

Detecting emotion in others: increased insula and decreased medial prefrontal cortex activation during emotion processing in elite adventure racers

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Understanding the neural processes that characterize elite performers is a first step to develop a neuroscience model that can be used to improve performance in stressful circumstances. Adventure racers are elite athletes that operate in small teams in the context of environmental and physical extremes. In particular, awareness of team member's emotional status is critical to the team's ability to navigate high-magnitude stressors. Thus, this functional magnetic resonance imaging (fMRI) study examined the hypothesis that adventure racers would show altered emotion processing in brain areas that are important for resilience and social awareness. Elite adventure racers ($n=10$) were compared with healthy volunteers ($n=12$) while performing a simple emotion face-processing (modified Hariri) task during fMRI. Across three types of emotional faces, adventure racers showed greater activation in right insula, left amygdala and dorsal anterior cingulate. Additionally, compared with healthy controls adventure racers showed attenuated right medial prefrontal cortex activation. These results are consistent with previous studies showing elite performers differentially activate neural substrates underlying interoception. Thus, adventure racers differentially deploy brain resources in an effort to recognize and process the internal sensations associated with emotions in others, which could be advantageous for team-based performance under stress.

Keywords: athlete; resilience; interoception; emotion detection

INTRODUCTION

Exposure to extreme stress can have profound effects on brain–behavior relationships that support the ability to respond to and maintain optimal performance during stress. In particular, high-magnitude stress impairs cognitive function (Lieberman *et al.*, 2005; Vasterling *et al.*, 2006), alters emotion regulation and processing (Van der Kolk *et al.*, 2005; Frewen and Lanius, 2006) and results in significant interpersonal challenges that can affect social support (Palinkas, 2001; Rosnet *et al.*, 2004; Schmidt *et al.*, 2004; Taylor *et al.*, 2004). Despite these negative effects of extreme stress, certain individuals are able to adapt to, recover from or even thrive in high-stress situations. A number of peripheral nervous system and psychosocial factors are associated with stress-resilience (Southwick *et al.*, 2005), but less understood are neural processes that promote optimal performance during high-magnitude stressors. Available evidence suggests that resilient individuals process information about their own internal physical condition differently (Paulus *et al.*, 2012; Simmons *et al.*, 2012); less clear is whether an optimal response to extreme stress is associated with altered neural processing of affective information about others. For team-based performance, it is critical that individual team members accurately detect emotion in others and appropriately integrate the internal sensations associated with processing emotion in others in order to increase the performance of the team (Palinkas, 1992). Therefore, as a first step toward discovering the neural signature of elite performers, we sought to further understand the neural mechanisms that underlie the recognition and categorization of affective information about others in highly resilient individuals. The present study extends the current research literature on the relationship between resilience and emotion by examining whether neural

processing of emotions is based on the goals of the team (Paulus *et al.*, 2010) or is a more general effect of being resilient.

Individuals who respond well to high-magnitude stressors may do so in part because of a well-contextualized interoceptive sense (Paulus *et al.*, 2009), i.e. these individuals maintain an accurate representation of their own internal state as it relates to the environmental challenges. Interoception is the brain's awareness and representation of internal physiological states (Craig, 2002). The interoceptive system is essential to maintaining homeostasis, as it utilizes a number of feedback systems to the brain to make it 'aware' of imbalances or conflicts in multiple internal systems. Greater awareness in one of these internal systems (e.g. pain or enteric sense) is associated with sensitivity to other internal systems (e.g. subjective feelings or saliency). For example, individuals who are better at detecting their own heartbeat are also more aware of their emotions (Barrett *et al.*, 2004). Interoception is mediated in part by the insula cortex, a paralimbic structure (Craig, 2009) believed to play a critical role in maintaining optimal performance under stress (Paulus *et al.*, 2009). For example, a study of special operations forces showed greater activation in the right insula while processing emotional information about others (Paulus *et al.*, 2010). In this study, elite warfighters showed increased insula activity while viewing angry faces, which suggests that they directed greater neural processing resources toward the most salient stimuli (e.g. threat-related stimuli). What remains unknown is whether or not this is a general effect of successful adaptation to stress (and therefore other team-based performers would show a similar pattern of activity while processing information about others) or if the goals of the team modify neural activity while processing emotion in others.

The insula processes interoceptive information and is likely to play an integral role in optimizing performance under stress, whereas other brain regions are important for processing information about the emotional status of others. For example, functional resting-state analysis has implicated several brain structures critical to evaluating

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personal and contextual meaning of emotional information, to include bilateral insula cortex, anterior cingulate, medial prefrontal cortex (mPFC), amygdala and hypothalamus (Seeley *et al.*, 2007). Thus, individuals who perform well in extreme situations may use these brain regions to differentially process interoceptive information that is generated when processing affective information about others.

Given that extreme stress alters emotional processing, and evidence suggests that elite performers process emotion information differentially, we hypothesize that elite Adventure Racers will direct increased neural resources to the insula while viewing emotional evocative faces in an effort to regulate their own internal affective state. The goal is to determine whether there is an overall emotion processing effect that is related to being an elite performer or whether processing efficiency is specific to the unique goals of the team as we have previously shown (Paulus *et al.*, 2010).

METHODS

Participants

This study was approved by the University of California San Diego (UCSD) Institutional Review Board and all subjects provided informed consent. Elite Adventure Racers ($N=10$, six males) were recruited for this study by word of mouth. Adventure Racers are a unique set of athletes who possess the ability to perform optimally for extended periods of time under a variety of physical, environmental and social stressors, which renders these individuals as an ideal population to elucidate the neural mechanisms underlying optimal performance in extreme circumstances. Inclusion criteria as an Adventure Racer required the following: (i) participation in multi-day events on an international level; (ii) placed among the top five performing teams in at least three races; (iii) completed international races within the past 5 years and (iv) at least 14 days since last race. The last criterion was used to minimize acute effects related to physical and psychological exhaustion. Age- and education-matched healthy volunteer subjects ($N=12$, eight males) were from studies focused on stress responses in Afghan and Iraqi war veterans as part of the research effort supported by the Center of Excellence for Stress and Mental Health (CESAMH). Twenty-two subjects completed the study. Specifically, 10 Adventure Racers age 37.5 years ($s.d.=6.1$) and 10 healthy volunteers age 36.7 years ($s.d.=6.6$) with 16.3 ($s.d.=1.8$) and 16.1 ($s.d.=1.8$) years of education participated in the study. All subjects were trained to perform the Hariri facial emotion detection task prior to testing during functional magnetic resonance imaging (fMRI) scanning and received \$50 for participation. No restrictions were placed on the consumption of caffeinated beverages; none of the subjects were smokers.

Measures

The Barratt Impulsivity Scale, Version 11 is a 30-item Likert-type self-report questionnaire designed to assess general impulsivity (Patton *et al.*, 1995). Factor analysis of the Barratt Impulsivity Scale (BIS) has revealed six sub-factors: attention, motor, self-control, cognitive complexity, perseverance and cognitive instability.

Zuckerman's Sensation Seeking Scale (SSS-V), form V, is a 40-item questionnaire designed to measure an individual's optimal level of stimulation. The SSS-V has demonstrated reliability and evidence of validity across age, sex and different cultures (Zuckerman *et al.*, 1978). Factor analysis has shown that the SSS measures four factors: thrill and adventure seeking, experience seeking, disinhibition and boredom susceptibility.

The International Physical Activity Questionnaire (IPAQ), short-form, is a seven-item self-report questionnaire designed to measure leisure-time physical activity and exercise levels (Craig *et al.*, 2003).

The IPAQ is scored by summing activity levels across self-reported time spent engaging in low-, moderate- and high-intensity physical activity or exercise, which are then converted to metabolic equivalent of task units per week.

Task

During fMRI, each subject was tested on a modified (Paulus *et al.*, 2005) version of the emotion face-processing task (Hariri *et al.*, 2002). During each 5-s trial, a subject was presented with a target face (on the top of the computer screen) and two probe faces (on the bottom of the screen) and was instructed to match the probe with the same emotional expression to the target by pressing the left or right key on a button box. A block consists of six consecutive trials where the target face is angry, fearful or happy. During the sensorimotor control task, subjects were presented with 5-s trials of either vertical or horizontal ovals or circles in an analogous configuration and instructed to match the shape of the probe to the target. Each block of faces and the sensorimotor control task was presented three times in a pseudo-randomized order. A fixation cross lasting 8 s was interspersed between each block presented at the beginning and end of the task (resulting in 14 fixation periods). For each trial, response accuracy and reaction time data were obtained. There were 18 trials (three blocks of six trials) for each face set as well as for shapes, and the whole task lasted 512 s.

Analysis

Acquisition of images

All scans were performed on a 3T GE CXX4 Magnet (General Electric Medical Systems, Milwaukee, WI, USA) at the UCSD Keck Imaging Center, which is equipped with eight high-bandwidth receivers that allow for shorter readout times and reduced signal distortions and ventromedial signal dropout. Each 1-h session consisted of a three-plane scout scan (10 s), a standard anatomical protocol (i.e. a sagittally acquired spoiled gradient recalled sequence) (field of view (FOV) = 25 cm, matrix = 192×256 , 172 sagittally acquired slices 1 mm thick, TR = 8 ms, TE = 3 ms, flip angle = 12°). We used an eight-channel brain array coil to axially acquire T2*-weighted echo-planar images (EPIs) with the following parameters: FOV = 23 cm, matrix = 64×64 , 30 slices 2.6 mm thick, gap = 1.4 mm, TR = 2000 ms, TE = 32 ms, flip angle = 90° .

Image analysis pathway

The basic structural and functional image processing were conducted with the Analysis of Functional NeuroImages (AFNI) software package (Cox, 1996). A multivariate regressor approach described below was used to relate changes in EPI intensity to differences in task characteristics (Haxby *et al.*, 2000). EPIs were coregistered using a 3D-coregistration algorithm (Eddy *et al.*, 1996) that has been developed to minimize the amount of image translation and rotation relative to all other images. Six motion parameters were obtained for each subject. Three of these motion parameters were used as regressors to adjust for EPI intensity changes due to motion artifacts. All slices of the EPI scans were temporally aligned following registration to ensure that different relationships with the regressors were not due to the acquisition of different slices at different times during the repetition interval.

Multiple regressor analyses

The four orthogonal regressors of interest were (1) happy, (2) angry, (3) fearful and (4) circle/oval (i.e. shape) sensorimotor condition. These 0–1 regressors were convolved with a γ -variate function

(Boynton *et al.*, 1996) modeling a prototypical hemodynamic response [6–8 s delay (Friston *et al.*, 1995)] and to account for the temporal dynamics of the hemodynamic response (typically 12–16 s) (Cohen, 1997). The convolved time series was normalized and used as a regressor of interest. A series of regressors of interest and the motion regressors were entered into the AFNI program 3DDeconvolve to determine the height of each regressor for each subject. The main dependent measure was the voxel-wise normalized relative signal change (or percent signal change for short), which was obtained by dividing the regressor coefficient by the zero-order regressor. Spatially smoothed (4 mm full-width half-maximum Gaussian filter) percent signal change data were transformed into Talairach coordinates based on the anatomical magnetic resonance images, which was transformed manually in AFNI.

Regions of interest

For a detailed description of the regions of interest analysis, see Paulus *et al.* (2010). As an example, the amygdala region of interest was defined by the Talairach Daemon atlas (Lancaster *et al.*, 2000) and functional neuroimage analyses were constrained to the *a priori* constrained regions of interest (Johnstone *et al.*, 2005). For the insular cortex, we extended this approach to use a probability mask. Briefly, to extract a mask for the insular cortex, we used Individual Brain Atlases using Statistical Parametric Mapping software (IBASPM, <http://www.thomaskoenig.ch/Lester/ibaspm.htm>), a toolbox for segmenting structural MR images. All programs in this toolbox are developed in MATLAB (<http://www.mathworks.com>), based on a widely used neuroimaging software package, SPM (Wellcome Trust Centre for Neuroimaging, London, UK). This package uses the non-linear registration and gray matter segmentation processes performed through SPM5 subroutines. Three principal elements for the labeling process are used: gray matter segmentation, normalization transform matrix, which maps voxels from individual space to standardized space, and MaxPro MNI Atlas. Data from a set of an existing set of 39 individuals, with similar sociodemographic characteristics as the target population, were processed using the SPM-based voxel-based morphometry approach (Ashburner and Friston, 2000). These data were subsequently processed using the IBASPM toolbox to obtain estimates of each individual's insula. The group insula mask was obtained by averaging across the individual insular masks and requiring that the insula voxels covered at least 50% of all subjects' gray matter.

Statistics

Groups were compared on demographic and trait characteristics data using independent *t*-tests, and where appropriate Cohen's *d* was calculated as an index of effect size (SPSS, Windows Version 18, Chicago, IL, USA). Performance (reaction time and accuracy) on the emotion processing task was evaluated using a 2 Group (Adventure Racer and healthy control) \times 4 Face (angry, fear, happy and oval) analysis of variance (ANOVA) in SPSS (Norusis, 1990). For fMRI data, whole brain data were clustered to account for multiple comparisons. Data were thresholded at $P < 0.05$ and clusters were retained that exceeded 1024 μL volume for continuous voxels based on Monte Carlo simulations using the AFNI function AlphaSim. All second-level analyses were conducted using the statistical programming language R (<http://cran.r-project.org/>). Specifically, a mixed-model analysis was conducted with the R program Linear Mixed Effects (LME). Fixed effects were emotion type (fear, anger and happy), group (Adventure Racer and control), education and response latency. Each subject comprised the random effects (i.e. an individual intercept was fitted for each subject). Moreover, we conducted voxel-wise multiple linear regression analyses with performance on the emotion-processing task

(latency to respond to angry, fearful or happy faces) as independent measures, and the percent signal change between faces and the sensorimotor control condition as the dependent measure using the lm program in R. Voxel-wise analyses using R were used to be able to use the mixed linear effects approach, which is not implemented in AFNI. LME has several key advantages to modeling advantages to the general linear model (GLM) models that are available in C-coded versions of AFNI. These include using unequal sample sizes as well as more subject data modeling rather than just group level. In fact, AFNI has recently adopted performing these second-level voxel-based analysis through R-coded statistical algorithms and has created an implementation of lme [3dlme] that uses the mixed linear effects approach. Brain-behavior relationships were evaluated by calculating Pearson correlations on changes in brain activity with key trait characteristic variables that differed between groups.

RESULTS

Demographics and personality characteristics

Demographics and personality characteristics are presented in Table 1. Adventure Racers did not differ from normal controls on age [$t(20) = 0.31$, $P = 0.76$] or years of education [$t(20) = 0.32$, $P = 0.76$]. There were significant differences in personality characteristics as measured by the BIS. Adventure Racers reported more perseverance [$t(20) = 3.31$, $P = 0.004$, $d = 1.52$], experience seeking [$t(20) = 2.12$, $P = 0.05$, $d = 0.66$], disinhibition [$t(20) = 2.68$, $P = 0.02$, $d = 1.06$], boredom susceptibility [$t(20) = 2.65$, $P = 0.02$, $d = 0.61$] and physical activity levels [$t(20) = 8.12$, $P = 0.01$, $d = 1.57$].

Behavioral performance during the emotion face processing task

Elite Adventure Racers did not differ from comparison subjects on speed or accuracy to respond to emotional faces (Figure 1). Response latency to target faces was not different between groups [$F(1,20) = 0.05$, $P = 0.82$, $\eta^2 = 0.002$], nor was there a group-by-face interaction [$F(3,60) = 0.33$, $P = 0.80$, $\eta^2 = 0.02$]. However, as previously reported (Paulus *et al.*, 2005, 2009), across groups, the latency to respond to a target varied by the type of target face [$F(3,60) = 130.20$, $P < 0.001$, $\eta^2 = 0.87$], such that both groups responded more quickly to shapes ($M = 831$ ms, *s.d.* = 141 ms) than happy ($M = 1100$, *s.d.* = 190,

Table 1 Demographics and trait characteristics

Gender	Control (8M, 4F) M (s.d.)	Athlete (6M, 4F) M (s.d.)	<i>t</i>	<i>P</i>	<i>d</i>
Demographics					
Age	36.66 (6.38)	37.5 (6.03)	0.31	0.76	0.13
Education	16.03 (1.82)	16.3 (1.82)	0.32	0.76	0.13
Impulsivity (BIS)					
Attention	11.00 (1.47)	12.73 (2.34)	1.95	0.06	0.36
Motor	15.08 (1.83)	16.5 (3.70)	1.14	0.27	0.51
Self control	16.66 (2.33)	15.87 (3.43)	0.59	0.56	0.26
Cognitive complexity	12.50 (2.50)	12.75 (2.37)	0.22	0.32	0.10
Perseverance	7.58 (1.37)	9.67 (1.30)	3.31	0.004**	1.52
Cognitive instability	3.66 (1.52)	7.12 (2.41)	1.50	0.15	0.67
Total	68.3 (7.20)	74.62 (6.16)	1.97	0.07	0.92
Seyizaticiy Seeking (SSS-V)					
Thrill and adventure seeking	7.92 (2.39)	9.33 (1.11)	1.64	0.12	0.54
Experience seeking	3.92 (1.62)	7.44 (1.66)	2.12	0.05*	0.66
Disinhibition	4.42 (2.33)	7.00 (1.93)	2.68	0.02*	1.06
Boredom susceptibility	2.33 (1.23)	4.00 (1.65)	2.65	0.02*	0.61
Total	20.33 (3.99)	27.77 (4.23)	3.99	0.001**	1.21
Physical Activity (IPAQ-SF)					
Total	2907.37	9606.14	8.12	0.01**	1.57

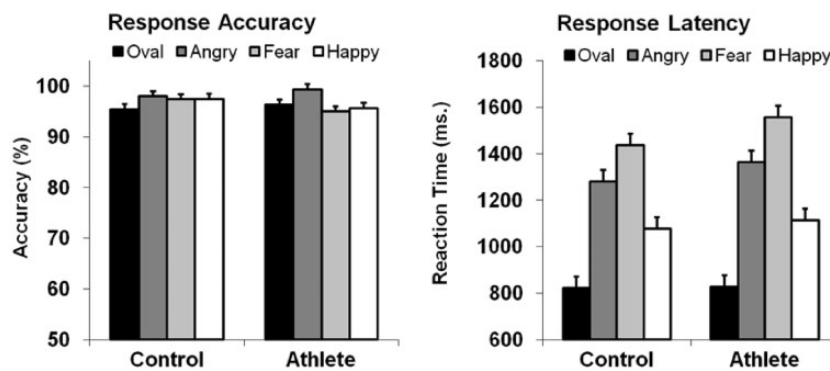


Fig. 1 Behavioral performance during the Face Processing Task. Elite Adventure Racers did not differ from comparison subjects on speed or accuracy to respond to emotional faces. Both groups showed accuracy rates and response latencies that were within typical ranges.

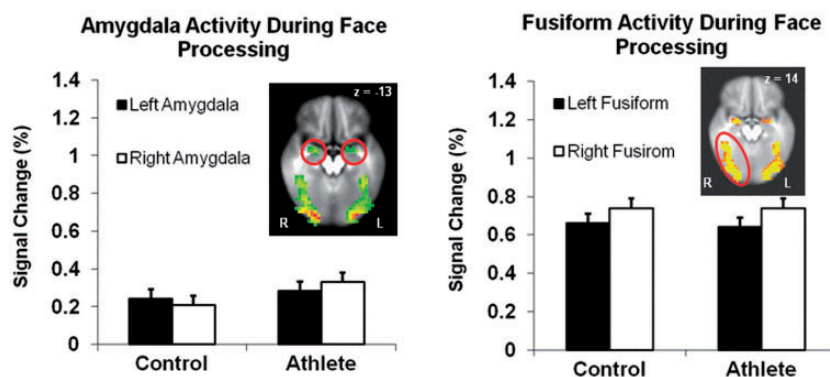


Fig. 2 Task-related activation. Groups were not different for task-related activation. Consistent with previous results, activation during the facial emotion detection task involved activity in structures in both limbic and paralimbic regions to include the amygdala and fusiform face area.

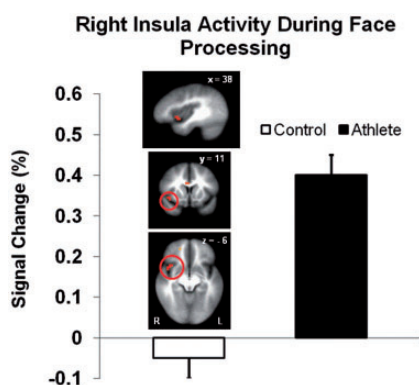


Fig. 3 Group differences in the insula. Elite Adventure Racers showed increased activation in the right insula during emotion face processing.

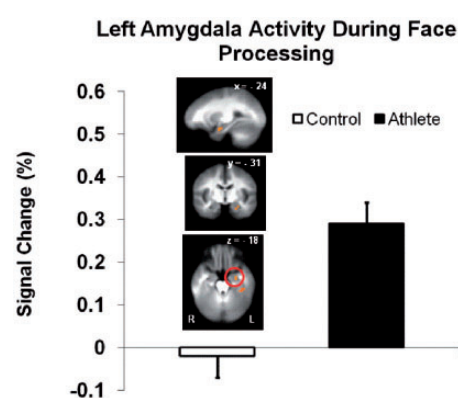


Fig. 4 Group differences in the left amygdala. Elite Adventure Racers showed increased activation in the left amygdala during emotion face processing.

$P < 0.001$), angry ($M = 1312$, $s.d. = 244$, $P < 0.001$) and fearful faces ($M = 1498$, $s.d. = 315$, $P < 0.001$). The groups did not differ on response accuracy [$F(1,20) = 0.13$, $P = 0.72$, $\eta^2 = 0.01$], nor was there an effect of the target face on accuracy [$F(3,60) = 2.60$, $P = 0.06$, $\eta^2 = 0.12$] or a group-by-face interaction [$F(3,60) = 1.10$, $P = 0.36$, $\eta^2 = 0.05$].

Task-related activation

Consistent with previous results (Paulus *et al.*, 2010), activation during the facial emotion detection task involved structures in both limbic and paralimbic regions to include fusiform gyrus, amygdala and bilateral insula (all P 's < 0.05) (Figure 2).

Group differences

Group differences in regional brain activation to facial emotions are shown in Figures 3–6. Specifically, Adventure Racers showed increased activation in right insula, left amygdala and dorsal anterior cingulate, but reduced activity in right mPFC (all P 's < 0.05).

Group-by-face interactions

There were no group-by-face interactions ($P > 0.05$), i.e. Adventure Racers did not process fear, anger or happy faces differently than comparison subjects.

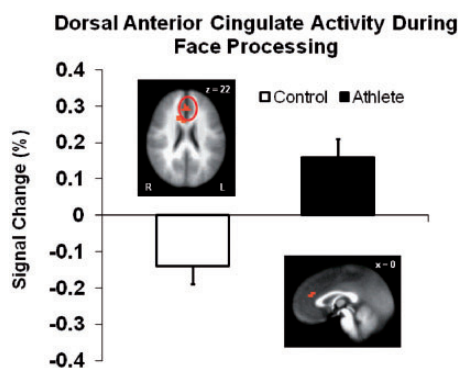


Fig. 5 Group differences in the dorsal anterior cingulate. Elite Adventure Racers showed increased activation in the dorsal anterior cingulate during emotion face processing.

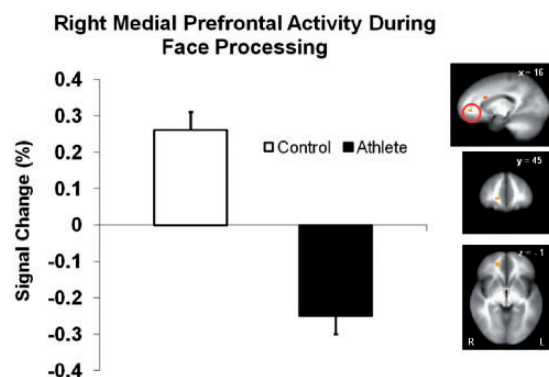


Fig. 6 Group differences in the mPFC. Elite Adventure Racers showed decreased activation in the right mPFC during emotion face processing.

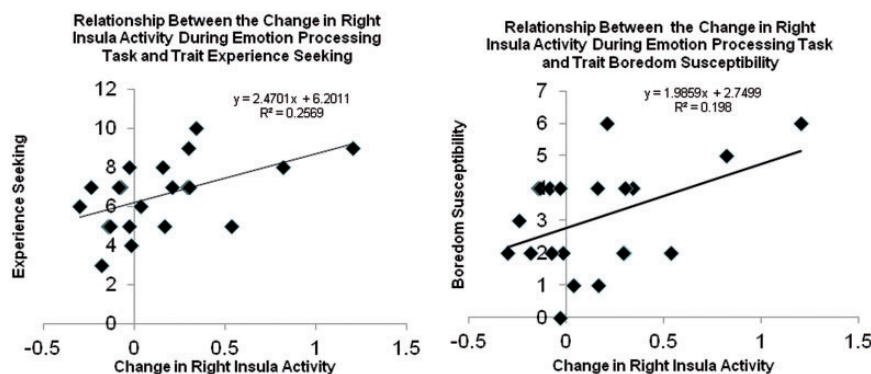


Fig. 7 Relationship between sensation seeking and right insula activity. Higher levels of experience seeking and boredom susceptibility were positively correlated with activity in the right insula during the emotion processing task.

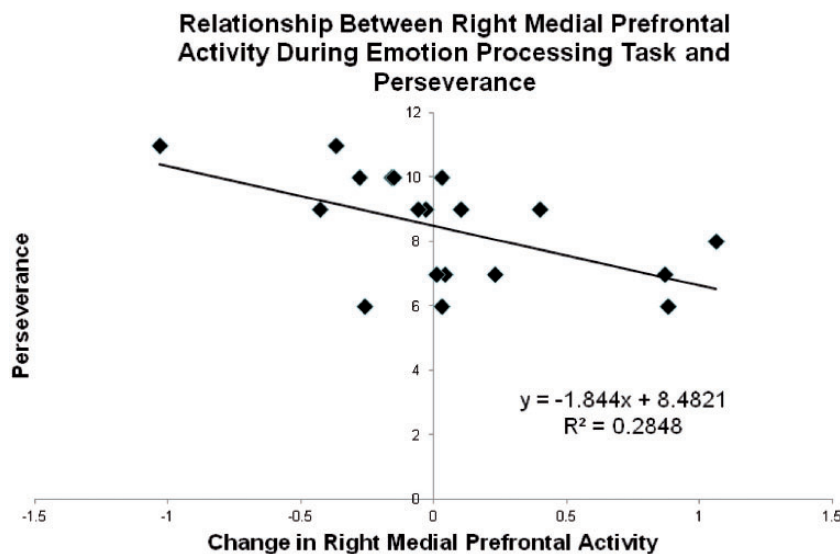


Fig. 8 Relationship between perseverance and mPFC activity. Individuals with higher perseverance scores showed relatively lower activation in the right mPFC.

Brain-behavior relationships

There were significant correlations between degree of activation and individual differences characteristics. Specifically, higher levels of experience seeking and boredom susceptibility were positively correlated with activity in the right insula during the emotion processing task ($r = 0.51$, $P < 0.05$; $r = 0.45$, $P < 0.05$) (Figure 7). In addition,

individuals with higher perseverance scores showed relatively lower activation levels in the mPFC ($r = -0.53$, $P < 0.05$) (Figure 8).

DISCUSSION

This study examined neural substrates that mediate a distinct aspect of interoception, namely the processing of internal sensations that arise

during recognition of emotion in others, in elite Adventure Racer athletes. These individuals showed increased activation in right insula (INS), left amygdala, dorsal anterior cingulate cortex and reduced activation in right mPFC. In addition, several brain-behavior relationships emerged. Greater perseverance was associated with lower activation in the mPFC, and higher levels of boredom susceptibility and sensation seeking were associated with increased right insula activation. This pattern of results suggests altered activation in substrates underlying recognition of emotions in others may be an indicator of those who operate well in groups in high-stress situations.

These results replicate previous findings showing differential insula activation in elite military personnel (Paulus *et al.*, 2010), and extends those results to team-based athletes who operate in a different type of high-magnitude, high-risk and stress. Similarly, others have found that activity in right insula differentiated high and low trait resilient individuals when anticipating threat (Waugh *et al.*, 2008). Right insula activation while viewing emotional faces has been interpreted as the 'gut reaction' to the face (Adolphs, 2002; Craig, 2002). Within that context, results from two separate studies of elite performers who operate in teams suggests that these groups allocate more processing resources to the initial reactions from the internal sensations generated by recognition of emotional states in others (Paulus *et al.*, 2010; Simmons *et al.*, 2012). In particular, right insula activation may be responsible for the re-representation of the state of the body that is critical for predicting how emotional states will alter decision-making to enhance survival, consistent with our model of performance (Paulus *et al.*, 2009) and Damasio's somatic marker hypothesis (Damasio, 1996). Hereby replicating this finding in another sample of elite performers suggests that increased right insula activation may be a neural marker of an optimal response to emotion for group-based performance. Moreover, right insula activation was associated with higher self-report of experience seeking and disinhibition which suggests that the most outgoing individuals also allocated the most processing resources toward integrating the emotional state of others with how they feel internally. What remains untested is whether this is an effect of training for adventure races, a more general adaptation related to optimal performance in highly stressful circumstances, or a characteristic that elite Adventure Racers are born with.

Adventure Racers also showed decreased activity in right mPFC (BA10 and 32) while viewing pictures of emotional faces. In humans, the mPFC, especially the antero-rostral portion (BA 10 and 32), supports the neural processing of the perception of others (Amodio and Frith, 2006). Perhaps elite Adventure Racers require less neuronal resources in the mPFC in order to perceive the emotional status of others, or their training and related goals (e.g. to win at the highest level) have led them to inhibit empathetic responses in favor of more rudimentary responses driven by the limbic system. In support of the latter interpretation, animal work has shown that the ventral-mPFC (vmPFC) exerts control over brainstem and limbic regions during stressful situations in a way that promotes resilience (Maier and Watkins, 2010). Viewing and categorizing emotional faces is not stressful, so perhaps the Adventure Racers take the mPFC offline while processing emotional facial information because it is not adaptive to use the mPFC to inhibit limbic regions under non-stressful conditions.

The combination of increased left amygdala activity, which helps interpret fine-grained details of emotional facial stimuli (Hariri *et al.*, 2003; Kilts *et al.*, 2003; Phillips *et al.*, 2001) and increased right insula activity suggest that elite team-based performers perceive the detailed emotional states of others as salient information, and therefore direct greater neural resources to the internal sensations that emotional faces produce. In addition, the associated decreased activity in mPFC suggests that they conserve activity in regions that engender empathy. In short, the goals of these elite athletes determine the way

they process emotional information about others. Further supporting this interpretation is the fact that mPFC activity and perseverance were inversely related. Similarly, elite warfighters have an enhanced neural response to salient threatening stimuli but use reduced processing resources to non-threatening stimuli (Paulus *et al.*, 2010).

The current results are also consistent with the notion that elite athletes pay close attention to bodily signals (Philippe and Seiler, 2005) as a way to maintain high levels of performance. For example, Marcora and colleagues have proposed a psychobiological model to explain the ability to maintain high levels of physical exertion, which focuses on the generation of a top-down or feed-forward signal as the basis for the perception of exertion (Marcora, 2008). These investigators have argued that a centrally generated corollary discharge of the brain is critical for optimal effort (Marcora, 2010) and that mental fatigue affects performance via altered perception of effort rather than afferent and body originating cardiorespiratory and musculoenergetic mechanisms (Marcora *et al.*, 2009). Interestingly, Williamson *et al.* (2006) have suggested that the neural circuitry of these central nervous mechanisms include the anterior cingulate and insular cortex that interact with thalamic and brainstem structures, which are important for cardiovascular integration. Moreover, these structures are important for the central modulation of cardiovascular responses (Williamson *et al.*, 2002) and can also function as a feedback system. Thus, these brain systems provide a contextualized body state that can inform the individual's sense of effort or exertion and does not require a parallel motor activation to exert its influence. These conceptualizations are similar to a neural processing model focused on both bottom-up interoceptive afferents and top-down cognitive control to modulate mood and anxiety (Paulus and Stein, 2010).

One potential challenge to this interpretation is that interoceptive sensitivity is not unique to elite performers. Several studies have shown that heightened awareness to interoceptive cues is mediated in part by differences in insula function, and may be a mechanism underlying vulnerability to anxiety spectrum disorders (Paulus and Stein, 2006, 2010; Domschke *et al.*, 2010). Accordingly, individuals who are highly adaptive to stress may share heightened sensitivity to interoceptive cues with individuals at the maladaptive end of the response to stress continuum. If so, how then do we reconcile the stark differences in behavioral response to stress given similar underlying interoceptive sensitivity? A plausible explanation has been offered by the early work of Folkman and Lazarus (1985; 1988) on the role of cognitive appraisal in response to stress. Cognitive appraisal is a top-down process that involves subjective perceptions and interpretations. Subjective appraisal of stressors effects subsequent down-stream physiological and neuroendocrine responses [for review see (Olf *et al.*, 2005)]. Research has also demonstrated that reappraising stress can modulate fear circuitry activation (Hariri *et al.*, 2003; Lemogne *et al.*, 2011). Within the context of elite performers, these individuals may have both heightened sensitivity to interoceptive cues, and then cognitively appraise such cues as useful information for adaptation, whereas anxiety prone individuals interpret these same cues as indicators of danger. For example, we found that anticipation of emotionally aversive visual stimuli activates the right anterior insula (Simmons *et al.*, 2004). Thus, elite performers may recognize interoceptive information more quickly, and also appraise this information in a way that prepares them to more efficiently respond to perturbations of the stress response system.

Taken together these results provide initial evidence for the role of the interoceptive system in aiding elite performance under extreme conditions. While these initial findings support our interoceptive model of elite performance, the ability to perform well under extreme conditions is a complex problem which requires further study.

Conflict of Interest

None declared.

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