Regional brain activity and strenuous exercise: Predicting affective responses using EEG asymmetry

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Abstract

Previous research using the model proposed by Davidson has shown that resting frontal electroencephalographic (EEG) asymmetry can predict affective responses to aerobic exercise at moderate intensities. Specifically, greater relative left frontal activity has been shown to predict positive affect (i.e., energy) following exercise. The purpose of this study was to determine if resting frontal EEG asymmetry would predict affective responses following strenuous exercise. Thirty participants (13 women, 17 men) completed a maximal graded exercise test on a treadmill. EEG was recorded prior to exercise. Affect was measured by the Activation Deactivation Adjective Check List prior to the graded exercise test, immediately following, 10 and 20-min following exercise. Greater relative left frontal activity predicted tiredness and calmness during recovery from exercise, but not tension or energy. Tiredness and calmness following exercise covaried, suggesting that tiredness following exercise might not have been linked with displeasure. These findings offer further support for the link between EEG asymmetry and affective responses to exercise.

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1. Introduction

Research has begun to examine individual variability in affective responses that occur when individuals are presented with similar situations or challenges (e.g., Ito and Cacioppo, 2005). Most exercise studies that examine affective responses have assumed a homogenous response and have failed to systematically examine individual difference variables that may account for divergence in affective reactivity. However, affective responses to exercise stimuli can exhibit markedly different patterns across individuals, even if the exercise intensity is adjusted to the same percentage of maximal capacity. For example, Van Landuyt et al. (2000) demonstrated five unique affective response patterns during cycling performed at 60% of predicted $VO_{2 max}$ (i.e., maximal volume of oxygen consumed) for 30 min. These five response patterns were: (1) an improvement in affective valence (pleasure–displeasure), coupled with an increase in perceived arousal ($n = 21$, 33.3% of sample), (2) decline in valence, increase in arousal ($n = 14$, 22.2%), (3) no change in valence, increase in arousal ($n = 8$, 12.7%), (4) improvement in valence, no change in arousal ($n = 6$, 9.5%), and (5) decline in valence, no change in arousal ($n = 11$, 17.5%). The findings suggest that, unlike most other affect-induction procedures (e.g., Velten, movie clips), exercise, despite holding its intensity equal (defined as a percentage of maximal capacity), can induce affective changes that differ between individuals not only in degree but also in direction.

One approach to examining these individual differences in affective responses, used in a series of studies in the context of exercise, comes from the theoretical model proposed by Davidson based on the extant research on frontal EEG asymmetry (1998, 2000a, 2000b, 2004; see also Allen and Kline, 2004). Davidson has coined the term "affective style" to discuss these individual differences in affective reactivity and has hypothesized that regional brain activity may account for these differences in affective responses. Specifically, Davidson's model hypothesizes that greater left anterior activity,

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relative to the right anterior region, is associated with an approach system and positive affect whereas greater right anterior activity, relative to left, is associated with an avoidance/withdrawal system and negative affect.

The major contribution of this model comes from the fact that such relative anterior activity asymmetries can be used to predict affective responses. Davidson (1993) proposes that ''anterior activation asymmetry functions as a diathesis that predisposes an individual to respond with predominantly positive or negative affect, given *an appropriate emotion elicitor*.'' (p. 145). For example, someone with greater relative right anterior activity may not necessarily be depressed; however, when this person is presented with a sufficient negative affective stimulus (e.g., death of a loved one), it is likely that s/he will experience greater negative affect than an individual with greater relative left anterior activity. Davidson and co-workers have demonstrated the ability of anterior asymmetry to predict affective responses to emotionally valenced film clips (Davidson et al., 1990; Tomarken et al., 1990; Wheeler et al., 1993). For example, Tomarken et al. (1990) found that resting frontal EEG asymmetry significantly predicted negative affect and affective valence (positive/negative, good/bad, pleasant/unpleasant) in response to film clips chosen to elicit either positive or negative affect. Davidson has proposed that these findings provide evidence for resting anterior asymmetry acting as a state-independent marker (i.e., not dependent on person's current affective state) of an individual's predisposition to respond affectively.

Petruzzello and co-workers (Hall et al., 2000; Petruzzello et al., 2006; Petruzzello et al., 2001; Petruzzello and Landers, 1994; Petruzzello and Tate, 1997; Van Landuyt, 1999) have utilized Davidson's model in predicting affective responses to acute exercise. Overall, these studies suggest that the intensity of exercise may influence the relationship between resting frontal asymmetry and affective responses to that exercise. When low intensities of exercise are used [walking at a self-selected pace (Hall et al., 2000); cycling at 55% $VO_{2\,max}$ (Petruzzello and Tate, 1997); or cycling at 60% predicted $VO_{2\,max}$ (Van Landuyt, 1999)] frontal EEG asymmetry does not predict affective responses following exercise. However, at higher intensities [cycling at 70% $VO_{2\,max}$ (Petruzzello and Tate, 1997); running at 70% $VO_{2\,max}$ (Petruzzello and Landers, 1994); running at 75% $VO_{2\,max}$ (Petruzzello et al., 2001)], frontal EEG asymmetry has been predictive of affective responses and this relationship appears to be influenced by fitness (Petruzzello et al., 2001).

The purpose of the present study was to clarify whether frontal EEG asymmetry could predict affective responses following an exercise stimulus that is unequivocally strenuous (i.e., leads to volitional exhaustion in all participants regardless of fitness). It was hypothesized that those subjects having greater relative left-sided anterior brain activity at rest would have a more positive (i.e., increased energy or calmness) and/or less negative (i.e., decreased tension or tiredness) affective response following exercise compared to those with greater relative right-sided activity.

2. Methods

2.1. Participants

Thirty healthy college students (13 women, *M* age = 23.2 ± 2.8 years, *M* weight = 73.3 ± 10.1 kg; *M* $VO_{2\,max}$ = 47.3 ± 4.0 ml kg^{-1} min^{-1}; 17 men; *M* age = 24.4 ± 4.1 years, *M* weight = 78.1 ± 7.1 kg; *M* $VO_{2\,max}$ = 51.5 ± 7.0 ml kg^{-1} min^{-1}) volunteered to participate in the study. Prior to their involvement, all participants read and signed an informed consent form approved by the University's Human Subjects Institutional Review Board.

2.2. Measures

2.2.1. Self-reported affect

Affect was assessed with the Activation Deactivation Adjective Check List (AD ACL; see Thayer, 1989). The AD ACL is a 20-item self-report measure that assesses multidimensional arousal via four subscales (energy, tiredness, tension, and calmness), each measured by 5 items. These subscales were used in the present study to measure affect. The reliability and validity of the AD ACL is well established (Thayer, 1978, 1986). Thayer (1978) found that the estimated reliabilities for the subscales of the AD ACL ranged from 0.89 to 0.92. Previous studies using the AD ACL before and after a walk found Cronbach alpha coefficients of 0.90, 0.91, 0.83, 0.76 before the walk and 0.88, 0.89, 0.76, 0.70 after the walk for energy, tiredness, tension, and calmness, respectively (Ekkekakis et al., 2005a).

2.2.2. Brain activity

Resting brain activity (i.e., EEG) was recorded from nine scalp locations. These included left, right, and mid-line recordings from the mid-frontal, central, and parietal brain regions.[1] Resting EEG activity has been shown to be a reliable index of regional brain activity (Tomarken et al., 1992). Raw EEG data were subjected to spectral analysis to decompose the complex EEG waveform into its component sine wave frequencies. The alpha frequency (8–13 Hz) was of interest because it is the primary basis of the Davidson model. Activity in this bandwidth is thought to be negatively related to the activity of the underlying cortex, such that greater alpha spectral power is related to less cortical activity, while less alpha spectral power is associated with greater activity (Oakes et al., 2004). Within Davidson's framework, alpha activity in the frontal regions is used to calculate an asymmetry index (F4–F3) to determine relative left versus right activity. A similar asymmetry index was calculated based on alpha activity from the parietal regions (P4–P3; see Heller, 1993) to determine the regional specificity of any effects.

2.3. EEG recording

A stretchable lycra electrode cap (Electro-Cap, Inc.) was fitted on the participant's head for electrode application and assessment of regional brain activity (i.e., EEG). Placement of the cap utilized anatomical landmarks (i.e., the inion and nasion) on the participant's head to insure proper location. Using this procedure, electrode placements have been shown to deviate negligibly from the International 10–20 System locations (Blom and Anneveldt, 1982). All leads were referenced to linked earlobes and all electrode impedances were below 5 KΩ. Impedances for homologous (e.g., F3, F4) sites were within 500 Ω of each other. Ocular artifact (e.g., eye movements, eyeblinks) was assessed by electro-oculogram (EOG) recording from electrodes placed laterally to both eyes as well as above and below the right eye.

EEG data were acquired using a Grass Model 12 Neurodata acquisition system equipped with Model 12A5 amplifiers. All bioelectric signals were amplified 20,000×, and high and low pass filters were set at 1 and 100 Hz, respectively (rolloff = 6 dB/octave; 60 Hz notch filter in). The amplified and filtered signal was digitized at 256 samples per second and stored on a Gateway

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[1] For the present study, in keeping with the theoretical predictions, only the right and left mid-frontal (F4, F3) and parietal (P4, P3) locations were used. Data from the other sites were collected as part of a larger investigation.

Table 1
Means and standard deviations ($M \pm$ S.D.) for the subscales of the AD ACL

	Energy	Tiredness	Tension	Calmness
Pre-exercise	11.41 ± 2.95	10.00 ± 3.42	8.28 ± 2.64	11.86 ± 2.07
Post-0 min	15.03 ± 3.51[a]	7.62 ± 2.24[a]	8.10 ± 2.45	10.24 ± 2.32[a]
Post-10 min	12.38 ± 3.13[b]	8.62 ± 2.62[b]	6.86 ± 1.90[a,b]	13.55 ± 3.00[b]
Post-20 min	11.38 ± 2.90[b]	9.55 ± 3.10[b,c]	6.62 ± 1.70[a,b]	13.83 ± 2.75[a,b]

[a] Significantly different ($p < 0.05$) than pre.
[b] Significantly different ($p < 0.05$) than post-0 min.
[c] Significantly different ($p < 0.05$) than post-10 min.

486/DX2 computer for later analysis using EEGSYS software (Version 5.5, Friends Medical Science Research Center, Baltimore, MD).

2.4. Procedures

Upon arrival at the laboratory, each participant was greeted, given an overview of the procedures to be followed, and asked to read and sign an informed consent form. The purpose of the study was described as an investigation of "some physiological and psychological responses to vigorous exercise." Participants were then prepped for EEG recording while seated in a comfortable chair. After signal integrity had been confirmed and recorded via impedance checks, participants were asked to sit quietly while baseline measures of EEG were collected. Resting EEG measures were obtained for four, 60 s baseline periods during which participants had their eyes closed. During the recording of these baselines, participants were instructed to be as "restful" as possible. The electrodes and electrode cap for EEG and EOG measurement were then removed so that the participants could complete the graded exercise test.

Participants were fitted with a heart rate monitor (model Vantage XL, Polar Electro, Finland) and asked to complete the AD ACL. Next, participants were shown to a treadmill, were presented with a description of the exercise protocol, and were fitted with a face mask equipped with a one-way valve (Hans Rudolph, Kansas City, MO) for collection of expired gases, ensuring that respiration was unobstructed and comfortable.

The graded exercise protocol was as follows. First, the O_2 and CO_2 analyzers (models S-3A/I and CD-3A, respectively; Ametek Applied Electrochemistry, Pittsburgh, PA) were calibrated using a gas with a known mixture of O_2 and CO_2 and room air. Participants were then seated on a stool for 2 min so that expired gases could be collected and analyzed to ensure the proper functioning of the various components of the metabolic cart. This was followed by a 3-min walk at 1.34 m s^{-1} (0% grade), which served as a warm-up. Once the warm-up was completed, the speed of the treadmill was increased to 2.24 m s^{-1} (0% grade). Beyond this point, the workload was increased every 2 min by alternating between increases in speed by 0.45 m s^{-1} and increases in grade by 2%. This procedure was continued until each participant reached the point of volitional exhaustion (American College of Sports Medicine, 2006). In all cases, this was verified by at least two of the standard criteria for reaching $VO_{2\,max}$, namely (a) reaching a peak or plateau in oxygen consumption (changes of less than 2 ml kg^{-1} min^{-1}) followed immediately by a decrease in oxygen consumption with increasing workloads; (b) attaining a respiratory exchange ratio equal to or higher than 1.1; and (c) reaching or exceeding age-predicted maximal heart rate (i.e., 220 – age). Participants then cooled down by walking on the treadmill for 2 min at 1.34 m s^{-1} and 0% grade. Finally, the participants sat in a chair doing nothing for a recovery period of 20 min. Immediately after the cool-down, as well as 10 and 20 min later, the participants again completed the AD ACL.

2.5. Data reduction and analysis

Off-line, EEG waveforms were visually inspected for artifact by comparing activity at the scalp leads with the EOG. EEG containing artifact was marked and excluded from each EEG trial prior to further analysis of the data. The artifact-free data were divided into epochs of at least 2.0 s in duration that did not overlap. These epochs were subjected to a fast Fourier transform (FFT) for decomposition of the EEG waveform into sine wave components using a cosine bell window. These components were used to estimate spectral power (in μV^2) which was then converted to a power density function (in μV^2/Hz) as a measure of the average spectral power in the alpha frequency band (8–13 Hz) across the trial. A natural log transformation was applied to all power density values to normalize the distribution (Gasser et al., 1982). All participants had a minimum of 10 artifact-free epochs (or 20 s) for each given 60 s baseline period (Gasser et al., 1985; Mocks and Gasser, 1984).

An EEG asymmetry index was derived (Davidson et al., 1990; Pivik et al., 1993) for both the frontal and parietal regions, which reflects the log alpha power density difference between corresponding regions of the two hemispheres (i.e., ln R − ln L alpha power). Thus, higher asymmetry scores represent lower amounts of alpha activity and relatively greater activity in the left hemisphere for a particular region. This asymmetry score has been demonstrated to have acceptable psychometric properties (Tomarken et al., 1992).

Regression analyses were used to examine the predictive power of asymmetry scores on post-exercise affect (i.e., AD ACL subscales) after partitioning out pre-exercise affect and $VO_{2\,max}$ (fitness levels).[2]

3. Results

The means and standard deviations for the self-reported affective measures before and following exercise are reported in Table 1. A repeated-measures MANOVA for the four subscales of the AD ACL was also performed. This showed a significant main effect of time [Wilks' $\lambda = 0.115$, $F(12, 17) = 10.94$, $p < 0.001$], which occurred for all four of the AD ACL subscales: energy [$F(3, 84) = 18.60$, $p < 0.001$], tiredness [$F(3, 84) = 6.95$, $p < 0.001$], tension [$F(3, 84) = 11.37$, $p < 0.001$], and calmness [$F(3, 84) = 21.24$, $p < 0.001$].

3.1. Resting EEG asymmetry predicting post-exercise affect

3.1.1. Frontal regions

To assess the extent to which resting frontal EEG asymmetry (F4–F3) predicted post-exercise affect, a set of hierarchical regression analyses were performed. Prior to these analyses, a one-way ANOVA by gender showed no significant gender differences in EEG asymmetry. Therefore, gender was not included as a factor in subsequent analyses. After controlling for fitness ($VO_{2\,max}$) and pre-exercise calmness (see Table 2), resting frontal EEG asymmetry (i.e., greater left activity relative to right) accounted for 18% ($\beta = 0.432$) of the variance in calmness at post-10, and 13% ($\beta = 0.375$) at post-20. Additionally, after controlling for fitness ($VO_{2\,max}$) and

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[2] Fitness levels were partialled out because previous work has shown fitness levels to influence the predictive ability of regional brain activity on affective responsivity (Petruzzello et al., 2001). In the present study, neither fitness levels nor weight were correlated with frontal asymmetry scores.

Table 2
Hierarchical regression analyses examining ability of frontal asymmetry to predict calmness

	β	$p^{\#}$	R	R^2_{change}	F_{change}	$p^{\dagger}$
Post-0						
$VO_{2\,max}$	−0.051	0.819	0.074	0.005	0.072	0.931
Pre-calmness	0.035	0.877				
$VO_{2\,max}$	−0.042	0.854	0.116	0.008	0.202	0.657
Pre-calmness	0.061	0.796				
Frontal asymmetry	0.092	0.657				
Post-10						
$VO_{2\,max}$	−0.004	0.987	0.145	0.021	0.280	0.758
Pre-calmness	0.144	0.519				
$VO_{2\,max}$	0.040	0.847	0.443	0.175	5.447	0.028
Pre-calmness	0.266	0.216				
Frontal asymmetry	0.432	0.028				
Post-20						
$VO_{2\,max}$	0.371	0.089	0.340	0.115	1.631	0.216
Pre-calmness	0.230	0.282				
$VO_{2\,max}$	0.387	0.062	0.495	0.130	4.126	0.053
Pre-calmness	0.341	0.109				
Frontal asymmetry	0.375	0.053				

[#] p value for β.
[†] p value for F_{change}.

pre-exercise tiredness (see Table 3), resting frontal EEG asymmetry accounted for 21% ($\beta = .459$) of the variance in tiredness at post-10, and 16% ($\beta = 0.405$) at post-20. Resting frontal EEG asymmetry did not predict any significant variance in post-exercise energy or tension.[3]

3.1.2. Parietal regions

Similar hierarchical regression analyses were performed to determine the extent to which resting parietal asymmetry (P4–P3) predicted post-exercise affect after controlling for fitness and pre-exercise affect. Resting parietal asymmetry did not significantly predict any post-exercise affective responses (all βs < 0.275). To further highlight the regional specificity of this effect, the regression coefficients for the frontal and parietal analyses were compared at 10 and 20-min post-exercise. As expected, the regression coefficients for the frontal analyses were significantly different than those for the parietal analyses for calmness at both time points (p's < 0.02) and for tiredness at 10-min ($p = 0.026$) and this difference approached significance at 20-min post-exercise ($p = 0.074$).

4. Discussion

The purpose of this study was to examine the theory proposed by Davidson (1998, 2000a,b, 2004) in the context of

strenuous exercise. Specifically, it was hypothesized that, as specified by the theory, individuals with greater left-than-right frontal activity would exhibit a diathesis (predisposition) to respond to the eliciting stimulus (i.e., exercise) with predominantly positive affect. Previous studies in the context of exercise had suggested that the intensity of exercise might be a critical factor in determining whether or not resting frontal asymmetry can predict post-exercise affective states, showing significant relationships when the intensity was higher, but no relationship when the intensity was lower. The present study was designed to extend this line of inquiry by examining the relationship at the highest end of the intensity range, using a maximal exercise test to volitional exhaustion as the stimulus.

The results showed that frontal EEG asymmetry at rest significantly predicted calmness and tiredness at the 10th and 20th minutes of recovery from the exercise test. These findings present a number of interpretational challenges that warrant scrutiny.

First, it seems paradoxical and inconsistent with Davidson's model that frontal asymmetry would predict calmness and tiredness, two states that appear to differ in terms of their affective valence (positive in the case of calmness, negative in the case of tiredness). In structural models of affect, such as the circumplex (Russell, 1980), calmness (a low-activation pleasant state) and tiredness (a low-activation unpleasant state) would be expected to be orthogonal (i.e., separated by 90°) and, therefore, be unrelated. However, in the present study, calmness and tiredness exhibited positive relationships at 10 min ($r = 0.527$, $p = 0.002$) and 20 min ($r = 0.292$, $p = 0.117$) of recovery. These findings suggest that, perhaps, tiredness did not necessarily reflect negative affect.

The second challenge, then, is to understand why calmness and tiredness covaried in this study. Although seemingly paradoxical, this finding is not entirely unexpected. In fact, this

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[3] Additional separate regression analyses using F3 and F4 natural log transformed alpha power to predict tiredness and calmness following exercise. The only significant β came at Post 0 for tiredness at F3 ($\beta = −0.435, p = 0.014$) and F4 ($\beta = −0.418, p = 0.018$). This suggests that alpha activity for the individual sites were inversely related to tiredness, but the asymmetry score did not predict tiredness Post 0. At all other time points where asymmetry significantly predicted tiredness or calmness, the individual sites did not predict tiredness or calmness (p's > 0.20).

Table 3
Hierarchical regression analyses examining ability of frontal asymmetry to predict tiredness

	β	$p^{\#}$	R	R^2_{change}	F_{change}	$p^{\dagger}$
Post-0						
$VO_{2\,max}$	−0.134	0.474	0.451	0.203	3.320	0.052
Pre-tiredness	0.391	0.044				
$VO_{2\,max}$	−0.144	0.447	0.470	0.018	0.572	0.456
Pre-tiredness	0.373	0.058				
Frontal asymmetry	0.135	0.456				
Post-10						
$VO_{2\,max}$	−0.240	0.226	0.351	0.123	1.832	0.180
Pre-tiredness	0.192	0.330				
$VO_{2\,max}$	−0.274	0.126	0.575	0.207	7.713	0.010
Pre-tiredness	0.131	0.457				
Frontal asymmetry	0.459	0.010				
Post-20						
$VO_{2\,max}$	−0.149	0.475	0.215	0.046	0.604	0.555
Pre-tiredness	0.114	0.583				
$VO_{2\,max}$	−0.202	0.305	0.454	0.160	4.829	0.038
Pre-tiredness	0.056	0.774				
Frontal asymmetry	0.405	0.038				

[#] p value for β.
[†] p value for F_{change}.

is precisely what is expected on the basis of Thayer's (1989, 1996, 2001) multidimensional arousal theory. In Thayer's (1996) words, "exhaustion represents a state of *calm tiredness*" (p. 72, emphasis added). He explains this phenomenon as follows:

> Substantial physical demand reduces energy to a very low level, and tension is reduced to such a degree that calm tiredness prevails. You become unresponsive to anything less than extreme tension-inducing circumstances. The dynamic interaction of energy and tension is especially clear with these experiences. The calm tiredness with exhaustion can be a very pleasant state. The usual concerns seem unimportant, unpleasant anxiety is eliminated, and rest or sleep is complete (Thayer, 2001, pp. 110–111; also see Thayer, 1989, p. 136).

In the present study, there was a continuous drop in energy over the course of recovery (from 15.03 to 12.38 and finally to 11.38), accompanied by a virtual elimination of tension (from 8.10 to 6.68 and finally to 6.62, with the low end of the possible range being 5.00). At the same time, tiredness kept creeping up (from 7.62 to 8.62 and finally to 9.55) while calmness showed a robust increase (from 10.24 to 13.55 and finally to 13.83). This pattern seems to match the scenario described by Thayer (1989, 1996, 2001) quite well. We believe that the affective state that prevailed during the recovery from the maximal exercise test can indeed be described as "calm tiredness."

In addition to Thayer's theory, another observation might also be relevant. In at least one previous study, involving a sample of middle-aged women participating in a maximal exercise test, researchers reported the co-occurrence of fatigue and self-esteem following the test (Pronk et al., 1995). Perhaps this finding, like ours, reflects what Acevedo and et al. have described as the "hurts so good" phenomenon (Acevedo et al.,

1996, 2003). Presumably, this means that, while symptoms of fatigue are undeniable (the "hurt" part), cognitive appraisal, most likely related to contentment, satisfaction, or a sense of accomplishment, produces a concurrent pleasant affective state (the "good" part). Ekkekakis (2003) has speculated that these seemingly incompatible responses "may originate from different levels of the affective hierarchy" (p. 217), the "hurt" or fatigue stemming from direct, cognitively unmediated somatic sensations, whereas the "good" stemming from the cognitive appraisal that one has just accomplished something beneficial or challenging.

The third interpretational challenge is to explain why, unlike previous exercise studies, frontal asymmetry failed to predict post-exercise energy. We believe that the explanation lies in the fact that, following a bout of strenuous exercise, it was "calm tiredness," this potentially "very pleasant state" (Thayer, 2001, p. 111), rather than energy, that was the prevalent affective state. After initial post-exercise drops, both calmness and tiredness gradually rose, with calmness surpassing pre-exercise levels by the 20th minute of recovery. On the contrary, the only noticeable change in energy compared to baseline was at post-0 but this quickly dissipated and, by the twentieth min of recovery, energy was no different than baseline (11.41 versus 11.38). This pattern of changes is unlike previous exercise studies, in which bouts of lower intensity were mainly followed by robust and persistent increases in energy (or activated pleasant affect, in general; Petruzzello et al., 2001; Petruzzello and Tate, 1997).

The fourth and final question is: why did frontal asymmetry not predict any affective variables immediately post-exercise? Our interpretation of this finding is based on the dual-mode theory of exercise-induced affective responses (Ekkekakis, 2003). According to this theory, affective responses to exercise are determined by the continuous interplay between two main

factors, namely interoceptive afferent cues (e.g., respiratory or muscular) that can reach the affective centers of the brain directly, via subcortical routes, and cognitive appraisals (e.g., of ability or accomplishment) mediated by the frontal cortex. Within this framework, it has been theorized that the earliest stages of recovery from strenuous exercise would be characterized by relatively homogenous changes in affective parameters and that this homogeneity reflects the continued influence of strong interoceptive cues (Ekkekakis et al., 2005b). On the other hand, as recovery progresses and the intensity of interoceptive cues subsides, affective responses tend to become more heterogeneous and this diversity presumably reflects the growing influence of cognitive appraisals. In the present study, immediately post-exercise, 71% of participants reported a decrease in tiredness, 77% reported an increase in energy, and 65% reported a decrease in calmness compared to baseline (there was little change in tension). However, by the twentieth min of recovery, the pattern had become more diverse, with 45% now showing increases in tiredness and 42% showing decreases, 42% showing decreases in energy and 32% showing increases, and 23% showing decreases in calmness and 52% showing increases. It is generally believed that EEG activity primarily reflects the workings of the cerebral cortex. Therefore, as Davidson and Fox (1988) have noted, *frontal* asymmetry is assumed to reflect "appraisal and coping" or, in other words, cognitive factors. If this is true, the fact that frontal EEG asymmetry in the present study was associated with affect during the late, but not the early, stages of recovery from strenuous exercise probably indicates that, consistent with the postulates of the dual-mode theory (Ekkekakis, 2003; Ekkekakis et al., 2005b), affect earlier on is dominated by the influence of interoceptive cues whereas later it becomes increasingly influenced by cognitive factors.

Davidson (1998, 2000a) has identified several issues that future studies on the relationship between frontal asymmetry and affect should address. These include affective chronometry, resilience, and threshold for reactivity. All three of these also represent important avenues of future inquiry for exercise studies. First, affective chronometry refers to the temporal dynamics of affective responding, such as rise time to peak (i.e., how quickly an individual reaches the peak of his or her response) and recovery time (i.e., how quickly an individual can recover from some perturbation). Although the present study only examined affect from before to 20 min after the exercise test, future studies could employ assessment protocols that track the entire trajectory of the affective response from initial onset, to peak, and ultimately to complete recovery. This should then allow the examination of the relationships of frontal asymmetry with the various aspects of the chronometry of the affective response to exercise. Second, Davidson (2000a) has defined resilience as "the maintenance of high levels of positive affect and well-being in the face of significant adversity" (p. 1198) and, presumably, in the face of an aversive stimulus such as strenuous exercise. Recent research has uncovered that, on average, a significant decline in pleasure is initiated when the intensity of exercise exceeds the ventilatory threshold (Hall et al., 2002). However, exercise intensities proximal to the

ventilatory threshold are characterized by substantial inter-individual variability in affective responses, with some individuals initiating the decline below and others persevering until considerably above the ventilatory threshold (Ekkekakis et al., 2005c). It is again an open empirical question whether frontal asymmetry could account for part of this variability. Finally, the third aspect of affective style discussed by Davidson is the threshold for reactivity, which refers to the intensity of the eliciting stimulus that is required for an affective response to occur (Davidson, 2000b). In response to exercise, some individuals exhibit a positive affective response with minimal intensities (such as a slow walk) whereas others desire much higher and more challenging intensities. It is again an interesting question whether frontal asymmetry could account for the variability in this threshold.

In sum, in the present study, frontal EEG asymmetry predicted calmness and tiredness during recovery (at 10 and 20 min) from an exercise test performed until volitional exhaustion. These two affective variables were found to be related, suggesting the emergence of what Thayer (1996, 2001) has characterized as a state of "calm tiredness." Therefore, inasmuch as tiredness was evidently not inherently unpleasant in this case, these results are interpreted as providing support for Davidson's model. It is also worth pointing out that this appears to be a regionally specific effect, as parietal asymmetry did not predict any post-exercise affective states, in agreement with previous exercise studies (e.g., Petruzzello et al., 2001). Overall, tests of Davidson's model in the context of exercise have shown that frontal symmetry is (a) unrelated to affect following stimuli of low intensity, (b) significantly related to energy and pleasant high-activation affect following exercise of vigorous intensity, and (c) significantly related to the correlated states of calmness and tiredness following strenuous exercise performed until volitional exhaustion.

Future research should more thoroughly examine how the relationship between frontal EEG asymmetry and affect changes over the entire duration of the exercise bout and recovery, delineate the components of the affective response (such as affective valence versus activation) more closely related to asymmetry, and continue to investigate the moderating role of exercise intensity. These issues become particularly important given the potential for self-regulation of affect through the use of exercise. Gaining a better understanding of the relationships between brain activity, exercise, and affect should help provide practical recommendations in this regard.

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