Emotion and Personal Space: Neural Correlates of Approach-Avoidance Tendencies to Different Facial Expressions As a Function of Coldhearted Psychopathic Traits

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Abstract: In social interactions, humans are expected to regulate interpersonal distance in response to the emotion displayed by others. Yet, the neural mechanisms implicated in approach-avoidance tendencies to distinct emotional expressions have not been fully described. Here, we investigated the neural systems implicated in regulating the distance to different emotions, and how they vary as a function of empathy. Twenty-three healthy participants assessed for psychopathic traits underwent fMRI scanning while they viewed approaching and withdrawing angry, fearful, happy, sad and neutral faces. Participants were also asked to set the distance to those faces on a computer screen, and to adjust the physical distance from the experimenter outside the scanner. Participants kept the greatest distances from angry faces, and shortest from happy expressions. This was accompanied by increased activation in the dorsomedial prefrontal and orbitofrontal cortices, inferior frontal gyrus, and temporoparietal junction for angry and happy expressions relative to the other emotions. Irrespective of emotion, longer distances were kept from approaching faces, which was associated with increased activation in the amygdala and insula, as well as parietal and prefrontal regions. Amygdala activation was positively correlated with greater preferred distances to angry, fearful and sad expressions. Moreover, participants scoring higher on coldhearted psychopathic traits (lower empathy) showed reduced amygdala activation to sad expressions. These findings elucidate the neural mechanisms underlying social approach-avoidance, and how they are related to variations in empathy. Hum Brain Mapp 38:1492–1506, 2017. © 2016 Wiley Periodicals, Inc.

Key words: interpersonal distance; facial expressions; empathy; psychopathic traits; fMRI

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INTRODUCTION

Keeping an appropriate distance from the surrounding physical world is a defensive mechanism that serves a variety of functions including preventing injury [Graziano and Cooke, 2006]. Similarly, to successfully navigate the social world, humans are required to regulate interpersonal distance in order to preserve their own and others' personal space boundaries [Hayduk, 1983; Horowitz et al., 1964]. The violation of those boundaries typically generates discomfort and anxiety, and may trigger defensive responses in others, resulting in avoidant or aggressive behaviour [Ng et al., 2001; Regoeczi, 2008]. Despite being a key process in normal social functioning, few studies have directly examined the neurocognitive processes implicated in normal and abnormal interpersonal distance regulation. In particular, little attention has been given to how distance varies as a function of emotional social cues, such as facial expressions. Here, we used fMRI in combination with a computerized interpersonal distance task to investigate, for the first time, the influence of both emotional context and individual differences in empathy on the neural processes involved in distance regulation.

Facial expressions are among the most powerful communication cues in humans. They convey not only the emotional state, but also the behavioural intentions of an individual [Blair, 2003; Horstmann, 2003; Parkinson, 2005; Schmidt and Cohn, 2001], and are constantly used to guide social behaviour. The ability to adequately adjust interpersonal distance as a function of the emotions manifested by others is thus of utmost importance, especially in potentially threatening interactions (for example, withdrawing from someone expressing anger may protect against aggression). In the past, approach-avoidance tendencies towards facial expressions have classically been examined using motoric tasks, wherein participants are instructed to either push or pull a joystick in response to different faces. The rationale behind such tasks was that pushing aversive stimuli (i.e., muscle extension) and pulling appetitive stimuli (i.e., muscle flexion) are automatic responses associated with shorter reaction times [Cacioppo et al., 1993; Marsh et al., 2005], although recent evidence suggests those responses may result from evaluative rather than purely automatic processes (see Laham et al., 2015 for a review). Studies using such paradigms have shown that angry faces generally motivate avoidance (faster pushing than pulling responses), whereas happy and fearful expressions elicit approach (faster pulling than pushing responses; Hammer and Marsh, 2015; Marsh et al., 2005; Seidel et al.,

Abbreviations

FDR False discovery rate IFG Inferior frontal gyrus

MNI Montreal Neurological Institute

OFC Orbitofrontal cortex ROI Region-of-interest 2010]. Yet, it is unclear how performance in these tasks is related to interpersonal distance in more naturalistic settings. Importantly, prior work does not elucidate what neurocognitive systems underlie approach-avoidance tendencies to distinct emotions. Our first goal was therefore to examine the neural activation patterns to approaching and withdrawing faces displaying different emotional expressions, and to assess their association with interpersonal distance preferences.

At the neural level, the amygdala is one of the candidate regions thought to be implicated in social approachavoidance mechanisms [Bliss-Moreau et al., 2011, 2013; Machado et al., 2009], and specifically in personal space regulation [Kennedy et al., 2009]. Existing neuroimaging studies have demonstrated an increase in amygdala activation in response to approaching relative to static faces, irrespective of emotion [Schienle et al., 2015], and to looming threatening stimuli [Mobbs et al., 2009; Mobbs et al., 2010]. Moreover, results obtained with both amygdala lesion patients and healthy participants suggested an association between amygdala function and interpersonal distance [Kennedy et al., 2009]. Based on these data, we hypothesized that activity within the amygdala would be enhanced in response to approaching compared to receding faces, and would be associated with greater interpersonal distance. A solid body of research has also supported a privileged role of the amygdala in processing fear-related stimuli [Adolphs et al., 1994; Aube et al., 2015; Kryklywy et al., 2013; Phillips et al., 1998], particularly fearful facial expressions [Fusar-Poli et al., 2009; Thomas et al., 2001; Whalen et al., 1998]. In light of this evidence, we also predicted the amygdala would be preferentially engaged in response to fearful faces relative to other expressions. In addition to the amygdala, animal and human studies have also suggested the involvement of a fronto-parietal network in the maintenance of personal space, which includes the margins of the intraparietal sulcus, as well as somatosensory and premotor cortices [Brozzoli et al., 2013; Ferri et al., 2015; Graziano and Cooke, 2006; Holt et al., 2014]. Hence, we additionally expected these regions to be preferentially engaged in response to approaching faces. We were interested in assessing whether facial expressions would modulate activity within this network, although no predictions were formulated regarding potential emotion effects.

Interpersonal distance preferences are also likely influenced by personality. Importantly, emotional context and personality appear to be interacting factors, with some traits selectively affecting approach-avoidance tendencies to specific emotions [Sambo and Iannetti, 2013; Schienle et al., 2015; Veenstra et al., 2016]. Personality traits associated with deficient emotional and empathic responses are characteristic of psychopathic personalities [Blair, 2015; Frick and White, 2008; Marsh, 2016], and may be particularly impactful in shaping interpersonal distance preferences in emotional contexts [Hammer and Marsh, 2015]. In

clinical populations, there is evidence that some of the severe interpersonal problems associated with psychopathy (e.g., instrumental aggression) may be linked to atypical social approach-avoidance mechanisms [von Borries et al., 2012]. Our second goal was to investigate whether psychopathic traits in a healthy community sample affects neural approach-avoidance patterns and interpersonal distance to different emotional expressions, particularly those signaling distress. Recent work has demonstrated that coldhearted psychopathic traits, in particular, are associated with a preference for shorter interpersonal distances in healthy individuals [Vieira and Marsh, 2014]. These traits have also been linked to impairments in processing distress cues such as fearful and sad expressions in developmental populations [Blair et al., 2001; Dawel et al., 2012], and are associated with atypical amygdala function in both youth [Lozier et al., 2014; Viding et al., 2012] and healthy adult samples [Han et al., 2012]. In light of these findings and of the putative involvement of the amygdala in interpersonal distance regulation, we hypothesized that coldhearted psychopathic traits would be associated with a preference for shorter interpersonal distances to distressrelated emotions such as fear and sadness, which would be accompanied by reduced amygdala engagement. To our knowledge, this is the first study to investigate the neural processes implicated in interpersonal distance preferences in a healthy population, and to examine how those processes are simultaneously influenced by emotional context and individual differences in empathy.

MATERIALS AND METHODS

Participants

Twenty-three participants (12 F, M = 20.96, SD = 2.48, range 18–29) were recruited through advertisements posted in the University of Western Ontario. All participants were right-handed, had normal or corrected-to-normal vision, and reported having no history of psychiatric or neurological diagnoses, brain injuries or substance abuse. The study was approved by the Health Sciences Research Ethics Board at the University of Western Ontario (London, ON, Canada). Participants provided written informed consent and were compensated for their time.

Psychopathic Traits Assessment

Psychopathic personality traits were assessed using the Psychopathic Personality Inventory – Revised [Lilienfeld and Widows, 2005], a self-report instrument designed to measure psychopathic traits in a dimensional manner. This is consistent with the idea that psychopathy is a set of traits continuously distributed in the general population rather than a clinical taxon and, like other personality disorders, it can be more reliably assessed using dimensional models of personality [Drislane et al., 2014; Marcus et al., 2004; Miller

et al., 2001; Skeem et al., 2011]. The PPI-R contains 154 items organized in seven subscales (social influence, fearlessness, stress immunity, Machiavellian egocentricity, rebellious nonconformity, blame externalization, and carefree nonplanfulness) that load onto two higher-order factors (PPI-I or fearless dominance, and PPI-II or Self-centered impulsivity) and an eighth subscale, Coldheartedness (C), that is believed to be largely independent of both these factors, and is therefore regarded simultaneously as a subscale and a higher-order dimension [Skeem et al., 2011]. Fearless dominance scores index interpersonal dominance and low anxiety (e.g., "When I'm in a frightening situation, I can "turn off" my fear almost at will"), whereas Self-centered impulsivity scores are related to disinhibition and impulsive behavior (e.g., "I like to act first and think later;" Lilienfeld and Widows, 2005].

Coldheartedness scores index callousness and lack of sympathy for others (e.g., "When someone is hurt by something I say or do, that's their problem;" [Lilienfeld and Widows, 2005]. It is the component that best taps onto the low empathic concern dimension of psychopathy, considered the precursor and core feature of the adult psychopathic phenotype [Frick, 2016]. Importantly, Coldheartedness has been previously associated with amygdala dysfunction [Han et al., 2012], abnormalities in fearful face perception [Oliver et al., 2015], preferences for shorter interpersonal distances [Vieira and Marsh, 2014], and increased approach to angry faces [Hammer and Marsh, 2015] in community populations. Because we were particularly interested in investigating how emotional contexts shapes interpersonal distance preferences, we hypothesized coldhearted psychopathic traits would have the largest influence. Therefore, our analyses were focused on this component. Coldheartedness raw scores were converted into T scores (range = 33–67; M = 45.83, SD = 9.39) based on sex and age group norms [Lilienfeld and Widows, 2005] and used in the analyses.

Computerized Interpersonal Distance Task

In this task, we assessed participants' preferred distance to faces displaying five different emotions. Participants were presented a series of facial expressions and asked to adjust their size on the screen, in order to manipulate the perceived distance from each face (Fig. 1B). Forty faces from eight Caucasian actors (four male, four female) displaying angry, fearful, happy, sad and neutral expressions were selected from the NimStim Set of Facial Expressions [Tottenham et al., 2009]. Images were converted to grayscale, cropped to remove extraneous features around the face, and the edges smoothed. Participants were instructed to use as reference the distance they would normally keep "when having a conversation with a stranger." The task comprised 40 approach (faces were initially small, simulating a greater distance) and 40 withdrawal trials (faces were bigger, simulating closer distance), presented randomly. In each trial, participants pressed "2" in a response box to bring the face closer (size increased by a factor of 1.13), and "3" to push it

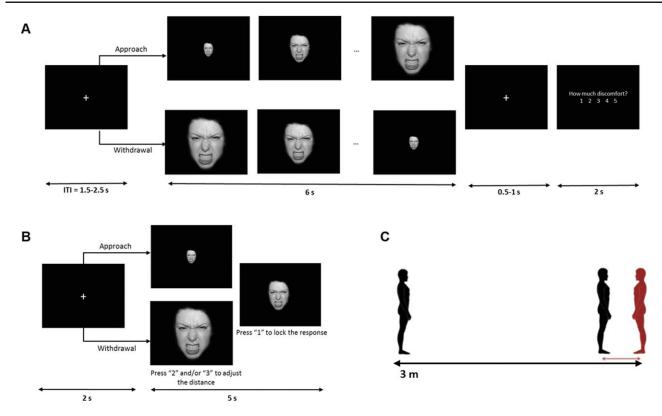


Figure 1. Schematic representation of the experimental tasks: imaging task (\mathbf{A}), computerized interpersonal distance task (\mathbf{B}) and "Stop-distance" task (\mathbf{C}). [Color figure can be viewed at wileyonlinelibrary.com]

back (size decreased by a factor of 1.13). They were given a 5-second interval to press the buttons as many times as necessary to achieve the desired distance, upon which they pressed "1" to lock their response and move on to the next trial. The task was programmed and delivered using E-prime 2.0 (Psychology Software Tools Inc.).

als of the task, 24 in each condition. The order of runs was randomized across participants. The task was programmed and delivered using E-prime 2.0 (Psychology Software Tools Inc.).

sadness, neutral) once in each direction (approach and

withdrawal). Thus, in total, participants performed 240 tri-

fMRI Task

To investigate BOLD responses to approaching and withdrawing emotional faces that were not contaminated by motoric responses, participants underwent fMRI scanning while they passively viewed facial expressions (same stimuli as in the computerized interpersonal distance task) that either increased (Approach) or decreased (Withdrawal) in size, appearing to move towards or away from or them, respectively. Images increased or decreased by a factor of 1.13, resulting in 20 frames per trial. In each trial, participants were instructed to stay focused on the face (6 s), and then rate their level of discomfort (2 s) using a 5-point scale (1—min, 5—max; Fig. 1A). Participants completed eight functional runs of 30 trials each (≈ 5 m). Each run included randomly presented faces from three actors displaying the five expressions (anger, fear, happiness,

"Stop-Distance" Task

We were interested in confirming whether performance in our computerized task predicted interpersonal distance preferences in real interaction settings. We therefore also asked participants to complete a "Stop-distance task" akin to that used in prior studies [Kennedy et al., 2009; Vieira and Marsh, 2014], which provided a more ecologically valid measure of preferred distance (Fig. 1C). In this task, performed outside the scanner, participants adjusted the distance between themselves and the experimenter across a series of trials. The task comprised an approach and a withdrawal block (4 trials each), counterbalanced across participants. In approach trials, the experimenter stood 3 m away and walked towards the participant at a natural gait (approximately 1m/s). In withdrawal trials, the experimenter started standing with her toes at about 3 cm from

the participant's, and walked backwards. In both, participants were instructed to tell the experimenter to stop at their preferred distance (*i.e.*, the distance at which they felt "the most comfortable"). Chin-to-chin distance was recorded in each trial using a digital laser tape measure (Bosch GLM 15).

Procedures

Functional neuroimaging took place in one session at the Centre for Functional and Metabolic Mapping of the Robarts Research Institute (University of Western Ontario). After providing written consent, participants were given a practice version of the experimental tasks on a laptop. They completed 8 practice trials of the scanning task and 16 trials of the computerized distance task, both featuring only neutral expressions of two actors not used in the experimental versions. For the "Stop-distance task," all participants were tested by the same experimenter in a room next to the scanner, either before or after the scan (counterbalanced). Following the scan, participants were administered the PPI-R; [Lilienfeld and Widows, 2005]. Additionally, in line with prior suggestions that interpersonal distance preferences in higher coldheartedness individuals could be associated with aggressive tendencies, we also administered a self-report measure of aggression (Reactive-Proactive Aggression Questionnaire, RPQ; [Raine et al., 2006].

fMRI Acquisition, Preprocessing, and Analysis

Subjects were scanned in a single session using a 3T Siemens Scanner with a 32-channel head coil. Whole-brain functional images were taken with an echo-planar T2*-weighted imaging sequence while participants performed the scanning task (TR = 1250 ms, TE = 30 ms, FoV = 192 mm, flip angle = 40° , 57 interleaved slices of 2.00 mm isovoxels, 267 volumes per run). Scan parameters were chosen to optimize the signal-to-noise ratio for the amygdala based on recent recommendations [Morawetz et al., 2008; Robinson et al., 2004]. After 4 functional runs, a high resolution T1-weighted anatomical scan was obtained (TR = 2300 ms, TE = 2.98 ms; FoV = 256 mm, flip angle = 9° , 192 axial slices of 1 mm isovoxels), during which participants performed the computerized distance task. Four more functional runs of the scanning task were collected after the anatomical scan.

Preprocessing of fMRI data was done using SPM12 (Well-come Trust Centre for Neuroimaging, www.fil.ion.ucl.ac. uk). After slice timing correction, images were realigned to the volume acquired immediately before the anatomical scan, using 6 parameter rigid-body transformations. They were then coregistered with the structural data, normalized to standard space using the Montreal Neurological Institute (MNI) template with a voxel size of $2 \times 2 \times 2$ mm, and smoothed using a Gaussian kernel with an isotropic full-width-half-maximum of 4 mm. The acquisition parameters

(namely slice thickness and TE) and spatial smoothing kernel were based on recommendations by Morawetz and colleagues (2008] and Robinson and colleagues (2004] to optimize signal-to-noise ratio in the amygdala: the use of 2 mm slices has been associated with fewer susceptibility artifacts, and moderate smoothing has been recommended to balance sensitivity and specificity. Similar parameters have been employed in prior fMRI studies investigating the involvement of the amygdala in socio-affective tasks in comparable populations [Han et al., 2012]. Additionally, a high-pass filter cutoff of 128 seconds was applied to remove slow signal drifts.

First-level analysis was based on the general linear model. Time-series of each voxel were normalized by dividing the signal intensity of a given voxel at each point by the mean signal intensity of that voxel for each run and multiplying it by 100. Resulting regression coefficients thus represent a percent signal change from the mean. Regressors were created by convolving the train of stimulus events with a canonical hemodynamic response function. Ten events of interest were modelled, corresponding to each of the five facial expressions (Anger, Fear, Happiness, Sadness and Neutral) in each direction (Approach, Withdrawal) (6 s). In addition, 10 more regressors were created to model the same conditions during the response slides (discomfort ratings; 2 s). The six motion parameters estimated during realignment were also included in the model as regressors of no interest.

Statistical Analysis

Behavioural data

Our behavioural measures were the distance set in the computerized task, which were operationalized as [100 – percentage of face maximum size], and the discomfort ratings. We investigated the effects of Emotion and Direction on these measures through two 5 (Anger, Fear, Happiness, Sadness and Neutral) by 2 (Approach, Withdrawal) repeated-measures ANOVAs. In addition, for the "Stop-distance task," we averaged all trials and performed a correlation analysis to test whether overall preferred distance outside the scanner predicted the overall distance set in the computerized task.

Finally, we used correlations to test the hypothesized association between Coldheartedness and distance to fearful and sad expressions, following evidence suggesting callous psychopathic traits are associated with impairments in processing distress cues. To isolate emotion-related effects, we computed difference scores between each emotion and Neutral for each direction, and then averaged across approach and withdrawal scores. We performed bivariate correlations between the two resulting average difference scores and Coldheartedness. The threshold for statistical significance was set at P < 0.05 two-tailed for all behavioural analyses. Greenhouse-Geisser procedure was used to correct departures from sphericity, when necessary, and Sidak correction

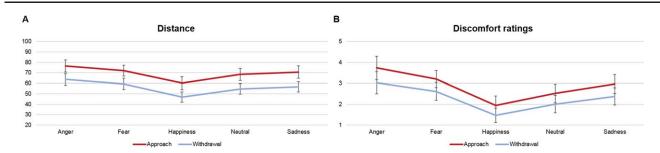


Figure 2.

Mean distances set to each emotional expression in the computerized task (**A**), and mean discomfort ratings during the scanning task (**B**). [Color figure can be viewed at wileyonlinelibrary.com]

was used to adjust the significance level when multiple correlations were performed. Analyses were performed in SPSS Version 23 (IBM Corp).

fMRI data

To investigate the neural activation patterns to approaching and withdrawing emotional faces (6-second interval), we performed a whole-brain 5 (Anger, Fear, Happiness, Sadness and Neutral) by 2 (Approach, Withdrawal) ANOVA, with emotion and direction as withinsubject factors. To minimize Type I errors, only results found with a false discovery rate (FDR)-corrected threshold of P < 0.05 are reported. To test hypothesized associations between brain activation and behaviour, we extracted the percent signal change of significant clusters and performed correlational analyses with both behavioural difference scores and Coldheartedness using SPSS. Sidak correction was used to adjust the significance level of multiple correlations.

To further investigate the association between Coldheartedness and amygdala activation to distress cues we performed region-of-interest (ROI) analyses using anatomically defined masks of the left and right amygdala. ROIs were created using the Automated Anatomical Labeling atlas (aal, + 1 dilation; Tzourio-Mazoyer et al., 2002] within the WFU PickAtlas toolbox [Maldjian et al., 2004; Maldjian et al., 2003]. For each ROI, we performed regression analyses on the Approach-Withdrawal average image for Fear and for Sadness, using Coldheartedness T scores as predictor. Significant clusters at a corrected threshold of P < 0.05 are reported.

RESULTS

Behavioural Results

In the computerized task, we found main effects of direction [F(1,22)=95.82, P<0.001] and emotion [F(4,88)=31.52, P<0.001], but no significant interaction. The main effect of direction was characterized by greater preferred distances in the Approach than the Withdrawal condition. For the main effect of emotion, with the exception of

neutral and sadness, all other emotions differed significantly from each other (all ps < 0.05), with greatest preferred distances for anger, followed by fear, sadness, neutral and happiness (Fig. 2A).

Finally, for ratings of discomfort, there were main effects of direction [F(1,22) = 9.98, P = 0.005], emotion [F(4,88) = 35.06, P < 0.001], and a significant interaction [F(4,88) = 3.41, P = 0.016]. Greater discomfort was reported during Approach trials, and all emotions differed significantly from each other (all ps < 0.05), with highest discomfort ratings for angry expressions, followed by fear, sadness, neutral and happiness. To explore the interaction, we compared the approach—withdrawal discomfort difference scores per emotion in a repeated measures ANOVA, and found that the difference score for anger was greater than for happiness (P = 0.020); no other difference scores differed significantly (Fig. 2B).

To verify whether distances in the computerized task predicted interpersonal distance preferences, we examined the correlation between those distances and that chosen in the Stop-distance task. We found that overall Stop distance was correlated at trend level with overall computerized distance (r = 0.396, P = 0.06).

Coldheartedness and distance

Correlation analysis revealed a trend for shorter distance to fearful faces in participants scoring higher in Coldheartedness (r = -0.403, P = 0.057). No correlation was found for sadness.

fMRI Results

Effects of direction and emotion on whole-brain activation

As hypothesized, activation in the right amygdala (xyz = 24, 0, -14) was increased for approaching versus receding facial expressions, irrespective of emotion. The same pattern was found in the margins of the intraparietal sulcus, including the left superior (SPL; -28, -58, 44) and right inferior (IPL; 40, -56, 46) parietal lobules. Other regions with increased activation for approaching versus

TABLE I. Descriptive statistics for age and PPI-R factor

T scores

	M(SD)	Range
Age	21 (2.5)	18–29
PPI-R total T	47.9 (9.2)	40-68
Fearless dominance T	47.7 (11.1)	27-68
Self-centered impulsivity T	46.7 (7.1)	36-61
Coldheartedness T	45.8 (9.4)	33-67

withdrawing faces included the bilateral insula (L: -28, 26, -2; R: 44, 20, -2), bilateral DLPFC (L: -50, 32, 30; R: 50, 34, 32), and a large cluster (8, -98, 18) that encompassed occipital, temporal and parietal visual areas (Table II, Fig. 3).

Contrary to our predictions, whole brain analysis found no main effect of emotion in the amygdala. Instead, results showed emotion affected activation in a prefrontal and parietal network that included the dorsomedial prefrontal cortex (dmPFC; 0, 64, 28), bilateral inferior frontal gyrus (IFG; L: -50, 36, -8; R: 44, 38, -8), right orbitofrontal cortex (OFC; 28, 62, 16), bilateral inferior parietal lobule (IPL; L: -42, -30, 44; R: 50, -52, 50), and angular/supramarginal gyrus (60, -50, 32) (Table II, Fig. 4A). Percent signal change was extracted from significant clusters to delineate the nature of these effects. The largest frontal clusters (located in the dmPFC and OFC) showed increased activation to faces of anger and happiness relative to other expressions (all ps < .05), with parietal clusters located in the temporoparietal junction (IPL and angular/supramarginal gyrus) exhibiting a similar activation pattern (Fig. 4B).

Results also revealed clusters with a significant *Emotion* \times *Direction* interaction. Of note, these regions included the right anterior insula (42, 6, -6) and left mid insula (-40, 2, 18), bilateral ventrolateral PFC (vlPFC; L: -34, 52, 24; R: 36, 44, 4), and left IFG (-40, 22, -12) (Table II, Fig. 5). Percent signal change was extracted from each cluster and paired t-tests were performed to compare activation in approach versus withdrawal trials, per emotion. In the insula (bilaterally),

results showed increased activation to approach versus withdrawal for happy and angry faces, and an opposite pattern for sadness. Results also showed opposite activation patterns to approaching versus withdrawing faces for happy and sad expressions in the vIPFC (bilaterally), such that activation was greater for withdrawing versus approaching sad faces, and for approaching versus withdrawing happy faces. Finally, in the left IFG, results showed a more pronounced activation increase for approach versus withdrawal for angry and happy faces (all ps < 0.05; see S1 for a more detailed description of the interaction).

Amygdala activation and distance. We extracted the percent signal change from the right amygdala cluster identified in the ANOVA (main effect of direction) and tested the association between activation within this region and distance in the computerized task. As hypothesized, right amygdala activation was significantly associated with greater distances to angry (r = 0.61, P = 0.002), sad (r = 0.527, P = 0.010) and, at trend level, fearful (r = 0.504,P = 0.014) expressions (Fig. 6). We also performed exploratory correlations between amygdala percent signal change and discomfort ratings. Results showed trends for increased amygdala activation and higher discomfort to angry (r = 0.421, P = 0.045), sad (r = 0.462, P = 0.027) and **fearful faces** (r = 0.375, P = 0.078). No associations were found between amygdala activation and preferred distance (r = 0.006, P = 0.98) or discomfort ratings (r = 0.192,P = 0.381) to happy expressions.

Amygdala activation and coldheartedness

Whole-brain analysis showed enhanced activation in the right amygdala to approaching versus receding faces. Following evidence that callous psychopathic traits are associated with abnormal amygdala activity to distress cues [Han et al., 2012; Lozier et al., 2014], we hypothesized activation within this cluster in response to fearful and sad faces would be modulated by Coldheartedness. To test this

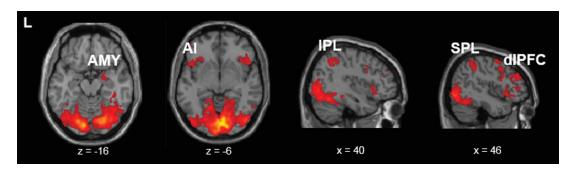


Figure 3.

Clusters showing a main effect of Direction in the 5 \times 2 ANOVA, including the bilateral visual cortex, fusiform gyrus, right inferior (IPL) and superior parietal lobules (SPL), right amygdala, bilateral anterior insula (AI) and bilateral dorsolateral prefrontal cortex (dIPFC; FDR-corrected P < 0.05). [Color figure can be viewed at wileyonlinelibrary.com]

TABLE II. Results of the 5 (emotion) by 2 (direction) ANOVA (FDR corrected P<0.05; MNI coordinates are reported)—effects of direction and emotion

Location	R/L	k	х	у	Z	BA	Nature of effect
Main effect of emotion							
Cerebellum	L	55	-10	-88	-28	_	HA > FE, NE , SA
Inferior parietal lobule	R	158	50	-52	50	40	AN = HA > FE, NE, SA
Angular gyrus	R	47	60	-50	32	40	AN > FE, NE
Inferior parietal lobule	L	51	-42	-30	44	40	AN = HA > SA
Precentral gyrus	R	78	28	-22	76	6	HA > FE, SA
Postcentral gyrus	L	49	-46	-18	48	4	HA > AN, FE, NE
Premotor cortex	R	215	38	6	54	6, 8	AN > SA; $HA > FE$, NE , SA
Ventrolateral prefrontal cortex	R	62	56	20	18	45	HA > NE, SA
Inferior frontal gyrus	L	54	-50	36	-8	47	AN > FE, HA , NE
Inferior frontal gyrus	R	114	44	38	-8	47	AN > FE, NE ; $HA > NE$; $SA > NE$
Dorsolateral prefrontal cortex	L	111	-20	50	24	10	AN > FE, NE ; $HA > FE$
Orbitofrontal cortex	R	289	28	62	16	10	AN > FE, NE , SA ; $HA > NE$, SA
Dorsomedial prefrontal cortex	L/R	415	0	64	28	9, 10	AN > FE, SA ; $HA > FE$
Main effect of direction							
Middle occipital gyrus	R/L	18624	8	-98	18	17, 18, 19, 30, 31, 37	A > W
Cerebellum	L	53	-12	-76	-44	_	A > W
Intraparietal sulcus	L	87	-28	-58	44	7	A > W
Inferior parietal lobule	R	506	40	-56	46	40	A > W
Amygdala	R	48	24	0	-14	_	A > W
Premotor cortex	L	49	-48	6	38	9	A > W
Supplementary motor area	L	287	-6	8	50	32	A > W
Inferior frontal gyrus	L	394	-44	16	-4	47	A > W
Anterior insula/IFG	R	638	44	20	-2	46, 9	A > W
Anterior insula	L	43	-28	26	-2	47, 13	A > W
Dorsolateral prefrontal cortex	L	173	-50	32	30	9, 46	A > W
Dorsolateral prefrontal cortex	R	1407	50	34	32	46	A > W
Direction × Emotion							
Precuneus	R	47	14	-66	32	31	
Rolandic operculum/mid-insula	L	57	-40	2	18	44	
Anterior insula	R	44	42	6	-6	13	
Inferior frontal gyrus	L	65	-40	22	-12	47	
Ventrolateral prefrontal cortex	R	272	36	44	4	10	
Ventrolateral prefrontal cortex	L	123	-34	52	24	10	

hypothesis, we performed correlations between percent signal change in the right amygdala in response to approaching sad and fearful faces and Coldhearteness scores. Results showed a significant negative association between activation to sad faces and Coldheartedness (r = -0.47, P = 0.027) (Fig. 6B). No association was found for fear.

To confirm the relation between Coldheartedness and amygdala activation, we created bilateral anatomical masks of this region and performed regression analyses within SPM using Coldheartedness scores as predictors. The ROI analysis confirmed a cluster within the right amygdala (14 voxels; 22, -10, -12) wherein activation in response to sad faces was negatively associated with Coldheartedness (Fig. 7).

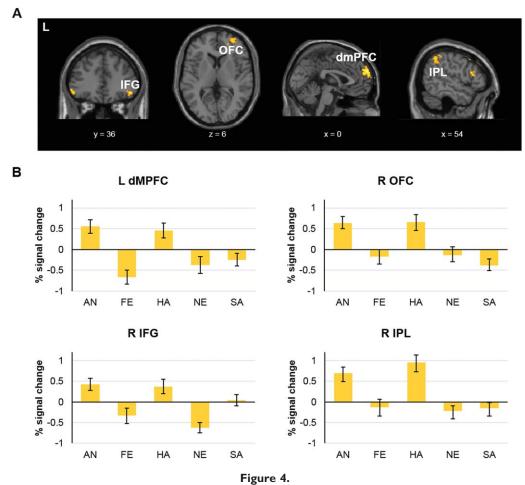
DISCUSSION

Successful social interactions rely on our ability to adequately adjust the distance from others based on relevant

emotional cues. In this study, we used fMRI to investigate the neural systems implicated in regulating interpersonal distance to different emotional expressions. Our findings revealed that a network of regions, including the amygdala, insula, dlPFC and IPS, was preferentially activated to approaching versus receding faces. Also, prefrontal and parietal regions, such as dmPFC and TPJ, were modulated by emotion, showing increased activity in response to facial expressions of anger and happiness. Finally, our results suggested that characteristics of the perceiver may moderate these effects, with coldhearted psychopathic traits being associated with differential limbic responses to approaching sad expressions.

The Amygdala and Interpersonal Distance

As hypothesized, we found greater right amygdala activity in response to approaching relative to withdrawing faces. These findings are in agreement with prior work



(A) Clusters showing a main effect of emotion in the 5 \times 2 ANOVA, including the bilateral IFG right OFC, left IPL and left dorsomedial prefrontal cortex (dmPFC; FDR-corrected P < 0.05). (B) Graphs depicting the percent signal change per facial expression in clusters showing a main effect of emotion (left dmPFC, right OFC, right IFG and right IPL). [Color figure can be viewed at wileyonlinelibrary.com]

demonstrating the amygdala responds preferentially to looming versus receding threatening stimuli (Coker-Appiah et al., 2013; Mobbs et al., 2010], and suggest this extends to salient social information, such as emotional faces. However, contrary to our predictions, amygdala effects were not modulated by emotional expression. This result may be surprising in light of evidence that the amygdala is more reliably activated in response to fearful faces than to other expressions [Fusar-Poli et al., 2009], but it is consistent with previous studies showing greater amygdala activation to approaching faces irrespective of emotion [Schienle et al., 2015]. Existing accounts implicate the amygdala—particularly its basolateral nucleus—in encoding salient, ambiguous or unpredictable information [Davis et al., 2016; Whalen, 1998], and in evaluating and representing the intensity of emotional stimuli [Kryklywy et al., 2013]. Both these processes are likely brought to bear in our paradigm; when approached by other

individuals, it is likely advantageous to both identify and assess the intensity of their emotional states, in order to infer their behavioural intentions and adjust our behavior accordingly. Our results suggest that, in the context of our task, spatial proximity was perhaps a more salient cue than emotion, as any approaching facial expression is potentially relevant. Furthermore, participants were required to rate their discomfort as facial stimuli approached their personal space. Judgements of discomfort may have caused generalized engagement of the amygdala, irrespective of the facial expression. Our correlational findings appear to support this interpretation; as predicted, we found a significant association between amygdala activity and interpersonal distance, in line with previous suggestions that this region is involved in personal space maintenance [Kennedy et al., 2009]. Specifically, our results showed increased amygdala activation to approaching faces predicted greater discomfort (at trend

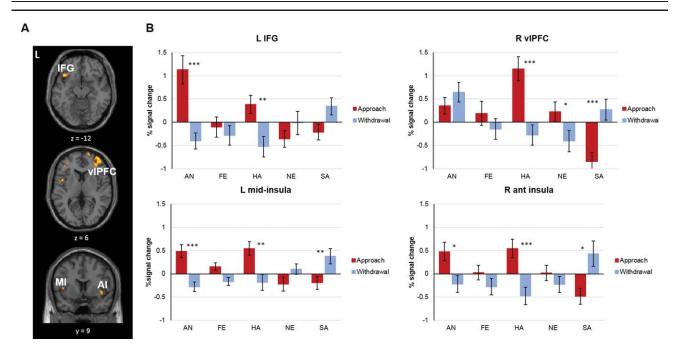


Figure 5.

(A) Clusters showing a direction \times emotion interaction in the 5 \times 2 ANOVA, including the left IFG, right ventrolateral prefrontal cortex (vIPFC), left mid-insula (MI) and right anterior insula (AI; FDR-corrected P<0.05). (B) Graphs depicting the

percent signal change per facial expression and direction in clusters showing a significant interaction (left IFG, right vIPFC left MI and right AI) (*P<0.05, ** P<0.01, *** P<0.001). [Color figure can be viewed at wileyonlinelibrary.com]

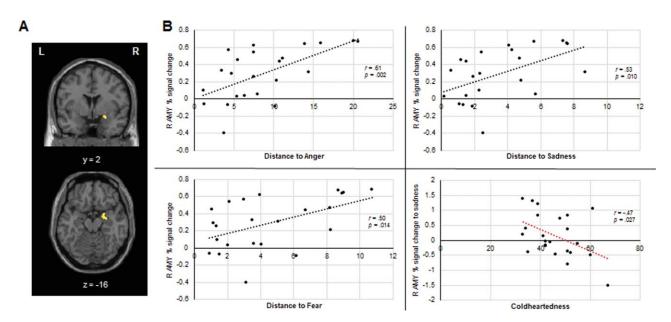


Figure 6.

Scatter plots depicting the association between right amygdala activation (24, 0, -14) and distance set to angry (top left), sad (top right) and fearful expressions (bottom left); scatter plot depicting the association between right amygdala activation to sad faces and Coldheartedness scores (bottom right). [Color figure can be viewed at wileyonlinelibrary.com]

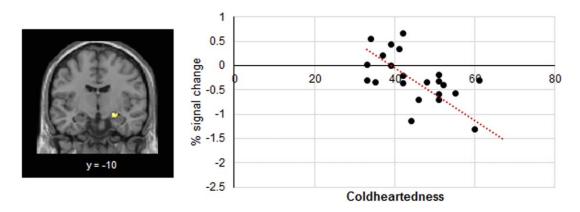


Figure 7. Scatter plot depicting the association between activation to sad faces in the right amygdala ROI and Coldheartedness (FWE-corrected P < 0.05). [Color figure can be viewed at wileyonlinelibrary.com]

level) and distance to angry, fearful and sad faces. This is consistent with previous suggestions that the amygdala contributes to interpersonal distance regulation by generating feelings of discomfort when personal space is breached [Kennedy et al., 2009]. Taken together, our data implicate the amygdala in interpreting the behavioural significance of facial expressions as a function of their proximity, potentially as a means of preserving a safety margin around the individual while appropriate behavioural responses are selected and initiated.

Impact of Emotion and Direction on Parietal and Prefrontal Responses to Faces

Besides the amygdala, approaching faces elicited increased widespread activation that was independent of emotional expression across occipital, parietal, temporal and prefrontal regions. This included brain regions involved in defensive responses, such as the anterior insula [Mobbs et al., 2007; Mobbs et al., 2010], and regions previously implicated in personal space maintenance, such as the margins of the intraparietal sulcus (Holt et al., 2014].

Additionally, we examined whole-brain approach-avoidance patterns to different emotions. Main effects of emotion emerged in the prefrontal (namely, dmPFC, OFC, IFG) and parietal (TPJ) cortices, with activation within these regions being increased in response to faces of anger and happiness relative to other expressions. Interestingly, these two emotions corresponded to the greatest and shortest behavioural distances, and the highest and lowest discomfort ratings, respectively. In spite of conveying opposite social signals, both anger and happiness are approach-oriented (i.e., both reflect a disposition to approach on behalf of the actor, Adams and Kleck, 2005] and dominant [Hess et al., 2000] emotions. It is plausible that personal space intrusions by individuals displaying dominant versus submissive expressions are interpreted differently by an observer. Hence,

unlike fearful or sad faces expressing greater vulnerability [Hess et al., 2000], observers may interpret approaching angry and happy expressions as more likely to result in behavioural action upon themselves. It is possible that, in our data, the greater recruitment of mentalizing regions (e.g., dmPFC, IFG and TPJ) in response to angry and happy faces reflects privileged processing of facial expressions with more probable behavioural consequences for the observer, and therefore demands to predict their intentions. However, more research is needed to formally test this hypothesis.

Finally, we have uncovered a direction by emotion interaction in the insula, vIPFC and IFG, driven by opposite approach-withdrawal patterns to sadness compared to angry and happy expressions. Specifically, across those regions, sad faces elicited greater activation in the withdrawal condition, whereas angry and happy faces were associated with enhanced activation during approach. Contrary to anger and happiness, sadness has been viewed as an avoidance-oriented emotion [Adams and Kleck, 2003; Adams and Kleck, 2005] that signals vulnerability, which could help explain the opposite activation patterns to sad versus angry and happy expressions, particularly in regions previously implicated in processing emotion [insula; Jerram et al., 2014] and social dominance [IFG/vlPFC; Marsh et al., 2009]. However, questions remain as to the motivational value of a receding sad expression. It is noteworthy that prior behavioural studies have reported more complex approach-avoidance patterns for sadness relative to other emotions. For example, Seidel and colleagues (2010] reported participants generally showed implicit approach to sad expressions (joystick task), but when asked to estimate how close/far they would get from a sad expression, their responses predominantly indicated avoidance. Taken together, these findings highlight remaining questions regarding the social value of sad expressions and call for addition research to be clarified.

Coldhearted Psychopathic Traits and Interpersonal Distance

A second goal of this study was to examine whether empathic abilities influenced interpersonal distance to emotional expressions signaling distress and its neural underpinnings. Our hypothesis was partially confirmed, with high Coldheartedness being associated with reduced right amygdala activation to sad expressions. To our knowledge, this is the first study reporting an association between amygdala hypoactivation to sad expressions and subclinical variation in coldhearted traits. The lack of additional empirical evidence for a link between coldhearted psychopathic traits and reduced amygdala sensitivity to sad faces could be due to the fact that most imaging studies on face processing, with either clinical or nonclinical populations, did not include sad expressions in their paradigms [Contreras-Rodriguez et al., 2014; Han et al., 2012; Jones et al., 2009; Mier et al., 2014], or did not perform contrasts with sadness [Gordon et al., 2004]. Nonetheless, psychopathic and callous-unemotional traits have been previously associated with atypical behavioural responses to sadness in youth [Blair et al., 2001; Woodworth and Waschbusch, 2008] and adult forensic samples [Dolan and Fullam, 2006; Hastings et al., 2008]. Additionally, there is evidence supporting the role of the amygdala in processing sad expressions [Fine and Blair, 2000]. Our findings thus lend support to the hypothesis that psychopathic personality traits related to low empathy are associated with diminished sensitivity to distress cues in others, possibly as a result of an amygdala dysfunction [Blair, 2013].

It should be noted that, at the behavioral level, we only found a trend level association between coldheartedness and distance to fearful expressions. This however, could have been due to reduced statistical power, especially given that our effect size (r = -0.4) was comparable to that of prior behavioral studies with larger sample sizes [r = -0.3; Vieira and Marsh, 2014]. Additional research with a larger sample and a greater range of Coldheartedness scores is needed to test the association between variation in these traits and behavioural responses to sad and fearful expressions. Overall, our results suggest dysfunctional social approach-avoidance patterns in individuals with low trait empathy may be associated with atypical amygdala responses to social cues signaling distress.

Caveats and Future Directions

Prior work suggests neural and behavioural response patterns to emotional stimuli may also reflect variation in core affective dimensions such as valence and arousal [Bonnet et al., 2015; Weymar and Schwabe, 2016; Wilson-Mendenhall et al., 2013]. A number of studies have provided a characterization of how different emotions map onto a valence/arousal space [Fontaine et al., 2007; Gerber et al., 2008; Mehu and Scherer, 2015; Yik et al., 2011]. These studies suggest that the dimensional profile

associated with each emotion is relatively stable across prototypical expressions of that emotion. Hence, some of the emotion-related effects in our data may reflect the inherent valence/arousal configuration of each emotion, as well as variations in other dimensions, such as dominance. Because dimensional ratings are not available for the experimental stimuli used in our study, we are unable to test the relative contribution of valence, arousal or dominance for the reported effects. Further research is needed to directly test the extent to which variation along different affective dimensions can account for approach/avoid preferences to distinct emotions. Regarding potential confounds, we have minimized the influence of gender and age on Coldheartedness by using sex and age-normalized T scores instead of raw scores. Also, it is unlikely that level of education has played a role in the reported effects, given that all participants were recruited from a relatively homogenous undergraduate population. However, it has been suggested that gender may also influence the recognition of facial expressions [Forni-Santos and Osorio, 2015] and empathic abilities [Christov-Moore et al., 2014], processes which may relate to interpersonal distance preferences [Perry et al., 2015]. Recent work has also reported differential neural activation patterns to personal space intrusions by men and women [Wabnegger et al., 2016]. In the present data, exploratory analyses revealed that females preferred greater distances than males in the approach condition only, irrespective of emotional expression. Given that we were primarily interested in emotion-specific effects on interpersonal distance and its neural substrates, no further gender differences were explored. Future research using larger mixed samples should assess how personal space preferences are affected by the gender.

One important limitation of this study is the relatively limited sample size for exploring individual differences, and consequently reduced statistical power, in comparison to prior work investigating neural correlates of socio-affective processes as a function of psychopathic traits [Han et al., 2012]. We have attempted to overcome this limitation by relying on correlational methods rather than group analysis to explore the effects of Coldheartedness in our data. Nevertheless, future work involving larger sample sizes would be valuable for further exploring these effects.

Conclusions

To our knowledge, this was the first study to explore the neural processes involved in regulating interpersonal distance in emotional contexts, and how those processes varied with individual differences in empathy. It differed from previous fMRI studies that examined the neural signatures of static emotional expressions [Fusar-Poli et al., 2009], or only contrasted approach and static stimuli [Schienle et al., 2015]. Present findings implicate the amygdala in approach-avoidance behaviour in social settings and, particularly, in interpersonal distance preferences to anger, sadness and fear displays. Moreover, we have

demonstrated that individual differences in empathy may selectively affect approach-avoidance tendencies to distress cues. Our hypotheses for this study were specific for low trait empathy as described and assessed for psychopathic personalities, given prior evidence of an association between those features and both interpersonal distance and amygdala dysfunction. Our findings concern community samples of individuals scoring high on coldhearted traits, and may not generalize to all psychopathic populations. However, in light of suggestions that the core deficits in psychopathy include reduced responsiveness to emotional cues in others [i.e., low empathy; Blair, 2015], the present findings may shed light on the potential neurobiological mechanisms disrupted in psychopathic individuals. Overall, the present work contributes to a better understanding of how people use emotional cues to guide social behaviour, and how individual differences in empathy influence this process.

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