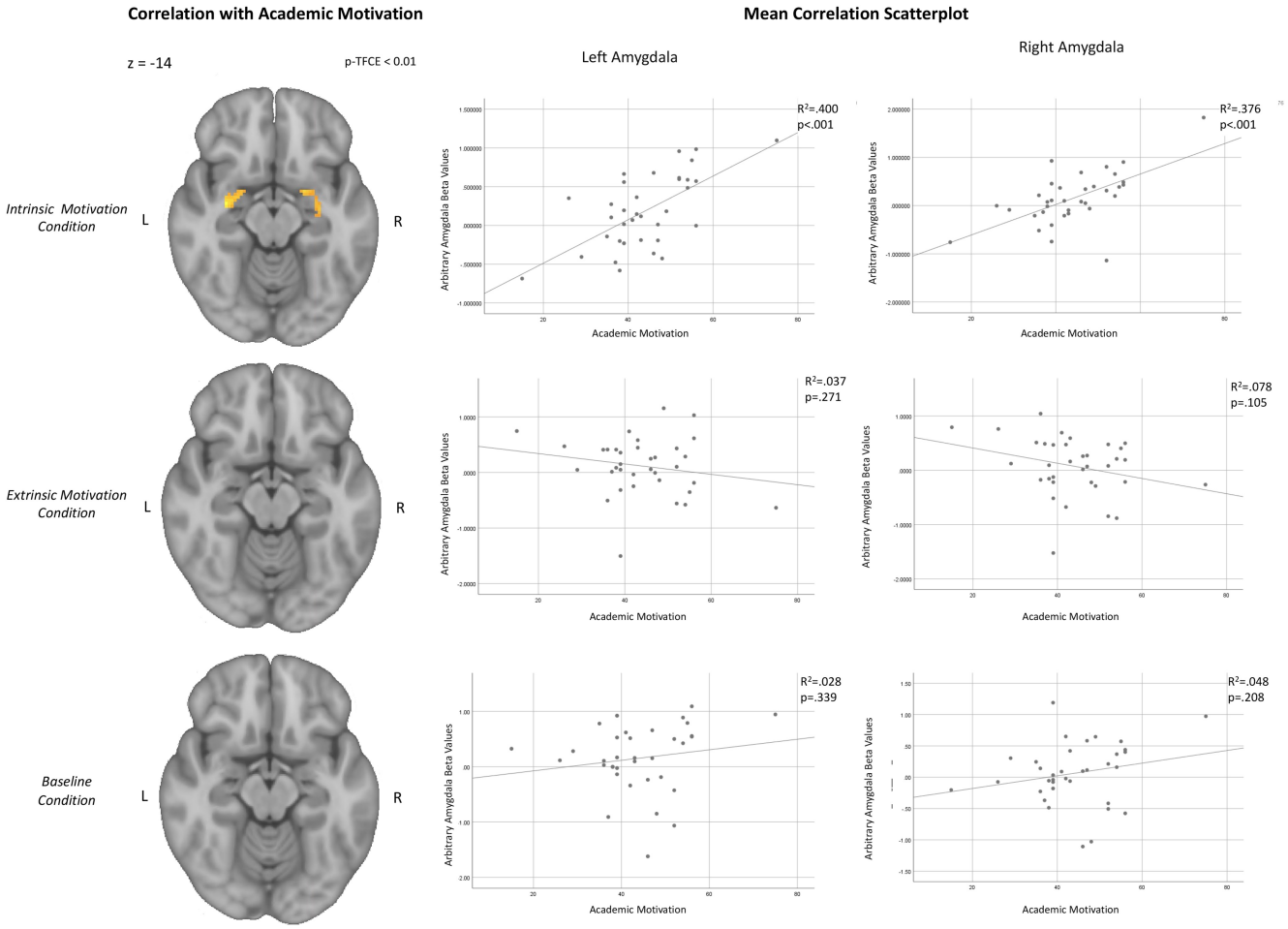
and Brown (2017) that the amygdala would be key for threat detection and defensive response rather than for the experience of fear is consistent with the general idea that the amygdala is important in the *detection* of relevant stimuli, but, we argue, such relevance detection goes beyond threat detection to include all stimuli that are relevant for the personal concerns of an individual. Adopting this latter approach may allow for deeper and more personalized insights when investigating normal amygdala functioning in affective processing (see Sander et al., 2018), in the modulation of several cognitive mechanisms such as attention (see Vuilleumier, 2005), memory (Chaaya et al., 2018), or decision-making (De Martino et al., 2006), and more generally in mechanisms subserving both appetitive- and aversive-related behaviors (Everitt et al., 2003), but also when investigating altered amygdala responding in affective disorders. Social motivation, such as maintaining social rank and bonding, is prominent in individuals suffering from social anxiety (e.g., Kashdan, 2007; Kashdan et al., 2008; Weisman et al., 2011). Importantly, socially anxious individuals often exhibit elevated amygdala responses to socially threatening information (cf. Cremers & Roelofs, 2016 for an extensive review), which could signal obstruction of such social goals (e.g., rejection). Furthermore, individuals suffering from emotion dysregulation disorders, such as borderline personality disorder, often show pervasive deficits in self-relevance processing as well as altered amygdala responses to social-affective information (e.g., Ripoll et al., 2013). To the best of our knowledge, little research has hitherto investigated the link between personal concern-relevance and amygdala response in these populations. Thus, considering amygdala sensitivity as driven by intrinsic motivations and concerns, rather than specifically by "fear" or "arousal," may account for interindividual differences relating to concern-relevance, both under typical or clinical conditions.

Limitations

Certainly, defendants of the "fear module" or "arousal" hypotheses may claim that amygdala response to targets in our study arise not because they were motivation-relevant; rather participants were "afraid of making errors" or were "aroused by targets." Addressing this argument requires future testing wherein participants' state anxiety and arousal to Ts are measured following each task and analyzed relative to their concerns. Although the "fear module" or "arousal" posthoc explanations cannot formally be disqualified, it seems plausible that the more parsimonious explanation holds that the amygdala subserves appraised concern-relevance of otherwise neutral stimuli. Furthermore, future studies should recruit a larger sample of participants in order to further test the relationship between individual differences in intrinsic motivation and amygdala response. It would indeed be useful to replicate our results with a larger sample, and with a focus on several types of motivations and individual differences (see Wuensch et al., 2021). Therefore, given our relatively small sample of participants, we consider our current results to be consistent with the hypothesis that the amygdala is involved in the appraisal of concern-relevance, but highlight that our results represent preliminary evidence in terms of individual differences. It is also worth reminding that

Figure 6

Amygdala Response to Concern-Relevant Targets as a Function of Academic Motivation



Note. The figure shows (left) ROI-based bilateral amygdala response to Ts > NTs in three separate conditions (*intrinsic motivation*, *extrinsic motivation*, and *baseline*) as a function (i.e., correlating with) academic motivation composite scores and (right) mean correlation scatterplots between ROI-based bilateral amygdala beta values during each separate condition (T > NT) and academic motivation composite scores. ROI=region of interest; T=target; NT=nontarget; p-TFCE = probability threshold-free cluster enhancement. See the online article for the color version of this figure.

one participant with excessive amygdala activity (which was more than 3 *SD* above the mean of the entire sample) was removed from the analysis, but retaining this participant still results in a significant Condition × Stimulus interaction, modulated by the influence of the covariate Academic Motivation, $F(2, 68) = 3.138$, $p = .050$, partial $\eta^2 = .084$, with the similar, albeit weaker, trend in the *intrinsic motivation* condition as with our results with 35 participants.

In conclusion, our results thus illustrate that adopting an appraisal-based perspective may contribute to a deeper understanding of the emotional brain (Brosch & Sander, 2013b; Sander et al., 2018), which holds important implications for advancing our understanding of emotion within both healthy and clinical populations. This research holds the promise that a concern-based approach informed by psychological appraisal theories can better appreciate interindividual differences, as it integrates a principled approach to the mechanisms underlying the elicitation of an emotion and is not restricted to the emotional response itself.

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