Title: Self-reported tolerance influences prefrontal cortex haemodynamics and affective responses

Running head: Self-reported tolerance of exercise

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ABSTRACT

The relationship between cognitive and sensory processes in the brain contributes to the regulation of affective responses (pleasure-displeasure). Exercise can be used to manipulate sensory processes (by increasing physiological demand) to examine the role of dispositional traits that may influence an individual's ability to cognitively regulate these responses. With the use of near infrared spectroscopy, this study examined the influence of self-reported Tolerance upon prefrontal cortex (PFC) haemodynamics and affective responses. The haemodynamic response was measured in individuals with high- or low-Tolerance during an incremental exercise test. Sensory manipulation was standardized against metabolic processes (ventilatory threshold [VT]; and respiratory compensation point [RCP]) and affective responses recorded. Results showed that the high-Tolerance group displayed a larger haemodynamic response within the right PFC above the VT (which increased above the RCP). The low-Tolerance group showed a larger haemodynamic response within the left PFC above the VT. The high-Tolerance group reported a more positive/less negative affective response above the VT. These findings provide direct neurophysiological evidence of differential haemodynamic responses within the PFC associated with Tolerance in the presence of increased physiological demand. This study supports the role of dispositional traits and previous theorising into the underlying mechanisms (cognitive vs. sensory processes) of affective responses.

INTRODUCTION

Affective responses (pleasure-displeasure) are proposed to be regulated in the brain by the prefrontal cortex (PFC) and subcortical regions, including the amygdala (Davidson and Irwin, 1999). Research has shown an inverse coupling between PFC activation and activity in the amygdala (Hariri et al., 2000, 2003; Quirk et al., 2003). The relationship between the PFC and amygdala is strengthened when individuals are instructed to cognitively-control negative (aversive) affective responses (Phan et al., 2005; Banks et al., 2007; Goldin et al., 2008). A transient disruption, or reduced activation, of lateralised regions of the PFC is associated with a reduced ability to exert cognitive-control to alleviate negative affective responses (Ochsner et al., 2004; Beauregard, 2007; Ochsner & Gross, 2008).

During increased physiological demand (i.e. exercise) affective responses become less positive/more negative as the intensity of exercise increases (for reviews see Ekkekakis & Petruzzello 1999; Ekkekakis et al., 2011). According to a theoretical framework (the dual mode model: Ekkekakis, 2003; Ekkekakis & Acevedo, 2006), at intensities below the ventilatory threshold (VT; the point of transition from aerobic to anaerobic metabolism), individuals are able to maintain PFC activation to override negative affective responses driven by sensory (interoceptive) input from the body. Interoceptive cues provide the brain with information from the body and include nociceptors (pain), metaboreceptors (chemical), thermoreceptors (temperature), mechanoreceptors and baroreceptors (touch, pressure, tension; see Ament & Verkerke, 2009). Above the VT (proximal to the respiratory compensation point: RCP; the point where physiological steady state cannot be maintained), competition between the PFC and subcortical regions, which receive sensory input from the body, becomes increasingly challenging. At this intensity, an individual's ability to maintain PFC activation becomes threatened. Recent work, using EEG (Robertson & Marino, 2015) and NIRS (Jung et al., 2015), has shown a redistribution of brain activation in PFC and motor regions as the intensity of exercise is increased. Since exercise influences PFC activation, it may be used to manipulate sensory input from the body (presumably to the amygdala) to examine the role of the PFC in the regulation of affective responses.

One potential factor that may impact PFC activation, and therefore an individual’s level of cognitive-control to regulate affective responses, is the role of dispositional traits. The Preference for and Tolerance of Exercise Intensity Questionnaire (PRETIE-Q) is an inventory created to assess arousability and sensory modulation-related traits for interoceptive (as opposed to exteroceptive) stimuli (see Ekkekakis et al., 2005 for full details). The authors define Preference as ‘a predisposition to select a particular level of exercise intensity when given the opportunity’ (p354), and Tolerance as ‘a trait that influences one’s ability to continue exercising at an imposed level of intensity even when the activity becomes uncomfortable or unpleasant’ (p354). The identification of Preference and Tolerance as dispositional traits is supported by no change in these scores after a 6-week training program which resulted in improvements in physical fitness (Hall et al., 2014). Conceptual validation of the scales (Ekkekakis et al., 2005) showed that neither Preference nor Tolerance was associated with affective responses reported during exercise at intensities below VT. However both scales were positively associated with affective responses at VT, but only the Tolerance scale above the VT (Ekkekakis et al., 2005; Ekkekakis et al., 2007). Therefore, a higher Tolerance was associated with a more positive affective response at intensities of exercise above the VT, which is predominantly aversive or negative (Ekkekakis et al., 2011).

It is proposed that Tolerance influences affective responses through cognitive processes in the PFC (Ekkekakis et al., 2005). Consistent with the dual mode model, sensory input to the body is biologically hard-wired; however the perception and modulation of the interoceptive input by the PFC may be influenced by predisposed traits. In other words, individuals with high-Tolerance may be more capable of cognitively regulating how sensory information from the body is perceived during exercise at physiologically challenging intensities (i.e. above VT), than those with low-Tolerance. Individuals with high-Tolerance would report less negative affective responses than those with low-Tolerance. In addition, individuals with high-Tolerance may exercise for longer at an imposed level of intensity (i.e. above VT) that is uncomfortable or unpleasant (Ekkekakis et al., 2005; Ekkekakis et al., 2007).

The present study investigates if Tolerance of the intensity of exercise influences PFC haemodynamics and affective responses during incremental exercise. Bilateral measures of the PFC (right and left) are measured due to evidence of lateralisation involved in cognitive-control processes (Ochsner et al., 2004). Prefrontal haemodynamics can be recorded by a non-invasive neuroimaging technique, near infrared spectroscopy (NIRS), suitable for use during exercise (Ferrari & Quaresima, 2012; Perrey, 2012). Changes (Δ) in cerebral haemodynamics; oxygenation (O_2Hb; oxygen delivery and blood flow), deoxygenation (HHb; oxygen extraction) and total blood volume (tHb = O_2Hb+HHb), reflect metabolic changes associated with functional (neural) activation and metabolism (Perrey, 2012). Cerebral activation is defined by a slight decrease in oxygen extraction (HHb) and an increase in oxygenation (O_2Hb; two-fold of HHb), leading to hyper-oxygenation (i.e. greater oxygen availability; Perrey, 2012). A meta-analysis of studies examining the haemodynamic response using NIRS during exercise shows a quadratic trend of cerebral oxygenation as the exercise increases: oxygenation increases from low to moderate and remains stable from moderate to hard, but declines at very hard (approx. RCP to exhaustion) intensities (Rooks et al., 2010). However, the authors indicate that the decline near exhaustion is less pronounced in trained, as opposed to untrained individuals.

Three hypotheses are examined: 1) Prefrontal cortex haemodynamics are different between individuals with high- or low-Tolerance; 2) Individuals with high-Tolerance report less negative affective response at intensities above VT; and 3) Individuals with high-Tolerance exercise for longer than those with low-Tolerance at intensities above VT.

METHODS

Participants

A university cohort of sports science students (*n* = 259) completed the PRETIE-Q (Ekkekakis et al., 2005) during a timetabled session. Following quantitative analysis of haemodynamic variables (ΔO_2Hb and ΔHHb) measured during exercise intensities up to exhaustion with an optode (transmitter-detector) distance of 4 cm (Rooks et al., 2010; assuming statistical power = .80 and α = .05), and allowing for attrition, at least 14 participants were required per group. Therefore, participants with the highest and lowest Tolerance scores were invited to participate in the study (*n* = 28; see Table 1). All except two participants were right-handed. The volunteers read and signed an informed consent form which was approved by the departmental Ethics Committee. The Physical Activity Readiness Questionnaire (Canadian Society for Exercise Physiology, 2002) was used to ensure suitability to exercise.

Measures

Preference for and Tolerance of the intensity of exercise questionnaire (PRETIE-Q)

Tolerance was assessed using the PRETIE-Q (Ekkekakis et al., 2005). The 16-item questionnaire contains eight items for Preference (4-high, 4-low) and similarly eight items for Tolerance (4-high, 4-low). Each item comprises a 5-point response scale (1= 'I totally disagree', 2= 'I disagree', 3= 'Neither agree nor disagree', 4= 'I agree' and 5= 'I strongly agree'). Alpha coefficients of internal consistency ranged from 0.82 to 0.87 for the Tolerance scale and test-retest reliability of coefficients of 0.85 and 0.72 after 3- and 4- month intervals (see Ekkekakis et al., 2005, for the complete questionnaire). Alpha coefficients of internal consistency in the present study ranged between 0.76 and 0.81 for the Tolerance scores of the high and low groups, respectively.

Near infrared spectroscopy (NIRS)

Cerebral haemodynamics were measured using NIRS (NIRO 200 Hamamatsu Photonics, Hamamatsu, Japan). The emitter and detector were encased in a rubber holder with a separation distance of 4 cm. A differential path length factor of 5.93 for the adult forehead was used (van der Zee et al., 1992) to provide a measure of concentration changes (Δ) in micromolar (µM) units of O_2Hb, HHb and tHb (sample rate 2Hz). The probes were placed approximately over the left and right dorsolateral PFC (between Fp1-F3 and Fp2-F4 respectively, of the international 10-20 system for EEG electrode placement) and secured to the skin using a double adhesive sticker. Elastic surgical tape (Kinesio Tex Gold) and a dark bandage were placed over the holders around the forehead.

The Feeling Scale

Affective responses were measured using the Feeling Scale (Hardy & Rejeski, 1989). The uni-dimensional 11-point scale (ranging from -5 to +5 with verbal anchors at all odd integers, and at the zero point; -5 very bad, -3 bad, -1 fairly bad, 0 neutral, 1 fairly good, 3 good, 5 very good) allows multiple assessments to be made during exercise. The Feeling Scale corresponds to one of the two dimensions of the circumplex model of feeling states (Russell et al., 1999) and is recommended to measure basic affect (pleasure-displeasure) (Ekkekakis & Petruzzello 1999).

Procedures

The study required individuals to visit the exercise physiology laboratory (approximate temperature 24°C, and relative humidity 40%) on one occasion. Upon arrival, participants completed the informed consent form and exercise testing questionnaire and initial assessments were taken (age, height and body mass). The procedures for the exercise tests were explained and a description of the Feeling Scale was provided. Participants were seated on a recumbent cycle ergometer (Lode Angio, Groningen, the Netherlands) and the NIRS optodes were carefully positioned. A facemask was fitted to measure metabolic data via online gas analysis (Cortex Metalyzer 3B, Biophysik, Leipzig, Germany). The participants then completed an incremental (20 $W \cdot min^{-1}$; pedal cadence 70 rpm) cycling exercise test to exhaustion. The end of the test was determined by volitional cessation of exercise or failure to maintain pedal cadence despite strong verbal encouragement. The achievement of VO_{2peak} was verified by a) a peak or plateau in oxygen consumption (changes < 2 $ml \cdot kg^{-1} \cdot min^{-1}$) with increasing workload; and b) a respiratory exchange ratio of at least 1.10. Cerebral haemodynamic responses and expired gases were measured continuously and affective responses were recorded pre-, during (every minute) and at the end of exercise.

Data and statistical analyses

The peak oxygen uptake (VO_{2peak}) was determined by the highest 30 second average of oxygen uptake (VO_2 $ml \cdot kg^{-1} \cdot min^{-1}$). The VT was determined using the three method procedure proposed by Gaskill et al. (2001) and the RCP was determined according to Beaver et al. (1986).

Thirty second baseline measures of cerebral haemodynamics (ΔO_2Hb, ΔHHb and ΔtHb) were recorded prior to exercise. Data were exported every 10 seconds and normalised to express the magnitude of changes from the baseline period (arbitrarily defined as 0 µM) at the start of exercise. Cerebral haemodynamic variables were selected at time points corresponding to intensities of exercise; 80% of VT (below VT), VT, RCP and end of exercise (End). Affective responses were extracted at time points corresponding to pre- and each of the intensities of exercise.

To examine hypothesis 1, a Group (2; high, low) by Hemisphere (2; right, left PFC) by Time (4; below VT, VT, RCP, End) mixed model analysis of variance (ANOVA) was conducted for each of the NIRS variables (ΔO_2Hb, ΔHHb and ΔtHb). To examine hypothesis 2, a Group (2; high, low) by Time (5; pre-exercise, below VT, VT, RCP, End) mixed model ANOVA was conducted for affective responses. Finally, to examine hypothesis 3, two independent sample t-tests, with Bonferoni correction (alpha of .05 / 2 [number of tests] = .025), were conducted for the duration of exercise (from VT to RCP, RCP to End) of the high- and low-Tolerance groups. All statistical analyses were performed using SPSS v. 18.0 (IBM Corp., Armonk, NY, USA). Greenhouse Geisser corrections were applied if the assumption of sphericity was not met. All significant main and interaction effects ($p < .05$) were followed by Bonferroni adjusted pairwise comparisons and simple main effects. Effect sizes associated with *F* statistics (ANOVAs) were expressed as partial eta squared (η_p^2) defined as small (.01), medium (.06) and large (.14) (Cohen, 1988). Values are mean ± *SD* unless otherwise stated.

RESULTS

Preliminary analyses

To ensure Tolerance scores were different between the two groups (high, low) and to verify if there was a difference in overall time to exhaustion, two independent t-tests were conducted. These tests showed that Tolerance scores were significantly different between high- (*M* = 33.1, *SD* = 2.3, range 30 to 38) and low- (*M* = 21.1, *SD* = 1.9, range 18 to 24) Tolerance groups, $t(26) = 15.07$, $p < .001$. No difference in overall time (sec) to exhaustion between high- (M = 676, SD = 116) and low- (M = 646, SD = 93) Tolerance groups was shown (p > .05).

To examine if there were differences in fitness (indicated by $\dot{V}O_2$ ml·kg^{-1}·min^{-1}) between males and females in the high- and low-Tolerance groups at time points corresponding to intensities of exercise (below VT, VT, RCP, End), a Group (2) by Gender (2) by Time (4) mixed model ANOVA was conducted. The analysis showed no differences in $\dot{V}O_2$ (ml·kg^{-1}·min^{-1}) between groups (main and interaction effects; p > .05). However, as expected $\dot{V}O_2$ (ml·kg^{-1}·min^{-1}) was (a) higher in males (M = 32.4, SD = 5.1) than females (M = 29.1, SD = 2.7), $F(1,24) = 4.73$, $p < .05$, $\eta_p^2 = .17$, and (b) significantly different at each intensity: below VT (M = 19.0, SD = 2.7), VT (M = 23.7, SD = 3.2), RCP (M = 36.1, SD = 5.3) and End of exercise (M = 43.8, SD = 6.4), $F(1, 26) = 1141.48$, $p < .001$, $\eta_p^2 = .98$. A Gender by Time interaction indicated that males had a disproportionately higher $\dot{V}O_2$ (ml·kg^{-1}·min^{-1}) at RCP than females, $F(1,26) = 4.52$, $p < .05$, $\eta_p^2 = .16$ (see Table 1).

*** INSERT TABLE 1 AROUND HERE ***

Cerebral haemodynamics (hypothesis 1)

As a result of the Gender by Time interaction for VO_2 (ml·kg^{-1}·min^{-1}) preliminary analyses of covariance were conducted for ΔO_2Hb, ΔHHb and ΔtHb to include Gender as a covariate. Additional analyses were also conducted using handedness as a covariate. The analyses showed no influence of Gender or Handedness upon the significant main and interaction effects for Group, Hemisphere and/or Time (p > .05). However, as expected significant Gender by Time interactions were recorded for ΔO_2Hb and ΔtHb (males higher than females at RCP; p < .05). The ANOVA and unadjusted means for ΔO_2Hb, ΔHHb and ΔtHb are presented.

Cerebral oxygenation (ΔO_2Hb)

A significant main effect of Time, $F(1,33) = 99.39$, $p < .001$, $\eta_p^2 = .79$, and significant Group by Hemisphere, $F(1,26) = 4.37$, $p = .047$, $\eta_p^2 = .14$, and Group by Hemisphere by Time, $F(1,34) = 4.14$, $p = .039$, $\eta_p^2 = .14$, interactions were recorded for ΔO_2Hb (µM). Cerebral ΔO_2Hb remained stable from below VT (*M* = 2.04, *SD* = 2.39) to VT (*M* = 2.71, *SD* = 2.82), then increased from VT to RCP (*M* = 12.14, *SD* = 5.51) and RCP to End (*M* = 13.49, *SD* = 6.87) in both groups. In the left PFC, ΔO_2Hb was larger in the low- (*M* = 8.33, *SD* = 3.88) than the high-Tolerance (*M* = 6.80, *SD* = 4.36) group. In the right PFC, ΔO_2Hb was similar between the low- (*M* = 7.46, *SD* = 4.01) and high-Tolerance (*M* = 7.78, *SD* = 4.27) groups. The three factor interaction indicated that from VT to RCP, the low-Tolerance group indicated a significantly larger ΔO_2Hb in the left than the right PFC at RCP (and when compared to both hemispheres in the high-Tolerance group). From RCP to End, ΔO_2Hb remained stable in both hemispheres in the low-Tolerance group, but significantly increased in both hemispheres in the high-Tolerance group. Therefore, at End, ΔO_2Hb remained larger in the left than the right PFC in the low-, whereas ΔO_2Hb was larger in the right than the left PFC in the high-Tolerance group (see Figure 1).

Cerebral deoxyhaemoglobin (ΔHHb)

Significant main effects of Hemisphere, $F(1,26) = 5.33$, $p = .029$, $\eta_p^2 = .17$, and Time, $F(1,31) = 50.99$, $p < .001$, $\eta_p^2 = .66$, were recorded for ΔHHb (µM). Follow up tests indicated that ΔHHb was larger in the right (*M* = 1.32, *SD* = 1.23) than the left (*M* = 1.01, *SD* = 1.32) PFC in both groups. Cerebral ΔHHb remained stable from below VT (*M* = .16, *SD* = .53) to VT (*M* = .06, *SD* = .68), then increased from VT to RCP (*M* = 1.03, *SD* = 1.68) and RCP to End (*M* = 3.41, *SD* = 2.53) in both groups.

Cerebral blood volume (ΔtHb)

A significant main effect of Time, $F(1,32) = 128.66$, $p < .001$, $\eta_p^2 = .83$, and a Group by Hemisphere by Time, $F(1,37) = 3.67$, $p = .049$, $\eta_p^2 = .12$, interaction were recorded for ΔtHb (µM). Cerebral ΔtHb remained stable from below VT (*M* = 2.20, *SD* = 2.33) to VT (*M* = 2.77, *SD* = 2.80), then increased from VT to RCP (*M* = 13.16, *SD* = 6.26) and RCP to End (*M* = 16.89, *SD* = 7.50) in both groups. The three factor interaction indicated that from VT to RCP, ΔtHb was significantly smaller in the left PFC in the high-Tolerance than low-Tolerance group. From RCP to End, ΔtHb was larger in the high-Tolerance than the low-Tolerance group. At End, ΔtHb remained similar in both hemispheres in the low-, whereas ΔtHb was larger in the right than the left PFC in the high-Tolerance group (and when compared to both hemispheres in the low-Tolerance group) (see Figure 1).

*** INSERT FIGURE 1 AROUND HERE ***

Affective responses (hypothesis 2)

A significant main effect of Time, $F(2, 39) = 38.35$, $p < .001$, $\eta_p^2 = .56$, and a significant Group by Time, $F(4, 104) = 3.57$, $p = .009$, $\eta_p^2 = .05$, interaction were recorded for affective responses. Affective responses declined from pre-exercise (*M* = 2.43, *SD* = 1.35) to below VT (*M* = 1.86, *SD* = 1.24), remained stable until VT (*M* = 1.68, *SD* = 1.44) and declined from VT to RCP (*M* = -.11, *SD* = 2.04) and RCP to End (*M* = -1.04, *SD* = 2.52). The interaction indicated that the decline in affective responses from pre-exercise to below VT was a result of the responses in the low-Tolerance group. Both groups reported similar affective responses from below VT to VT, at which point there was a larger decline in the low- than the high-Tolerance group. Therefore, despite positive affective responses in both groups at VT, affective responses were negative at RCP and End in the low-Tolerance group (see Figure 2).

*** INSERT FIGURE 2 AROUND HERE ***

Exercise Duration (hypothesis 3)

There was no difference in the duration (sec) of exercise from VT to RCP between the high- (M = 250, SD = 44) and low- (M = 260, SD = 53) Tolerance group ($p > .025$). However, the duration of exercise from RCP to End was significantly longer in the high- (M = 145, SD = 39) than the low- (M = 113, SD = 24) Tolerance group, $t(26) = 2.62$, $p < .025$. A significant positive correlation was shown between the duration of exercise from RCP to End and Tolerance scores ($r = .48$, $p < .001$).

DISCUSSION

Exercise was used to manipulate sensory processes (by increasing physiological demand) to examine the influence of a dispositional trait upon PFC haemodynamics and affective responses. Tolerance is proposed to influence an individual's ability to cognitively regulate affective responses. In addition, Tolerance impacts an individual's ability to continue exercising at levels of intensity associated with feelings of displeasure and discomfort (Ekkekakis et al., 2005; Ekkekakis et al., 2007). There are three main findings in this study. Firstly, individuals with high- and low-Tolerance showed asymmetrical PFC haemodynamics during exercise at intensities above VT (hypothesis 1). Secondly, individuals with low-Tolerance reported negative affective responses at intensities of exercise above VT (hypothesis 2). Finally, despite no differences in fitness (VO_2 ml·kg^{-1}·min^{-1}) between the two groups, individuals with high-Tolerance exercised for longer above their individually determined RCP compared to those with low-Tolerance (hypothesis 3).

In line with the dual mode model, it was proposed that active involvement of the PFC suppresses aversive stimuli theorised to be mediated by the amygdala driven by intensified sensory (interoceptive) input from the body (Ekkekakis, 2003; Ekkekakis & Acevedo, 2006). At intensities below VT, no differences in PFC haemodynamics were observed between the high-and low-Tolerance groups and affective responses were positive. According to the model, sensory input from the body does not threaten homeostasis and affective responses are predominantly positive. Tolerance was not expected to influence PFC haemodynamics and has not previously been shown to correlate with affective responses below VT (Ekkekakis et al., 2005).

At intensities from VT to RCP, there were no differences in cerebral blood flow and volume in the right PFC between the high-and low-Tolerance groups. However, in the left PFC, the low-Tolerance group indicated larger blood flow (ΔO_2Hb) and volume (ΔtHb) than the high-Tolerance group. This implies that the haemodynamic response in the left PFC in the low-Tolerance group was larger than those observed in the high-Tolerance group at RCP due to the increase in oxygen availability. Oxygen extraction (ΔHHb) increased in both hemispheres in both groups. Affective responses were negative in the low-Tolerance group but remained positive in the high-Tolerance group. Therefore, in the low-Tolerance group a larger haemodynamic response in the left PFC may have been required to maintain cognitive-control processes as the intensity of exercise started to become challenging (Ekkekakis, 2003; Ekkekakis & Acevedo, 2006). This would allow the individual to continue exercise despite the presence of negative affective responses (Ekkekakis et al., 2005).

At intensities from RCP to End, there were differences in cerebral blood flow and volume in both hemispheres between high- and low-Tolerance groups. Individuals with low-Tolerance indicated a smaller haemodynamic response at intensities above RCP. This was shown by stable cerebral blood flow (ΔO_2Hb) in the presence of increases in oxygen extraction (ΔHHb; i.e. lack of oxygen supply relative to demand). Individuals with high-Tolerance had an increased haemodynamic response at intensities above RCP. This was shown by increases in cerebral blood flow (ΔO_2Hb) and oxygen extraction (ΔHHb; i.e. adequate oxygen supply relative to demand). The low-Tolerance group indicated deregulation (hypofrontality effects;

Dietrich, 2003, 2006) in the PFC and reported a more negative affective response than the high-Tolerance group. In addition, the duration of exercise was positively associated with Tolerance scores at these intensities (RCP to End). The high-Tolerance group showed an ability to continue exercise at a level of intensity associated with feelings of displeasure and discomfort (Ekkekakis et al., 2005; Ekkekakis et al., 2007). However, due to the larger haemodynamic response in the high-Tolerance group, it may be that these individuals are able to maintain PFC function more efficiently as their affective responses are not as negative.

Consistent with the dual mode model, the intensified sensory (interoceptive) input, presumably to the amygdala, provided a greater challenge to those individuals with low-Tolerance to maintain PFC activation (Ekkekakis, 2003; Ekkekakis & Acevedo, 2006). As previously reported, affective responses were less positive/negative at intensities above the VT (Ekkekakis et al., 2011), but these were distinctly more negative in the low- than the high-Tolerance group. Therefore, Tolerance potentially influenced the individual's ability to exert cognitive-control in the attempt to alleviate negative affective responses (Ochsner et al., 2004; Beauregard, 2007; Ochsner and Gross, 2008).

Asymmetrical PFC haemodynamics were shown between the high- and low-Tolerance groups. Previous research investigating affective and motivational (approach-avoidance) processes using EEG has indicated that avoidance/withdrawal-related behaviours are associated with greater activity within the right relative to the left PFC (Davidson, 1993). However, the larger haemodynamic response within the right PFC observed in those individuals with high-Tolerance presumably does not reflect withdrawal-type behaviour due to their perseverance of exercise at intensities above the RCP. It is postulated that, in this study, the larger haemodynamic response (reflecting greater activity) in the right PFC is potentially due to active avoidance of withdrawal-type behaviour (as opposed to promoting an approach-related behaviour i.e. larger activity in the left PFC) in the presence of negative affect (Woo et al., 2009). This would allow individuals with high-Tolerance to continue exercising and indicates differential cognitive and motivational processes used by individuals with low-Tolerance.

Alternatively, Craig's theory of forebrain emotional asymmetry (2005) may explain the larger haemodynamic response within the right PFC of the individuals with high-Tolerance. Craig proposes lateralisation of interoceptive input from afferent cues. Parasympathetic afferents activate primarily the left and sympathetic afferents the right insular cortices. Due to the increased sympathetic activity exercise induces, heightened activation of the right insular may have had an impact on the overlying regions of the right PFC measured in this study (Woo et al., 2009). Although there were no physiological differences between the two groups, the perceptual representation of the afferent input may be influenced by the individual's Tolerance of the intensity of exercise (Ekkekakis et al., 2005). It is plausible that the individuals with high-Tolerance had a more acute ability to regulate their somatosensory perception.

It is important to highlight a range of factors which may have contributed to the differences in haemodynamic and perceptual responses between the high- and low-Tolerance groups. In this cross-sectional study, the training status of the participants was not assessed, however as previously indicated, no differences in aerobic power between the two groups were shown. Rooks et al. (2009) showed a decline in cerebral oxygenation at very hard intensities (i.e. above RCP), which was influenced by training status. In the present study, no decline in cerebral oxygenation was observed at a similar intensity; cerebral oxygenation increased in the high- and remained stable in the low-Tolerance group. The lack of drop in PFC oxygenation near exhaustion has recently been observed by others (Jung et al., 2015). A potential explanation of this discrepancy may be due to differences in the placement of the optodes over the PFC (Jung et al., 2015), as prior work has shown region specific changes in PFC haemodynamics (Tempest et al., 2014). Finally, both males and females took part in this study and no gender effects were observed (other than those likely explained by fitness). Future research should interrogate the potential influence or relationship of training status, gender and Tolerance upon haemodynamic responses.

The influence of the dispositional trait of Tolerance upon PFC haemodynamics has been highlighted in this study. However, no measures of the exact cognitive-control mechanisms proposed have been assessed, nor have measures of subcortical areas of the brain (i.e. the amygdala) been recorded. Future studies should utilise study designs from emotion research (i.e. to include appraisal/suppression paradigms) to understand an individual's cognitive and motivational strategies involved in the regulation of affective responses during increased physiological demand (such as exercise). Prior work has shown that the use of imagery as a cognitive strategy can maintain activation (larger haemodynamic response) of the PFC and results in a more positive affective response at intensities above the VT, but not the RCP (Tempest & Parfitt, 2013). In addition, the relationship between oxygenation in different regions (right-left, dorsal-ventral) of the PFC and affective responses is influenced by increases in the intensity of exercise above the VT (Tempest et al., 2014).

Summary

This study used methods to standardise sensory input from the body induced by exercise to investigate the regulation of affective responses in the PFC. Tolerance is a dispositional trait associated with cerebral blood flow during exercise. It appears that those individuals with low-Tolerance may utilise cognitive mechanisms in the left PFC during exercise at intensities above the VT and proximal to the RCP. Those individuals with high-Tolerance do not appear to utilise the left PFC until higher intensities of exercise (i.e. above the RCP). Additionally, individuals with high-Tolerance induce a larger haemodynamic response in the right PFC during exercise at intensities near exhaustion. Tolerance potentially influences, or is influenced by, the way an individual perceives and self-regulates somatosensory information during exercise. It is proposed that Tolerance influences the interplay between cognitive and sensory processes which influences the regulation of affective responses.

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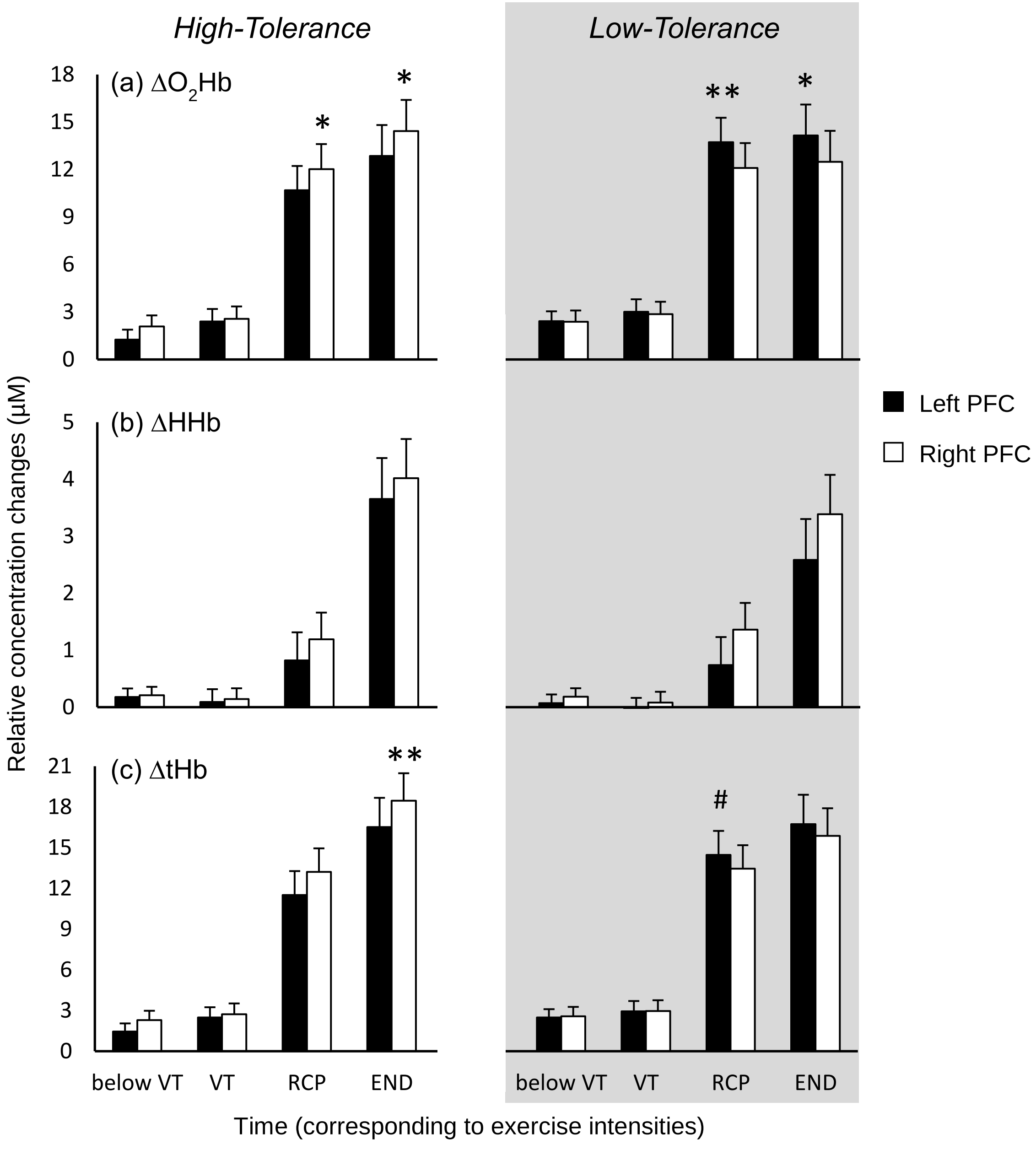
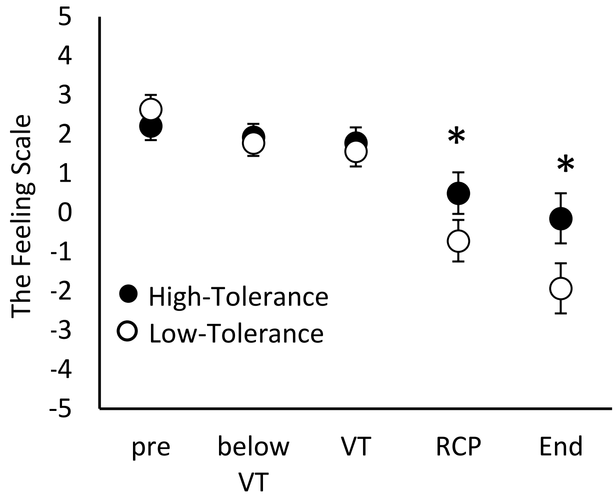
Figure 1: Change in cerebral (a) oxygenation (ΔO_2Hb), (b) deoxygenation (ΔHHb) and (c) blood volume (ΔtHb) in the right and left PFC at each time point for the high- and low-Tolerance groups, *M* and *SEM*.



Time points corresponding to: 80% ventilatory threshold (below VT), VT, respiratory compensation point (RCP) and end of exercise (End). * Significantly higher than the other hemisphere within group; ** significantly higher than the other hemisphere within and between groups; # significantly higher than the other hemisphere between groups ($p < .05$). The pattern of the haemodynamic data (ΔO_2Hb, ΔHHb and ΔtHb) were relatively linear between the time points examined.

Figure 2: Affective responses at each time point for the high- and low-Tolerance groups, *M* and *SEM*.



Time points corresponding to: pre-exercise (pre), 80% ventilatory threshold (below VT), VT, respiratory compensation point (RCP) and end of exercise (End). * Significantly more positive affective responses in the high- than the low-Tolerance group (p < .05).

Table 1. Participant demographics and oxygen uptake ($\dot{V}O_2$ ml·kg^{-1}·min^{-1}) for the high- and low-Tolerance groups, *M* and *SD*.

	High tolerance group			Low tolerance group		
	Males[#] (*n* =7)	Females (*n* =7)	Total* (*n* =14)	Males[#] (*n* =7)	Females (*n* =7)	Total* (*n* =14)
Demographics						
Age (yrs)	20.1 (1.1)	20.7 (1.4)	20.6 (1.4)	21.3 (2.7)	20.8 (3.8)	21.5 (3.4)
Height (cm)	177.1 (5.0)	164.8 (3.1)	171.0 (7.5)	179.0 (8.4)	167.4 (5.5)	173.2 (9.1)
Body mass (kg)	71.5 (4.1)	65.0 (7.1)	69.3 (7.3)	77.6 (9.1)	57.5 (3.8)	68.6 (12.8)
BMI	22.8 (1.4)	23.9 (2.5)	23.4 (2.0)	24.2 (2.2)	20.6 (1.9)	22.4 (2.7)
$\dot{V}O_2$ ml·kg^{-1}·min^{-1}						
below VT	20.9 (2.8)	18.1 (1.7)	19.5 (2.7)	18.8 (3.2)	18.0 (1.6)	18.4 (2.5)
VT	26.1 (3.5)	22.7 (2.3)	24.4 (3.4)	23.6 (4.0)	22.5 (2.0)	23.0 (3.1)
RCP	40.1 (4.7)	34.8 (3.5)	37.8 (5.1)	36.7 (7.0)	34.2 (3.6)	35.4 (5.5)
End (VO_{2peak})	49.4 (5.9)	41.7 (4.2)	45.6 (6.3)	43.0 (8.2)	41.1 (4.0)	42.1 (6.3)

Oxygen uptake ($\dot{V}O_2$ ml·kg^{-1}·min^{-1}) at time points corresponding to: 80% ventilatory threshold (below VT), at VT, respiratory compensation point (RCP) and end of exercise (End) indicating maximal oxygen uptake ($\dot{V}O_{2peak}$). * Significant increase in $\dot{V}O_2$ at each time point; [#] significantly higher $\dot{V}O_2$ in males than females at each time point, ($p < .05$).