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Gender differences in the cortical electrophysiological processing of visual emotional stimuli

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The processing of visual emotional stimuli has been investigated previously; however, gender differences in the processing of emotional stimuli remain to be clarified. The aim of the current study was to use steady-state probe topography (SSPT) to examine steady-state visually evoked potentials (SSVEPs) during the processing of pleasant and unpleasant images relative to neutral images, and to determine whether this processing differs between males and females. Thirty participants (15 males and 15 females) viewed 75 images low on the arousal dimension (categorised as pleasant, neutral or unpleasant) selected from the International Affective Picture System (IAPS), whilst a 13-Hz sinusoidal white visual flicker was superimposed over the visual field and brain electrical activity was recorded from 64 electrode sites. Results suggest that pleasant and unpleasant images relative to neutral images are associated with reductions in frontal latency and occipital amplitude. In addition, electrophysiological gender differences were observed despite there being no differences found between males and females on subjective mood or behavioural ratings of presented images (valence and arousal dimensions). The main gender difference reported in the current study related to the processing of unpleasant images (relative to neutral images) which is associated with widespread frontal latency reductions (predominantly right sided) in females but not in males. Our results suggest that gender differences do exist in the processing of visual emotional stimuli, and illustrate the importance of taking these differences into account during investigations of emotional processing. Finally, these gender differences may have implications for the pathophysiology of mood disorders such as depression.

Keywords: Gender; Sex; Emotional processing; Emotion; Unpleasant; Pleasant; IAPS; Valence; Arousal; Electrophysiology; SSPT; Imaging

Introduction

Gender differences in the brain have been well characterised in animals and to a lesser extent, in humans (Cooke et al., 1998; Rabinowicz et al., 1999, 2002; Supprian and Kalus, 1996). Although the functional significance of these differences are unclear (Rabinowicz et al., 1999; Supprian and Kalus, 1996), research is now beginning to examine the gender differences in emotion. This is an important endeavour considering that emotion has been described as the key component in personality and vulnerability factors governing risk for psychopathology (Davidson, 2002). With regards to the disorders of emotion, it is known that the lifetime risk for depression is 10–25% for women but only 5–12% for men (American Psychiatric Association, 1994). A more recent survey based on the ICD-10 classification found 6% of adults to suffer from depressive disorders and that twice as many females as males experience depression (Australian Bureau of Statistics, 1997). Differences in biology as well as gender-related environmental experiences are regarded as the key to understanding these gender differences in depression (Kessler, 2003).

'Emotion' may be defined as a relatively brief episode of synchronised response involving multiple components including cognitive processes, physiological responses, motivation changes, motor expression and subjective feeling (Borod, 1993; Ekman, 1984, 1992; Lang, 1968, 1984; Scherer and Peper, 2001). By contrast, 'mood' is generally considered to be a more diffuse state, characterised by low intensity but relatively long duration (lasting hours to days) (Ekman, 1992; Ketter et al., 2003; Scherer and Peper, 2001). Although, these terms relate to different behavioural constructs, it is possible that chronic or repeated activation of certain underlying neurophysiological mechanisms may be the connection between emotional experience and mood disorders such as depression and anxiety. For example, theories have been proposed which describe certain neurophysiological processes as they relate to longer-lasting affective phenomena such as depressed and anxious mood (e.g. Heller, 1993). Furthermore, brain activation resulting from the use of certain mood induction techniques in healthy participants is regarded as similar to that seen in mood disorders such as depression (see Lawrence and Grasby, 2001, for discussion).

A limited but growing number of studies have investigated whether gender differences in brain activation exist on tasks designed to assess a broad range of emotional processes. These studies are important to enable researchers to move beyond employment of behavioural methodologies which have been criticised for their inability to illuminate processes inaccessible to consciousness (e.g. Davidson et al., 2003). Studies that have investigated emotional perception have reported either no gender differences (Meyers and Smith, 1986), subtle differences between males and females (Morita et al., 2001; Wildgruber et al., 2002), or

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sex-specific areas of brain activation (Killgore and Yurgelun-Todd, 2001; Lee et al., 2002). Tasks that involve more the experience of emotion (e.g. Del Parigi et al., 2002; George et al., 1996; Pardo et al., 1993; Pendergrass et al., 2003; Schneider et al., 2000) have reported more consistent gender differences. Healthy women have been shown to display more activity (i.e. larger number and more widespread significant differences between transient induced negative mood states and baseline) than healthy men in anterior limbic structures such as the inferior frontal, orbital and prefrontal cortices, during transient induced sadness (e.g. George et al., 1996 and Pardo et al., 1993). These studies have also demonstrated that women show more bilateral activation without asymmetries during induced sadness. For example, in a female-only study, increases in activity were reported within the thalamus and medial prefrontal using both film as well as recall-induced emotional states (Lane et al., 1997a). Pardo et al. (1993) demonstrated left-sided activation of inferior frontal and orbitofrontal cortices in males, whilst bilateral activation of these areas was reported in females. In addition, sadness has been associated with amygdala activation in males but not females (Schneider et al., 2000). The authors suggested that females produce less concentrated and less lateralised brain activation than males. Bilateral findings in females are consistent with a widely held neuropsychological theory on the organisation of the brain, which posits that females are more bilateralised than men (Iaccino, 1993; Levy and Heller, 1992; McGlone, 1986). Whilst these studies examining emotional experience have shown gender differences, inconsistent differences have been reported. For example, George et al. (1996) report that women activate a greater portion of their limbic system than men during transient sadness, whilst Schneider et al. (2000) report that processing of sadness is more focal and subcortical in men. The literature focusing on transient happiness has also been inconsistent. For example, decreases as well as increases in activity have been reported for happiness (see George et al., 1995 and Lane et al., 1997a, respectively). Gender differences in transient happiness however may be more subtle. This is supported by previous studies which report either slight or no differences for happiness (George et al., 1996 and Schneider et al., 2000, respectively).

It should be noted however that many problems arise when attempting to compare studies that have investigated gender differences in emotion. First, brain imaging studies have used a variety of different paradigms. These paradigms have included recollection of sad events (Pardo et al., 1993), perception and experience of human emotional nonverbal sounds (Meyers and Smith, 1986; Smith et al., 1995), recollection of affect-specific events (George et al., 1996), viewing of faces with either happy or sad facial expressions to aid mood induction (Schneider et al., 2000), the recognition of facial affect (Kesler-West et al., 2001; Killgore and Yurgelun-Todd, 2001; Lee et al., 2002; Morita et al., 2001), the processing of emotionally evocative images (Canli et al., 2002; Pendergrass et al., 2003), the detection of emotional intonation (Wildgruber et al., 2002), and the experience of hunger and satiation (Del Parigi et al., 2002). Second, there are a large number of different neuroimaging techniques used, which range from PET (Del Parigi et al., 2002; George et al., 1996; Pardo et al., 1993), fMRI (Canli et al., 2002; Kesler-West et al., 2001; Lee et al., 2002; Killgore and Yurgelun-Todd, 2001; Pendergrass et al., 2003; Schneider et al., 2000; Wildgruber et al., 2002) and different electroencephalographic techniques (Meyers and Smith, 1986; Morita et al., 2001; Smith et al., 1995).

The International Affective Picture System (IAPS) (Lang et al., 1999) has become increasingly used amongst brain imaging studies to investigate emotional processes as it allows for systematic selection of images that range in emotional content. Specifically, these images are associated with standardised ratings for valence and arousal which allows researchers to easily replicate published findings for a specific selection of images and also aid interpretation of and allow conclusions to be drawn from multiple studies using this task. Previous studies using the IAPS have investigated emotional processing with haemodynamic imaging techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) (e.g. Canli et al., 1998, 2002; Lane et al., 1997b,c; Lang et al., 1998; Paradiso et al., 1999; Pendergrass et al., 2003; Taylor et al., 1998; Wrase et al., 2003), electroencephalographic-based techniques (e.g. Aftanas et al., 2001a,b, 2002; Junghofer et al., 2001; Kawasaki et al., 2001; Kemp et al., 2002; Mini et al., 1996; Palomba et al., 1997; Schupp et al., 2000, 2003) as well as magnetoencephalography (Northoff et al., 2000, 2002).

However, few of these studies have examined gender differences (Canli et al., 2002; Pendergrass et al., 2003; Wrase et al., 2003). These studies suggest gender differences in several neural structures including the insular, prefrontal and parietal cortices, bilateral visual processing areas, thalamic nuclei, amygdala, caudate, putamen and pons regions, and the postcentral and parahippocampal gyri during the processing of visual emotional stimuli. By contrast, a recent behavioural study that examined gender differences in IAPS images in terms of valence and arousal ratings, facial EMG, skin response and heart rate suggests that ‘remarkable congruence’ was displayed in the physiological profile between the two genders when viewing images having less arousing appetitive and defensive contexts (Bradley et al., 2001). In addition, Wrase et al. (2003) have recently reported that although no significant differences were found between males or females in valence, arousal, skin conductance response and startle modulation, men displayed stronger brain activity for positive visual stimuli in the inferior and medial frontal gyrus, whilst women displayed stronger brain activity for negative visual stimuli in the anterior and medial cingulate gyrus. These findings suggest that although males and females may not differ in terms of behavioural and peripheral physiological measures of emotional responsivity, the two genders may well differ in neurophysiology.

The present study focuses on aspects of *emotion* that relate to the processing of emotional stimuli or *emotional processing*. Emotional processing may be defined as the perception and evaluation of emotional stimuli which may or may not involve emotional experience. For example, emotional processing may involve recognition of emotional facial expressions (emotional perception), recollection of an emotional event (emotional experience), or the viewing of emotional film or images (emotional perception and experience). Note however, that such categorisations are a simplification as studies have clearly demonstrated the presence of autonomic arousal during tasks involving recognition of emotional facial expressions (e.g. Williams et al., 2001). Although the present study involves presentation of images rated low on the dimension of arousal, these pictures do appear to involve aspects of emotional experience, such as alterations in heart rate (Kemp and Nathan, in press).

It has been suggested that techniques with a superior temporal resolution may better address gender differences in emotional processing (e.g. Schneider et al., 2000). Event-related potential techniques however are unable to elucidate time-extended processes following stimulus presentation (Silberstein et al., 1990). Two other techniques, magnetoencephalography (MEG) and steady-state probe topography (SSPT) provide such information; however, relatively few studies using these techniques have investigated how the brain differentially responds to emotional stimuli over time. In the current study, SSPT was used to investigate gender differences during the viewing of emotional stimuli selected from the IAPS. SSPT may be characterised by three features which include (1) the presentation of a rapid and repetitive visual flicker distinct from and irrelevant to the cognitive task undertaken by the participants, (2) the recording of brain electrical activity from 64 scalp-electrode sites within the area defined by the International 10-20 system and (3) a relatively short integration period which enables the rapid changes in brain electrical activity as well as the time-extended processes following stimulus presentation to be tracked (Gray et al., in press; Kemp et al., 2002; Silberstein et al., 1990). We have previously shown that transient widespread and bilateral frontal SSVEP latency and occipital amplitude reductions are associated with the cortical processing of pleasant and unpleasant emotional stimuli in a mixed-gender sample (Kemp et al., 2002). The aim of the current study was to investigate how cortical steady-state visually evoked potentials (SSVEPs) recorded using the SSPT technique are modulated by pleasant and unpleasant images (relative to neutral images) in a larger sample size, and to investigate whether this processing differs between males and females. Based on the extant literature reviewed above, we hypothesise (1) that males and females will not differ in subjective verbal report, (2) that females will display bilateral frontal latency reductions during the processing of both unpleasant and pleasant images relative to neutral images, and (3) that males will display more focal changes.

Methods

Participants

Thirty healthy participants (mean age 23.00 ± 4.21 years), consisting of 15 males (mean age 23.73 ± 5.04 years) and 15 females (mean age 22.27 ± 3.20 years), were included in the current study. All participants were right handed as assessed by the Edinburgh Inventory (Oldfield, 1971), nonsmokers, drug-free, and had no history of epilepsy, head injury, stroke, psychiatric disorders, neurological conditions or alcoholism. A medical examination was conducted by a physician who, from physical- and question-based assessment, screened and excluded potential participants according to these exclusion criteria. Participants were recruited by advertising on noticeboards and word of mouth, were generally from a university population and gave informed consent to participate in the current study.

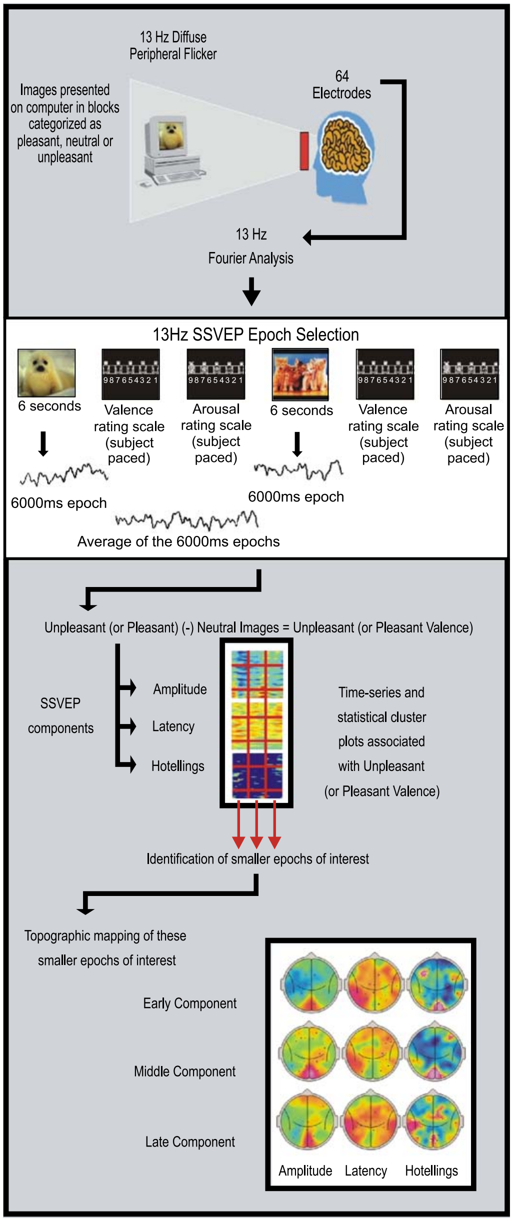
Procedure

All participants were informed that they should not drink alcoholic or caffeinated beverages in the 12 h before the experiment being conducted. Participants then arrived for testing in the morning at approximately 8 am after which a standard breakfast was provided. Participants were then brought to the testing room and the recording procedure explained. Participants completed a short in-house questionnaire relating to standard demographics such as age, gender, years of education and exclusion criteria, the Oldfield handedness inventory (Oldfield, 1971), and the Profile of Mood States (POMS; McNair et al., 1988) before the SSPT recording (see Table 1). Participants indicated how they felt "RIGHT NOW" on the POMS questionnaire to determine current mood state. As outlined by Kemp et al. (2002), 75 images selected from the International Affective Picture System (IAPS) were then presented to participants in three blocks (categorised as pleasant, neutral or unpleasant) of 25 images. The images were carefully selected so that images were relatively low on the dimension of arousal and did not contain high arousal content such as violent death and erotica. Pleasant (P) stimuli included kittens, puppies, babies, flowers, sailing, etc; unpleasant (U) stimuli included cemeteries, smoke, garbage, dead cows, handicapped individuals, etc.; neutral (N) stimuli included mushrooms, animals, abstract art, buildings, kitchen objects, etc. Neutral images were always presented between pleasant and unpleasant image categories, and the presentation order of the categories was counterbalanced (i.e. P, N, U or U, N, P). There were no statistical differences in brightness and contrast between any of the image categories. Following each image, the Self Assessment Maniken (SAM) valence rating scale, ranging from 1 (maximally unpleasant) to 9 (maximally pleasant), and the SAM arousal rating scale, ranging from 1 (low arousal) to 9 (high arousal), appeared on the computer screen requiring the participant to rate each image corresponding to how they felt whilst viewing the previously presented image. Participants had been specifically asked to focus on emotional content and to refrain from emotive inhibition. Recording of brain electrical activity was made from 64 electrodes, located in International 10/20 positions and sites midway between these positions, whilst participants viewed the images and a diffuse 13-Hz sinusoidal white visual flicker was presented over the visual field.

Signal processing and presentation of data

The major methodological steps taken to analyse and present the SSVEP data are presented in Box 1. Signal processing involved calculation of the 13-Hz Fourier coefficients (FC) for each stimulus cycle, smoothing the subsequent time series by averaging overlapping blocks of 10FCs, extracting the 6-s SSVEP associated with each image, averaging across categories, averaging across subjects and then subtracting the averaged SSVEP associated with the neutral category from that associated with the emotional categories to produce activity interpreted as reflecting emotional valence.

Data are presented firstly to efficiently summarise the activity associated with the electrophysiological processing of unpleasant and pleasant valence. Rather than selecting a specific time point through identification of the maximal difference between the emotional categories and the neutral category as described in our previous study (Kemp et al., 2002), we now present time-series plots (including both amplitude and latency SSVEP components) and statistical cluster plots (Hotellings T), which display all 64 electrodes and all seventy-eight 13-Hz time points. These time series and statistical cluster plots reflect the SSVEP associated with the processing of emotional valence for the entire 6-s image presentation. In all plots and topographic maps, warmer colours reflect reduced amplitude and latency during the presentation of emotional images relative to neutral images as well as larger t values in the Hotellings maps. The time series as well as the statistical cluster plots present electrodes on the y-axis and time points on the x-axis. Amplitude is always in the top row, latency on the second row and the Hotellings statistical cluster plots on the third row. Electrode numbers have been demarcated as having either frontal (including electrodes Fp1, Fp2, F7, F3,



Box 1. Methodological steps taken to analyse and present SSVEP data.

Fz, F4 and F8), centro-parieto-temporal (including electrodes T3, C3, Cz, C4, T4, T5, P3, Pz, P4 and T6) and occipital locations (including electrodes O1, Oz and O2) to aid in interpretation of these plots.

Statistical clusters of surrounding electrodes and consecutive time points were identified and used as a guide for determining epochs of interest within the larger 6-s epoch. Consecutive time points within these epochs were then averaged and represented in the form of topographic maps using a spherical spline interpolation procedure (Nunez et al., 1994). These epochs were normalised using normalisation factors (NFs) which were identical to those used for the amplitude and latency components in the 6-s epoch in order for the newly epoched data to be directly comparable to the 6-s epoched data. (For description of normalisation procedures, see Kemp et al., 2002.) The topographic maps display amplitude and latency components of the SSVEP for emotional images relative to neutral images (emotional valence), as well as the statistical strength of these differences.

Results are presented in the following way. Firstly, Fig. 1 displays the time series and statistical cluster plots for the entire sample (n = 30), whilst Fig. 2 displays the epochs of interest in the form of topographic maps. Fig. 3 presents time series and statistical cluster plots for males (n = 15) and females (n = 15) separately, whilst Fig. 4 presents male and female epochs of interest in the form of topographic maps. Results summarise all significant effects into the following regions: (1) left frontal region, (2) right frontal region, (3) left temporal, central and parietal regions, (4) right temporal, central and parietal regions and the (5) occipital region. In summarising the results displayed in the topographic maps, if an SSVEP component (amplitude or latency) did not appear to be either increased or decreased in the emotional condition relative to the neutral condition (as indicated by topographic difference maps) within the statistically significant region (as indicated by the Hotellings maps), then the other SSVEP component is reported only and it is this component that is interpreted as being responsible for this effect.

Statistics

Separate independent-sample t tests were firstly conducted on behavioural variables including age, education and each of the POMS subscales to determine whether differences existed between males and females. In addition, between-groups repeated-measures ANOVAs were conducted on participant's valence and arousal ratings to determine whether gender modified the main effects of these two variables. The statistical strength of the SSVEP differences between the emotional images (unpleasant, pleasant) and the neutral images were examined using the Hotellings T^2 parameter and presented in both statistical cluster plots and topographic maps. Due to the exploratory nature of this study, an alpha criterion for the Hotellings T was arbitrarily set at P = 0.01 (uncorrected for multiple comparisons) for the SSVEP data. It is assumed that real effects will have some degree of statistical continuity both in terms of surrounding electrodes and consecutive time points, and that if one particular electrode or point in time is statistically significant, then adjacent electrodes and consecutive time points will also be significant. The rationale that clusters of statistical significance are likely to reflect real effects has been used previously (e.g. Gray et al., in press; Guthrie and Buchwald, 1991; Murray et al., 2002).

The Hotellings T statistic illustrates statistical differences of within-subject effects. Although topographic mapping of within-subject statistical differences allow for a potentially useful, visual comparison between different groups (e.g. Silberstein et al., 1998, 2000), the Hotellings T statistic does not directly compare differences between males and females. Therefore, in addition to the Hotellings T statistics, the SSVEP was also analysed using six, 2 (male, female genders) × 3 (neutral, pleasant, unpleasant categories) × 2 (left, right hemispheres) × 2 (frontal, posterior regions), mixed-between and within-subject repeated-measures ANOVAs (RMANOVAs) for early, middle and late time points separately. Separate tests were conducted for each time-period to complement the effects displayed in the topographic maps and provide some means of comparison between the two statistical tests (and topographic maps) conducted on the SSVEP. To reduce the number of within-subject dependent variables (i.e. electrodes) entered into these analyses, three standard electrodes within each quadrant were selected and averaged, yielding four SSVEP (amplitude and latency) values per quadrant (i.e. left frontal: Fp1, F7, F3; right frontal: Fp2, F8, F4; left posterior: O1, P3, T5; right posterior: O2, P4, T6). Although Hotellings T statistics were conducted on complex numbers (combination of amplitude and phase) using in-house software, no in-house software is available at present for conducting repeated-measures statistics on such data. Therefore, RMANOVA statistics were performed on normalised amplitude and latency data (separately), which enabled the tests to be run using the Statistical Package for Social Sciences (SPSS) V.10 (SPSS Inc., 1999). In total, six RMANOVAs were conducted to examine effects of gender in amplitude and latency data at each of the three time periods. As these tests were run to examine effects of gender and to (partially) minimise the impact of experiment-wise type 1 error resulting from the running of multiple statistical tests, only gender-associated effects and their interactions are reported in this paper. An alpha level of 0.05 uncorrected for multiple comparisons was arbitrarily set for the repeated-measures ANOVAs conducted.

Results

Behavioural results

A series of independent-samples t tests were conducted on age, education and each of the POMS subscales separately to determine whether any differences exist between males and females. None of these variables were found to significantly differ between males and females ($P > 0.05$). Means (M), standard deviations (SD) and range are provided for age, years of education and all six POMS subscales for males and females (grouped as well as separated by gender) in Table 1.

Participants rated each image on valence and arousal scales. These ratings were averaged for each subject (25 images per category) and then averaged across subjects. Means (M), standard deviations (SD) and ranges for these ratings are provided below in Table 2 for the group averaged data, as well as males and females separately.

To determine whether gender modified the main effects for either valence or arousal, a between-groups repeated-measures ANOVA was conducted for both valence and arousal (separately). The tests revealed no significant Valence × Gender interaction [$F(1.19,33.31) = 1.51$, $P = 0.30$] (Greenhouse–Geisser adjusted), or Arousal × Gender interaction [$F(1.58,44.24) = 0.41$, $P = 0.62$] (Greenhouse–Geisser adjusted), indicating that gender did not modify the significant main effect of valence [$F(1.19,33.31) = 175.18$, $P < 0.001$] (Greenhouse–Geisser adjusted) or arousal [$F(1.58,44.24) = 30.52$, $P < 0.001$] (Greenhouse–Geisser adjusted). For the valence rating scale, planned comparisons revealed differences between pleasant and neutral categories, [$F(1,28) = 119.86$, $P < 0.001$, partial eta squared = 0.81] as well as unpleasant and neutral categories [$F(1,28) = 170.72$, $P < 0.001$, partial eta squared = 0.86]. For the arousal rating scale, significant differences between pleasant and neutral categories [$F(1,28) = 41.42$, $P < 0.001$, partial eta squared = 0.60], as well as unpleasant and neutral categories [$F(1,28) = 68.92$, $P < 0.001$, partial eta squared = 0.71] were also revealed, but not for pleasant and unpleasant categories [$F(1,28) = 4.08$, $P = 0.053$].

SSPT results

On examination of the amplitude, latency and Hotellings plots in Fig. 1, distinct significant clusters of activation differ between pleasant and unpleasant valence. To better examine these activations in terms of spatial scalp location, the data presented in the time-series plots below were averaged into three 2-s time periods [specified as early (0–2 s), middle, (2–4 s) and late components (4–6 s)], and examined topographically (Fig. 2). These maps reflect the SSVEP that corresponds with the mean difference [emotional category (−) neutral category] of early, middle and late components (each map containing an average of the twenty-six 13-Hz cycles) as demarcated in the time-series plots in Fig. 1. The statistically significant findings displayed in these topographic maps are summarised in Table 3 and discussed below.

Pleasant and unpleasant valence display similarities as well as differences across the 6-s epoch, suggesting that activation of both unique and common cortical areas occurs during the processing of pleasant and unpleasant stimuli (see Fig. 2 and Table 3). During both pleasant and unpleasant valence, reductions in amplitude and latency are observed within the left frontal region (latency only) and the occipital region. A number of differences are also observed and these indicate that pleasant valence unlike unpleasant valence is associated with increases in amplitude within left frontal and decreases in amplitude within right frontal regions; more persistent and widespread frontal latency decreases; and amplitude and latency changes within both left and right temporal, central and parietal regions. Finally, latency reductions during unpleasant valence occur during the early time period only, thus appearing as more of a transient phenomenon compared to pleasant valence in which latency reductions occur throughout all time periods.

To examine potential gender differences, amplitude and latency time series and statistical cluster plots are displayed in Fig. 3 for males and females for both pleasant and unpleasant valence. Inspection of the Hotellings T plots, particularly for unpleasant valence, suggests that the number and size of statistically significant clusters of activation differ between males and females. Again, to allow a better spatial scalp profile of these findings, early, middle and late epoch components are presented in the form of topographic maps (Fig. 4). Statistically significant results displayed in these maps are summarised in Table 4 and discussed below.

Males and females display both similarities as well as differences in the processing of emotional valence, suggesting that unique as well as common cortical areas are activated when males and females process emotional stimuli. During the processing of pleasant valence, both males and females display reductions in latency within the right frontal and left temporal regions. However, males display left frontal increases in amplitude and reductions in latency as well as reductions in occipital amplitude, whilst females display reductions in latency within left and right temporal, central and parietal regions and increases in occipital latency. During the processing of unpleasant valence, both males and females display amplitude increases within the right temporal region during the middle epoch,

Table 1
Participant characteristics: M ± SD (range)

	Grouped sample (n = 30)	Males (n = 15)	Females (n = 15)
Age (years)	23.00 ± 4.21 (18–39)	23.73 ± 5.04 (18–39)	22.27 ± 3.20 (19–31)
Education (years)*	15.88 ± 1.97 (12–21)	15.80 ± 2.30 (12–20)	15.96 ± 1.62 (14–21)
POMS			
Tension-anxiety	6.07 ± 4.03 (0–14)	5.67 ± 3.66 (0–11)	6.47 ± 4.47 (0–14)
Depression-dejection	5.17 ± 5.68 (0–21)	5.07 ± 5.35 (0–16)	5.27 ± 6.18 (0–21)
Anger-Hostility	4.37 ± 5.32 (0–26)	5.47 ± 6.46 (0–26)	3.27 ± 3.79 (0–13)
Vigor	15.27 ± 6.44 (0–28)	15.67 ± 6.81 (4–27)	14.87 ± 6.27 (0–28)
Fatigue	5.93 ± 5.21 (0–20)	4.87 ± 4.64 (0–15)	7.00 ± 5.68 (1–20)
Confusion-bewilderment	6.10 ± 4.23 (0–16)	5.33 ± 3.92 (0–13)	6.87 ± 4.52 (0–16)

*Missing data for one female.

although males display latency increases and females display latency decreases. A number of differences are also observed indicating that females display frontal SSVEP changes (predominantly latency reductions and distributed primarily in the right hemisphere), whilst males do not display frontal SSVEP changes. In addition, females display reductions in both amplitude and latency in left temporal, central and parietal regions, whilst males display occipital reductions in both amplitude and latency. In summary, the processing of pleasant valence was associated with latency reductions within right as well as left frontal regions in males, and latency reductions within right frontal regions (during the late time period only) in females. By contrast, the processing of unpleasant valence was associated with latency reductions within right frontal and temporal regions in females only.

A series of mixed-, between- (gender) and within-subject (category, hemisphere, region) repeated-measures ANOVAs were conducted for amplitude and latency data at early, middle and late time points to directly compare between males and females. These RMANOVAs revealed a significant Category × Hemisphere × Gender interaction [$F(2,56) = 3.172$, $P = 0.050$, partial eta squared = 0.102] for amplitude during the middle time period, a significant Category × Region × Gender interaction [$F(2,56) = 3.307$, $P = 0.044$, partial eta squared = 0.106] for latency during the middle time period and a significant Category × Hemisphere × Gender interaction [$F(2,56) = 3.899$, $P = 0.026$, partial eta squared = 0.122] for amplitude during the late time period. No other gender-associated effects or any overall between-subject effects (main effects of gender) were found to be significant.

The Category × Hemisphere × Gender interaction for amplitude during the middle time period indicates that Category modified a Hemisphere × Gender interaction. Tests of within-subject contrasts indicated that Category modified the Hemisphere × Gender interaction during presentation of unpleasant images relative to neutral images [$F(1,28) = 4.324$, $P = 0.047$, partial eta squared = 0.134], but not during pleasant images relative to neutral images [$F(1,28) = 0.402$, $P = 0.531$]. To investigate this effect further, two Hemisphere × Gender RMANOVAs were conducted on neutral [$F(1,28) = 0.262$, $P = 0.613$] and unpleasant [$F(1,28) = 6.830$, $P = 0.014$, partial eta squared = 0.196] images separately. These findings indicate that amplitude within the right hemisphere (anterior and posterior) in females is greater than the left hemisphere whilst viewing unpleasant images. This effect however, was not present in the male sample.

The Category × Region × Gender interaction for latency during the middle time period indicates that Category modified a Region × Gender interaction. Tests of within-subject contrasts indicated that Category modified the Region × Gender interaction during presentation of unpleasant images relative to neutral images [$F(1,28) = 6.000$, $P = 0.021$, partial eta squared = 0.176], but not during pleasant images relative to neutral images [$F(1,28) =$ c0.073, $P = 0.788$, partial eta squared = 0.003]. To investigate this effect further, two Region × Gender RMANOVAs were conducted on neutral [$F(1,28) = 2.753$, $P = 0.108$] and unpleasant images [$F(1,28) = 3.144$, $P = 0.87$, partial eta squared = 0.101] separately. The results for the latter ANOVA indicate a trend for a Region × Gender interaction during viewing of unpleasant images. As the initial ANOVA was significant however, further examination of the associated SPSS profile plot (not displayed) was warranted. This plot indicated that females may display latency reductions within the frontal regions, whilst males displayed small latency increases. An independent sample t test conducted on the average of left and right frontal locations indicated that this effect was significant [$T(28) = 2.242$, $P = 0.033$].

Finally, the Category × Hemisphere × Gender interaction for amplitude during the late time period indicates that Category modified a Hemisphere × Gender interaction. Tests of within-subject contrasts indicated that Category modifies the Hemisphere × Gender Interaction during the presentation of

Table 2
Valence and arousal behavioural rating scores for our Australian participants (M ± SD and range)

Category	Males and females (n = 30)	Males (n = 15)	Females (n = 15)
Unpleasant: valence	3.38 ± 0.65 (1.88–4.24)	3.57 ± 0.51 (2.52–4.24)	3.18 ± 0.72 (1.88–4.20)
Unpleasant: arousal	3.94 ± 1.40 (1.16–7.16)	3.97 ± 1.49 (1.96–7.16)	3.90 ± 1.35 (1.16–6.44)
Neutral: valence	5.15 ± 0.28 (4.28–5.80)	5.15 ± 0.32 (4.28–5.68)	5.16 ± 0.26 (4.80–5.80)
Neutral: arousal	1.75 ± 0.62 (1.00–3.48)	1.87 ± 0.58 (1.08–3.08)	1.63 ± 0.66 (1.00–3.48)
Pleasant: valence	6.33 ± 0.64 (5.28–7.84)	6.32 ± 0.64 (5.28–7.72)	6.35 ± 0.66 (5.44–7.84)
Pleasant: arousal	3.23 ± 1.43 (1.12–6.04)	3.10 ± 1.45 (1.12–6.04)	3.36 ± 1.44 (1.64–5.40)

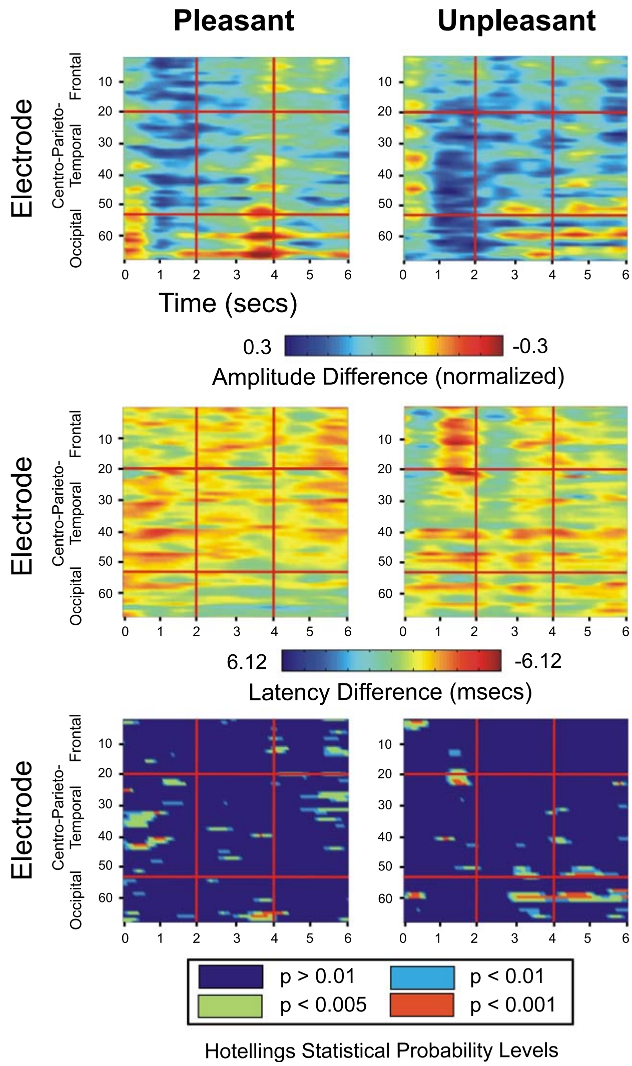


Fig. 1. Amplitude (row 1) and latency (row 2) time series plots illustrate the difference between emotional categories (pleasant and unpleasant) and the neutral category across time (*x*-axis) for each of the 64 electrode positions (*y*-axis) for 30 participants. Warmer colours in these maps represent reduced amplitude and latency during the presentation of emotional images. The Hotellings statistical cluster plots (row 3) illustrate the results of point-wise Hotellings t tests, which evaluated the differences between the emotional categories and the neutral category. These statistical cluster plots display four levels of probability (uncorrected for multiple comparisons) in which warmer colours illustrate larger t values in the Hotellings maps.

unpleasant images relative to neutral images [$F(1,28) = 7.110$, p0.013, partial eta squared = 0.203] but not during the presentation of pleasant images relative to neutral images [$F(1,28) = 0.452$, $P = 0.507$]. To investigate this effect further, two Hemisphere × Gender RMANOVAs were conducted on neutral [$F(1,28) = 0.006$, $P = 0.939$] and unpleasant [$F(1,28) = 7.726$, $P = 0.010$, partial eta squared = 0.216] images separately. Like those reported for the middle time period, these findings indicate that amplitude within the right hemisphere (anterior and posterior) in females is greater than the left hemisphere whilst viewing unpleasant images. This effect again was not present in males.

In summary, results indicate no overall between-subject (gender) differences; however, findings for amplitude during both the middle and late time periods indicate that only females display increased amplitude within the right hemisphere relative to the left hemisphere (after collapsing across frontal and posterior locations). In addition, findings for latency during the middle time period indicate that only females display latency reductions within frontal locations. All these effects were significant during viewing of unpleasant images only.

Discussion

The current study investigated the spatiotemporal characteristics of the SSVEP associated with the processing of low arousal, unpleasant and pleasant images relative to neutral images in males and females using the SSPT technique. SSVEP results support our previous study (Kemp et al., 2002) which reports that processing of emotional valence (pleasant and unpleasant) is associated with frontal SSVEP latency and occipital amplitude reductions; however, substantial gender differences exist particularly within the frontal regions during the processing of unpleasant valence and these are discussed below. Key findings demonstrate (1) that electrophysiological differences between males and females exist despite there being no differences in subjective mood (POMS questionnaire) or behavioural ratings (valence and arousal dimensions), (2) that the processing of pleasant valence is associated with left and right frontal latency reductions in males, but not in females, (3) that the processing of unpleasant valence is associated with widespread frontal latency reductions (predominantly right sided and most apparent during the middle time period) in females, but not in males, and (4) that only females display increased amplitude within the right hemisphere relative to the left hemisphere during unpleasant images in the middle and late time periods.

The SSVEP amplitude and latency components have been interpreted previously as being analogous to the amplitude of regional cortical activity within the alpha frequency range and as reflecting neural information processing speed, respectively (Kemp et al., 2002; Silberstein et al., 1990, 1995, 1996, 2000). In this framework, reductions in SSVEP amplitude may be considered comparable to the transient reduction in alpha activity, known as event-related desynchronisation (see Pfurtscheller and Lopes da Silva, 1999, for review), whilst reductions in SSVEP latency may be considered as increased neural information processing speed or more generally as either increased excitation or reduced inhibition. Supporting this interpretation, increases in visual attention are associated with decreases in SSVEP amplitude at occipital and prefrontal sites (Silberstein et al., 1990, 1995) and variations in reaction time in a visual vigilance task correlates with frontal SSVEP latency changes (Silberstein et al., 1996, 2000).

The literature implicates anterior frontal locations more in emotional valence and emotional experience, whilst posterior regions are implicated more in perceptual and arousal components of emotion (Davidson, 1992, 1998; Davidson and Irwin, 1999; Heller, 1990, 1993). This background in terms of the neural structures underlying experiential and perceptual components of emotion is important for the interpretation of the gender differences presented in the results, particularly within frontal

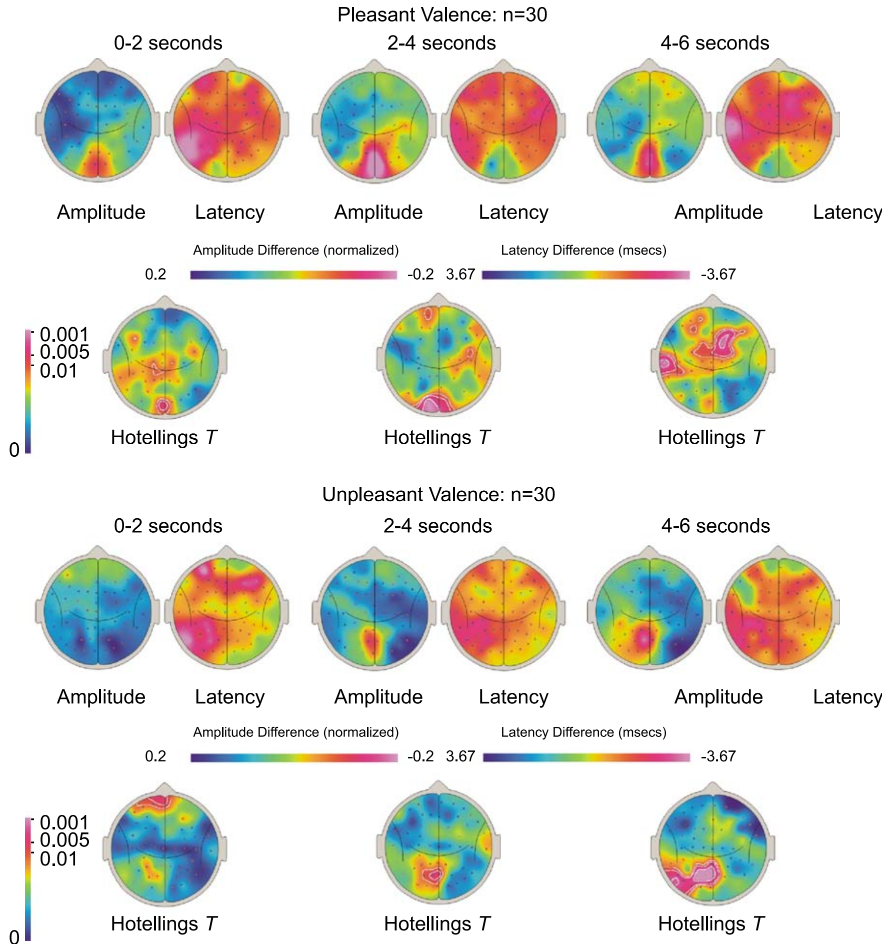


Fig. 2. Topographic maps associated with the difference between emotional categories (pleasant and unpleasant) and the neutral category are presented for amplitude and latency as well as Hotellings *T* values. Contours are plotted on the Hotellings *T* maps at three levels of probability ($P = 0.01$, $P = 0.005$ and $P = 0.001$) uncorrected for multiple comparisons. Three time periods are presented which relate to early (0–2 s), middle (2–4 s) and late (4–6 s) components of image viewing. Warmer colours represent reductions in amplitude and latency during presentation of emotional images relative to neutral images and larger *t* values in the Hotellings *T* maps.

regions. Right frontal activation during unpleasant emotion (e.g. disgust) and left frontal activation during pleasant emotion (e.g. happiness) has been reported extensively in the EEG literature, and activation of these regions may be specialised for withdrawal and approach behaviours, respectively (for review, see Davidson, 1998). These EEG findings have more recently been supported by PET, fMRI and electrophysiological studies (Canli et al., 1998; Sutton et al., 1997; Aftanas et al., 2001a,b, respectively), though others have reported overlapping activation and no hemispheric asymmetries (Baker et al., 1997; George et al., 1995; Kemp et al., 2002; Lane et al., 1997a,b,c; Pardo et al., 1993; Teasdale et al., 1999). Regardless, the prefrontal region is strongly implicated in emotional processing and the experience of emotion (Davidson and Irwin, 1999).

The processing of unpleasant valence is associated with widespread frontal latency reductions (predominantly right sided) in females but not in males. It is possible that males were less responsive to unpleasant stimuli, supporting previous studies which have reported greater activations particularly in frontal regions, in females relative to males. For example, Pardo et al. (1993) reported that whilst women displayed bilateral inferior and orbitofrontal activation in response to recalled sad mood, males displayed left-sided activation only. In addition, George et al. (1996) reported that whilst women displayed increased activity in the bilateral anterior cingulate, left medial prefrontal cortex, left insula and thalamus during the transient sadness, males activated only the left insula and right caudate, completely failing to activate the prefrontal cortex. Furthermore, women in this latter study displayed a greater number of significant changes from neutral to sadness tasks. It is important to note that SSPT is unable to acquire functional information from subcortical structures and it is possible therefore that the processing of unpleasant valence in males may be more subcortical than in females. This interpretation has been made previously in an fMRI study (Schneider et al., 2000) in which the authors speculated that men may have displayed increased amygdala involvement because they exerted greater effort to experience sadness.

These results are particularly interesting given that females are more susceptible to lowered mood as demonstrated in tryptophan depletion studies (e.g. Ellenbogen et al., 1996; Smith et al., 1997; Booij et al., 2002) and, more generally, that females are more likely to experience depression and anxiety (see Darlington, 2002, for

Table 3
Summary of the statistically significant SSVEP findings (amplitude and latency) as indicated by the Hotellings T ($P < 0.01$, uncorrected for multiple comparisons) for pleasant and unpleasant valence for 30 participants, where Amp = amplitude and Lat = latency

Valence	Region	Time periods		
		Early component (0–2 s)	Middle component (2–4 s)	Late component (4–6 s)
Pleasant	left frontal region	Amp ↑; Lat ↓	Lat ↓	Lat ↓
	right frontal region		Amp ↓; Lat ↓	Lat ↓
	left temporal, central and parietal regions	Amp ↑; Lat ↓		Amp ↑; Lat ↓
	right temporal, central and parietal regions			Amp ↑; Lat ↓
	occipital region	Amp ↓; Lat ↓	Amp ↓	
Unpleasant	left frontal region	Lat ↓		
	right frontal region			
	left temporal, central and parietal regions		Amp ↓; Lat ↓	Amp ↓; Lat ↓
	right temporal, central and parietal regions			
	occipital region		Amp ↓; Lat ↓	Amp ↓; Lat ↓

review). Nishizawa et al. (1997) reported that serotonin synthesis in normal females was 52% lower than normal males, indicating that females may be less able to maintain adequate stores of the serotonin neurotransmitter, particularly under stressful situations. In addition, it has been argued, on the basis of differing social and gender roles, that females are more likely to experience feelings of sadness, hurt and disappointment, which is likely to lead to excessive rumination and clinical depression (Brody 2001; Brody and Hall, 1993; Hankin and Abramson, 2001; Noelen-Hoeksema, 1991). Hankin and Abramson (2001) have posited a cognitive vulnerability-transactional stress theory to explain the 'big fact' that more girls become depressed than boys after the age of 13 or 'middle puberty' and that this difference persists throughout adulthood. On the basis of experimental data, these authors indicate that adolescent girls are more likely than boys to encounter negative life events, experience cognitive vulnerabilities to depression, personality traits such as neuroticism and environmental adversity such as sexual abuse. The model suggests that these experiences will lead to increased negative, anxious and depressive affect, which in turn generates more dependent negative life events, eventually leading to depression. Recent neuroimaging evidence has provided a direct relationship between depressed mood and regions of the frontal cortex following modulation of certain neurochemical systems. For example, PET suggests that both tryptophan and α-methylparatyrosine (AMPT)-induced return of depressive symptoms leads to decreases in metabolism within common brain circuitry including the orbitofrontal and dorsolateral prefrontal cortex (Bremner et al., 1997, 2003). Interestingly, Davidson (2002) has suggested that greater relative right-sided prefrontal metabolism is associated with higher metabolic activity within the amygdala and that such activations have been associated with mood disorders such as anxiety and depression. It is possible therefore that the gender differences observed within right frontal and anterior temporal regions reflect decreased and increased responsiveness in males and females, respectively, to unpleasant images (relative to neutral) despite similar ratings on verbal report.

By contrast, the processing of pleasant valence is associated with left and right frontal latency reductions in males but only the right frontal region (during one time period) in females. The literature has indicated that positive affect is much harder to elicit in the laboratory (Davidson, 2002) and given that the present study presented images previously rated as low on the arousal dimension, it is possible that our sample of females did not engage the cortical areas involved in the experiential components of emotion to the same extent as males. It could be argued that females do not need the same degree of cortical activation to have a subjective feeling comparable to those of males. However, several recent studies suggest that this is not the case. For example, a previous study which investigated sex differences in hunger and satiation concluded that men may have a brain response producing greater hedonic effects from eating and more rewarding feelings associated with satiation (Del Parigi et al., 2002). Whilst not directly comparable, it does suggest that brain responses in males may be more sensitive to pleasant valence than females. Most recently, another study using fMRI to investigate gender differences in the viewing of IAPS images reported that men display a stronger brain activity for positive visual stimuli than women within the inferior and medial frontal gyrus as well as the amygdala (Wrase et al., 2003). If we consider pleasant and unpleasant valence to lie on a continuum as previously hypothesised (Feldman-Barrett and Russell, 1999), it is possible that females are more orientated towards the unpleasant pole on this continuum further supporting female susceptibility to lowered mood. Although the Hotellings statistics provide support for the conclusion that males activate frontal regions more consistently than females during viewing of pleasant images, no gender differences were evident in the RMANOVA statistics for these images. Instead, the gender differences (as reported in the RMANOVA) in both amplitude and latency were specific to unpleasant emotional stimuli, suggesting perhaps that differences in males and females may relate more to unpleasant than pleasant stimuli. Gender differences therefore, relating to the neurobiological mechanisms underlying the processing of pleasant images and pleasant emotion more generally, will need verification in future studies.

A number of similarities between males and females were also observed in the processing of emotional valence. This is consistent with previous reports that there are both similarities and differences between males and females in resting state (e.g. Gur et al., 1995) as well as in the processing of emotional stimuli (e.g. Del Parigi et al., 2002; Pendergrass et al., 2003). During pleasant valence, both males and females display activations (reduced latency) within right frontal and left temporal regions. In addition, the left frontal region in females was close to, but did not reach significance within the late component of image viewing. Left temporal activation during the processing of pleasant valence may relate to findings reported in a previous study in which a more posterior distribution of activity, in the region of the pre- and post-

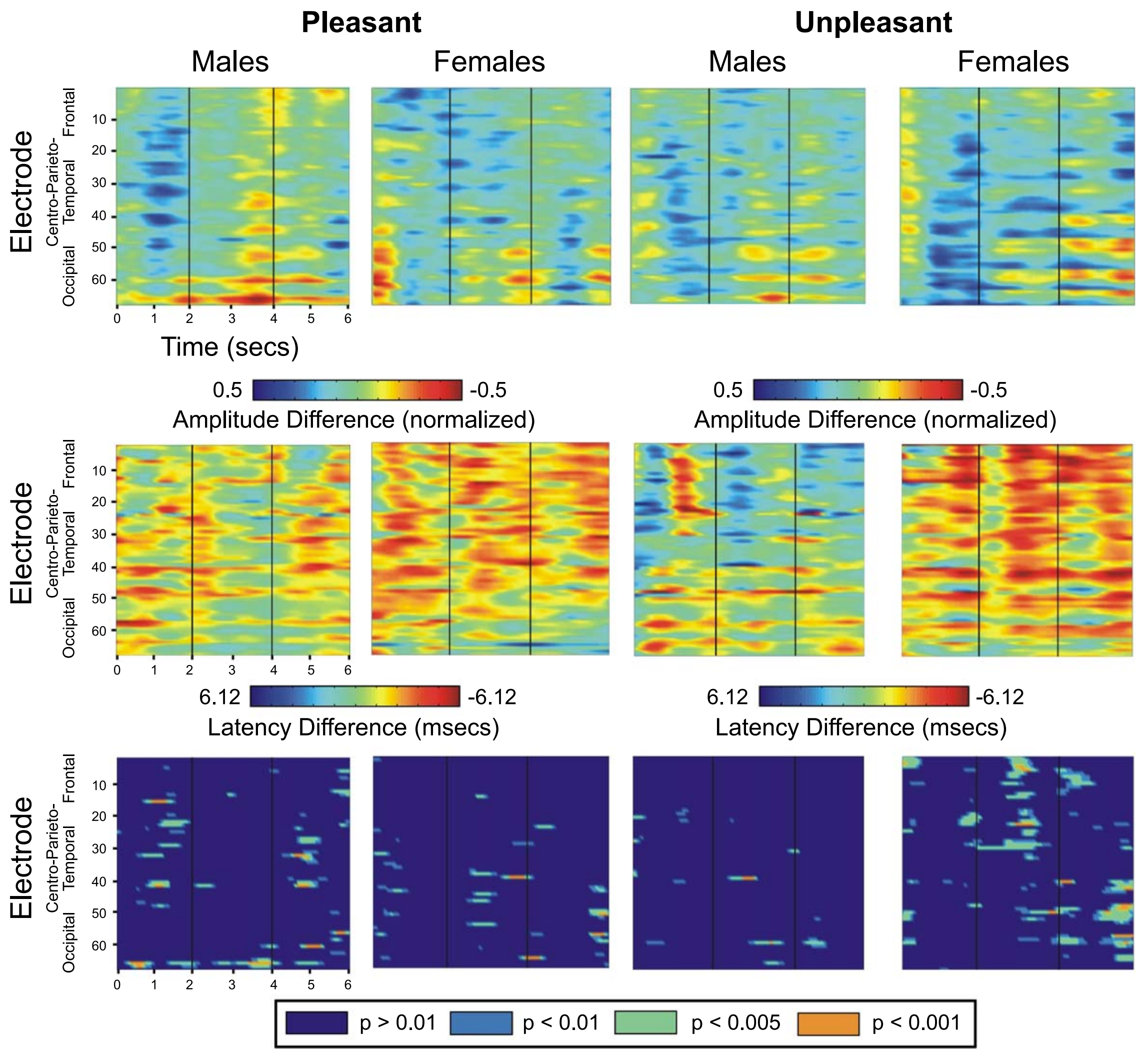


Fig. 3. Amplitude (row 1) and latency (row 2) time series plots and Hotellings T statistical cluster plots (row 3) for emotional valence in 15 males and 15 females. These maps display SSVEP activation across time (x-axis) for each of the 64 electrode positions (y-axis), in which warmer colours represent reduced amplitude and latency during presentation of emotional images, as well as larger t values in the Hotellings maps.

central gyri, was associated with an extended-picture presentation to evoke positive mood (Sutton et al., 1997). However, in the current study, females did not engage the frontal structures to the same extent as males during pleasant valence, which may reflect a lower responsiveness of neural structures involved in the experiential components of emotion in our female subjects. Finally, during unpleasant valence, both males and females display reduced activation (amplitude increases) within right temporal regions.

As discussed above, SSVEP amplitude may be interpreted in exactly the same way as the amplitude of regional cortical activity within the alpha frequency range. In this framework, an amplitude enhancement has been interpreted as a deactivated state in which the brain region is neither receiving nor processing sensory information and that this may be important for the introduction of inhibitory effects (Pfurtscheller and Lopes da Silva, 1999). Consistent with this model, males also display latency increases (increase in inhibitory processes) within this region, possibly reflecting a compensatory response to override expressions of emotion generated by limbic–subcortical structures (as discussed in Liotti et al., 2000). Unlike males however, the processing of unpleasant valence in females is associated with widespread reductions in latency (increases in excitatory processes) which may reflect increased responsiveness to unpleasant (relative to neutral) images and possibly an inability to successfully suppress activation associated with the presentation of unpleasant stimuli. This interpretation is consistent with the purported role of the right hemisphere in inhibitory control (Garavan et al., 1999) and its dense interconnectivity with the paralimbic core (Tucker, 2001).

The finding that only females displayed a more general increase in amplitude during viewing of unpleasant images within the right hemisphere deserves some comment as it could be argued that this finding contradicts traditional theorised patterns in the processing of emotion. For example, one of the oldest theories of emotions in the brain is the key role of the right hemisphere in the processing of emotion (e.g. Levine and Levy, 1986; Ross and Mesulam, 1979; Sackeim et al.,

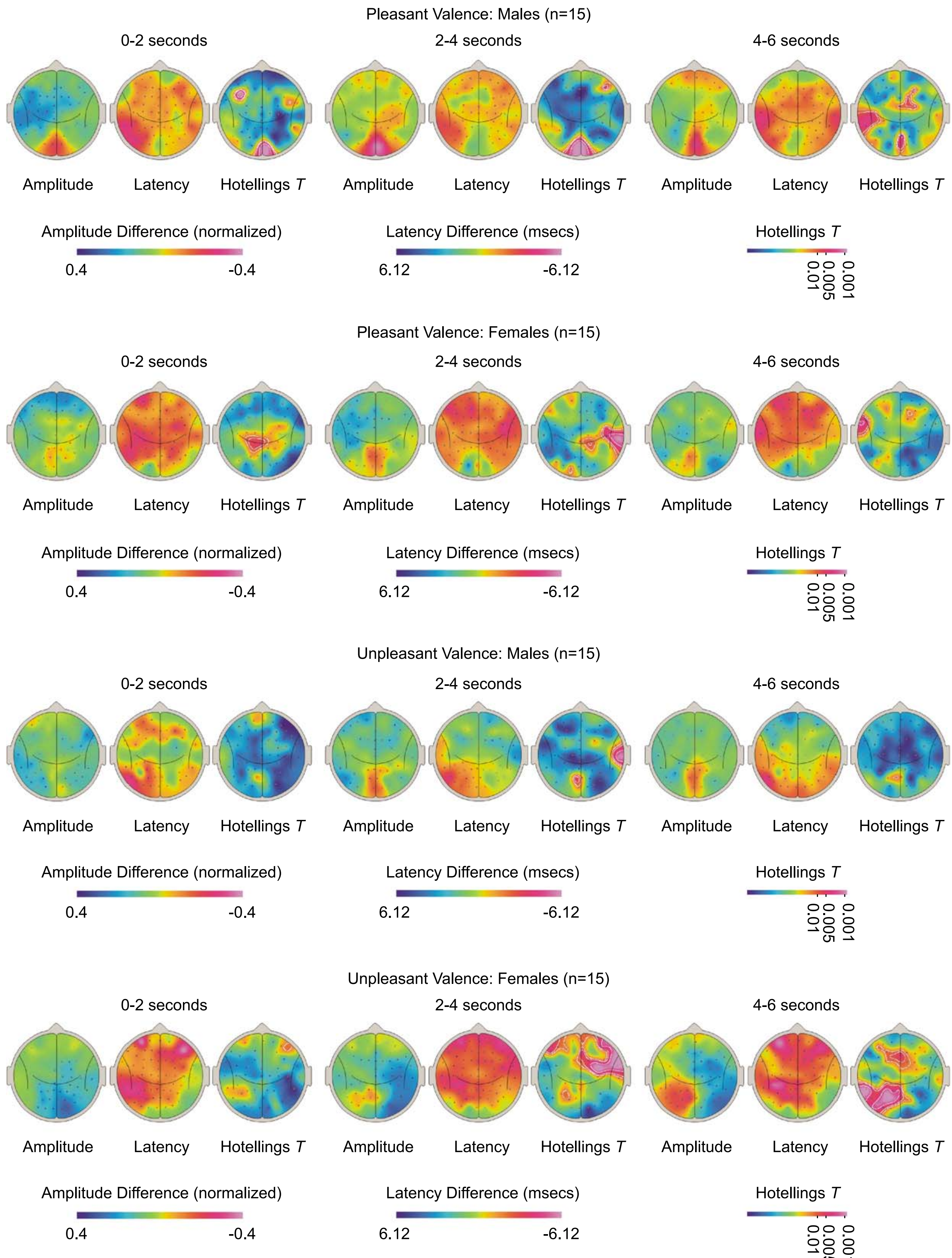


Fig. 4. Topographic maps associated with pleasant and unpleasant valence (pleasant and unpleasant image categories (−) neutral category) in males and females are presented which display the 13-Hz SSVEP data (amplitude and latency) as well as Hotellings T values which demonstrate the statistical significance for the difference data. Contours are plotted on the Hotellings T maps at three levels of probability ($P = 0.01$, $P = 0.005$ and $P = 0.001$) uncorrected for multiple comparisons. Three time periods are presented which relate to early (0–2 s), middle (2–4 s) and late (4–6 s) components of image viewing. Warmer colours represent reductions in amplitude and latency during presentation of emotional images relative to neutral images and larger t values in the Hotellings T maps.

Table 4
Summary of the statistically significant SSVEP findings (amplitude and latency) for 15 males and 15 females as indicated by the Hotellings T ($P < 0.01$, uncorrected for multiple comparisons) for both pleasant and unpleasant valence, where Amp = amplitude and Lat = latency

Valence	Gender	Region	Time periods		
			Early component (0–2 s)	Middle component (2–4 s)	Late component (4–6 s)
Pleasant	Males	left frontal region	Amp ↑; Lat ↓		
		right frontal region	Lat ↓	Lat ↓	Lat ↓
		left temporal, central and parietal regions			Lat ↓
		right temporal, central and parietal regions			
		occipital region	Amp ↓	Amp ↓	Amp ↓
	Females	left frontal region			
		right frontal region			Lat ↓
		left temporal, central and parietal regions	Lat ↓		Lat ↓
		right temporal, central and parietal regions		Lat ↓	
		occipital region		Lat ↑	
Unpleasant	Males	left frontal region			
		right frontal region			
		left temporal, central and parietal regions			
		right temporal, central and parietal regions		Amp ↑; Lat ↑	
		occipital region		Amp ↓; Lat ↓	Amp ↓; Lat ↓
	Females	left frontal region		Lat ↓	Amp ↑; Lat ↓
		right frontal region	Lat ↓	Amp ↓, ↑; Lat ↓	Amp ↑; Lat ↓
		left temporal, central and parietal regions		Amp ↓; Lat ↓	Amp ↓; Lat ↓
		right temporal, central and parietal regions		Amp ↑; Lat ↓	
		occipital region			

1978). In terms of brain activation and from the 'arousal' model of alpha amplitude, in which reductions in alpha amplitude are thought to reflect increases in activation (e.g. Lindsley and Wicke, 1974; Ray and Cole, 1985), it could be argued that decreases in amplitude within the right hemisphere should be displayed rather than the increases found in the current study. However, given that participants were requested to focus on emotional content and refrain from emotional inhibition, it is possible that as part of this process, females primed particular emotional circuits through imagining and remembering similar emotional events. Amplitude findings could therefore be considered to be consistent with previous reports of an increase in alpha activity associated with mental imagery (Ray and Cole, 1985; Tesche et al., 1995) and also the finding that this alpha increase is specific to the right hemisphere (Ray and Cole, 1985).

Finally, some limitations of the study are worth noting. Firstly, participant's ratings of arousal indicate that pleasant and unpleasant images significantly differed from neutral images, thereby making the interpretation that difference maps (emotional versus neutral images) reflect only 'valence', difficult. It is important to mention however, that pleasant and unpleasant images did not significantly differ from each other and also that this finding may reflect the more general difficulty of selecting positively or negatively valenced images which are equivalent to neutral images on the arousal dimension. Moreover, the current study did not select images containing high arousal content such as 'violent death' and 'erotica', which would have otherwise confounded emotional arousal with emotional valence. Secondly, the calculation of RMANOVA statistics required data reduction procedures, which limited the potential conclusions able to be drawn from the results of these tests. Although these statistics confirmed differences between males and females with respects to the processing of unpleasant images, the fact that no statistical differences were displayed for the pleasant stimuli does not rule out that differences for such stimuli may exist (as reported recently by Wrase et al., 2003). Thirdly, it is possible that a range of variables including psychological, cognitive and social variables, could in part, account for the observed effects. Authors have argued for example, that women may employ more cognitive strategies and internal cues, whilst men may focus on the external stimulus to generate emotion (e.g. Schneider et al., 2000). Future studies should examine these issues in more detail when investigating gender differences in emotional processing.

In summary, electrophysiological differences in the processing of pleasant and unpleasant valence between males and females were observed despite there being no differences in subjective mood or ratings of pleasant, neutral or unpleasant images. These results suggest that gender differences do exist in the processing of visual emotional stimuli, and illustrate the importance of taking these differences into account during investigations of emotional processing. The main gender difference reported in the current study relates to the processing of unpleasant valence which is associated with widespread frontal latency reductions (predominantly right sided) in females but not in males. This finding is consistent with the interpretation that females rather than males are more susceptible to negative life experiences and lowered mood, and may have implications for the pathophysiology of mood disorders such as depression.

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