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Time-dependent cortical asymmetries induced by emotional arousal: EEG analysis of event-related synchronization and desynchronization in individually defined frequency bands

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Abstract

Event-related desynchronization (ERD) and synchronization (ERS) in the individually defined theta, alpha-1, alpha-2 and alpha-3 frequency bands were measured in 20 healthy subjects in response to International Affective Picture System (IAPS) stimuli with low, moderate and high arousal (LA, MA and HA) content. The 62-channel EEG, skin conductance response (SCR) and heart rate (HR) were simultaneously recorded while subjects viewed sequentially presented pictures and subjectively rated them after each presentation. In the theta band, both MA and HA vs. LA stimuli induced larger synchronization over the left anterior and bilaterally over posterior cortical leads. However, rather unexpectedly, both MA and HA vs. LA stimuli yielded larger alpha-1 synchronization, predominantly over occipital leads. In both theta and alpha-1 bands, affectively salient stimuli prompted larger ERS against the background of the overall dominance in power synchronization of posterior regions of the right hemisphere, irrespective of stimulus category. Finally, in the alpha-3 band, HA stimuli induce a lateralized time-dependent power increase over anterior leads of the left hemisphere. The hemispheric asymmetries revealed point to recruitment of not only posterior regions of the right hemisphere (theta and alpha-1 bands), but also of anterior regions of the left hemisphere (theta and alpha-3 bands) in affect analysis beyond valence dimension. In terms of affective chronometry, the significant arousal \times time interactions clearly indicate that in the theta frequency band discrimination of affective stimuli has already started at 200 ms post-stimulus, whereas in the alpha-1 and alpha-3 bands this process is delayed by up to 800–1200 ms. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: EEG; Emotion; Emotional arousal; Theta; Alpha; Event-related desynchronization and synchronization; Hemispheric asymmetry; Skin conductance; Heart rate; Affective chronometry

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1. Introduction

Along with valence (pleasant/unpleasant), arousal (high/low) dimension of emotion experience has consistently emerged from multidimensional scaling and factor-analytical studies of self-reported emotion (e.g. Russel and Bullock, 1985; Watson and Tellegen, 1985). Contemporary research on cortical correlates of emotion function have started to take into account this distinction (e.g. Lang et al., 1998; Muller et al., 1999; Aftanas et al., 2001; Junghofer et al., 2001). Due to ambiguity of the arousal concept, repeatedly discussed in the psychophysiological literature (for review see Venables, 1984; Heller et al., 1997), the arousal dimension of emotion function has received little attention in EEG investigations. Consistent with the hypothesis that posterior regions of the right hemisphere are involved in the modulation of *emotion-related arousal* (Heller, 1993), scarce EEG (Nitschke et al., 1999; Davidson et al., 2000a), ERPs (Junghofer et al., 2001), autonomous (e.g. Heilman et al., 1978), neuropsychological (Heller et al., 1997) and fMRI (Lang et al., 1998) findings suggest this association. However, it is yet undetermined how cortical EEG asymmetries, emerging during affective processing, vary with the judged *arousal* of affectively salient stimuli. It is also unclear when, where and at which frequencies it occurs.

The experimental paradigm used in our prior study (Aftanas et al., 2001) was a good starting point for investigating how regional cortical activity varies as a function of arousal, EEG frequency and time course of affective responses. This paradigm controls for several potentially confounding variables. First, IAPS stimuli (Lang et al., 1999) enable control for valence and arousal dimensions. Stimuli are presented for 6 s. This standard time recommended for self-report rating of IAPS stimuli (Bradley and Lang, 1994) is acceptable for detecting both early (evaluative) and later (experiencing) aspects of affective processing in EEG investigations (e.g. Muller et al., 1999; Aftanas et al., 2001). Second, participants are instructed to attend to the pictures, but no overt response is required, so inherent affective reactions to these stimuli, rather than cognitive infor-

mation-processing, are enhanced. Third, cortical activity is investigated using the event-related synchronization/desynchronization (ERD/ERS) method (Pfurtscheller and Aranibar, 1977). Sensory, cognitive and motor processing can result in changes in the ongoing EEG in the form of event-related desynchronization (ERD) or synchronization (ERS). Both phenomena are time-locked to the event and highly frequency band-specific. Traditionally, ERD is interpreted as a correlate of an activated cortical area with increased excitability and the ERS in the alpha and lower beta bands can be interpreted, at least under certain circumstances, as a correlate of a deactivated cortical area. Spatial mapping of ERD/ERS can be used to study the dynamics of cortical activation patterns (Pfurtscheller and Lopes da Silva, 1999). Few previous studies on the ERD/ERS responses to emotion-related stimuli have examined the narrow frequency bands of the EEG and revealed that this EEG quantification method can uncover the cortical correlates of relatively small differences in emotion processing (Aftanas et al., 1996a,b, 2001; Krause et al., 2000) and personality (Aftanas et al., 1996b), as well as a dissociation between the neural correlates of the processing of different types of emotional stimuli (Aftanas et al., 1996a,b, 2001; Krause et al., 2000). However, since fixed frequency bands blur specific relationships between cognitive performance and power measurements, narrow theta, alpha-1, alpha-2 and alpha-3 frequency bands are individually defined in relation to the individual alpha frequency (Doppelmayr et al., 1998a). Fourth, the use of a high-resolution 62-electrode recording montage provides more adequate topography of regional hemispheric activation patterns during emotional processing. Fifth, the simultaneously recorded SCR and electrocardiogram (ECG) data give important support to the proposal that picture differences are attributable to emotional arousal.

The present experiment, based on the merits of both the ERD/ERS method and IAPS stimuli set, was undertaken to examine whether arousal dimension of an emotion function would be associated with ERD/ERS measures of interhemispheric asymmetries in the anterior–posterior di-

rection of the cortical plane. We contrasted changes in brain activity induced by IAPS pictures segregated into low, moderate and high arousal categories. We raised the following questions: do interhemispheric asymmetries, emerging during affective processing and indexed by ERD/ERS measures, vary with the judged *arousal* of an affective picture foreground? If so, when, where and at which frequencies does this occur?

Several predictions were made. In line with Heller's model (Heller, 1993; Heller et al., 1997), as well as with our pilot ERD/ERS study with IAPS pictures (Aftanas et al., 2001), we predicted that modulatory influences of emotional arousal would be restricted to posterior cortical regions, with the strongest impact of high arousal stimuli on right posterior activity. The modulatory influences of emotional arousal on anterior brain activity were difficult to anticipate. According to existing models of emotion, anterior cortical regions are uniquely involved in the valence dimension of emotion, with pleasant affect associated with greater left activity and unpleasant affect associated with greater right activity (Heller, 1993; Davidson et al., 2000a,b). The greater right than left anterior activity associated with unpleasant valence would probably serve to cancel the increase in left anterior activity expected for positive stimuli. Prediction in the frequency domain was related to findings that theta and alpha oscillations defined in narrow frequency bands are regarded as reflecting activity of multifunctional neuronal networks, differentially associated with sensory, cognitive and affective processing (for a review see Crawford et al., 1996; Aftanas et al., 1998; Klimesch, 1999; Basar et al., 1999, 2001). Desynchronization in the lower and medium alpha bands is associated with processes of external attention, such as alertness/vigilance (lowest alpha) and expectancy (medium alpha), whereas desynchronized upper alpha reflects enhanced cognitive processing (e.g. Klimesch et al., 1998a). In turn, previous research suggests that higher theta activity is best interpreted as an electrophysiological manifestation of higher activation, related to orienting, attention, memory, affective and cognitive processing (Klimesch et al., 1996;

Doppelmayr et al., 1998b; Sakowitz et al., 2000; Aftanas et al., 2001; Aftanas and Golosheikine, 2001; Basar et al., 2001). The prediction was that cortical influences of arousal would be predominantly associated with the theta and the lowest alpha bands, indexing involvement of orienting, stimulus decoding and memory (theta), as well as alertness/vigilance (lowest alpha) mechanisms in affective processing. In terms of affective chronometry (Davidson, 1998), according to our recent pilot study (Aftanas et al., 2001) among the four frequency bands, the theta band was assumed to be the fastest in detecting affective salience of incoming stimuli.

2. Method

2.1. Subjects

Subjects (Ss, $n = 20$) were right-handed college students (13 males, 7 females) between the ages of 18 and 26 years. All the Ss signed an informed consent to participate in a study and the research received prior approval of the institutional ethics committee. All the Ss had normal or corrected-to-normal vision. The day before the investigation, the Ss were reminded to refrain from exercise and consumption of alcohol during this day. All the Ss were paid for participation in the study.

2.2. Stimuli (IAPS)

The IAPS pictures as scanned color images (CSEA-NIMH, 1999) were selected by normative arousal (ARO) and valence (VAL) ratings (Lang et al., 1999) and arranged into five subsets (eight stimuli per category): (1) emotionally neutral — low arousal pictures (NeutLA: $ARO \leq 3.11$; $VAL \geq 4.87$ and ≤ 5.74); (2) emotionally positive — moderate arousal pictures (PosMA: $ARO \geq 3.37$ and ≤ 4.39 ; $VAL \geq 6.35$ and ≤ 7.85); (3) emotionally negative — moderate arousal pictures (NegMA: $ARO \geq 3.89$ and ≤ 4.67 ; $VAL \geq 2.65$ and ≤ 4.15); (4) emotionally positive — high arousal pictures (PosHA: $ARO \geq 3.57$ and ≤ 5.39 ; $VAL \geq 6.41$ and ≤ 7.89); and (5) emotionally negative — high arousal pictures (NegHA: ARO

≥ 5.04 and ≤ 5.72 ; $VAL \geq 1.87$ and ≤ 2.50)¹. Resulting arousal and valence ratings of the subsets constructed are basically in line with earlier demonstrations for IAPS stimuli and exhibit a quadratic relationship between valence and arousal dimensions; pictures receiving higher arousal ratings also reveal extreme (either positive or negative) valence ratings (Lang et al., 1993; Lang, 1995).

2.3. Electrophysiological recording

2.3.1. Electroencephalogram

SCAN 4.1.1 software, a 128-channel electrical signal imaging system (ESI-128, NeuroScan Labs), a modified 64-channel QuikCap with embedded Ag/AgCl electrodes (NeuroSoft Inc) and ElectroCap Gel (Weaver and Co) were used to record EEGs from 62 active scalp sites referenced to the tip of the nose (see Fig. 1 for the cap layout). The ground electrode was attached to the center of the forehead. The impedance was kept below 5 k Ω . The EOGs were measured to control for ocular artifacts using the QuikCap electrodes. Vertical EOG was measured with electrodes placed 2 cm above and below the middle of right eye. Horizontal EOG electrodes were placed as close as possible to the left and right outer canthi of the eyes. Calibration was carried out at 100 μ V at 10 Hz. The EEG and EOG signals were digitally filtered at 0.3–50 Hz (–6-dB gain, ≥ -12 -dB/octave slope) and amplified (gain 1000, resolution 0.084 μ V/bit, range 5.5 mV) via SynAmps amplifiers, sampled at 500 Hz and stored for off-line analyses.

2.3.2. Skin conductance response (SCR)

After an appropriate cleaning procedure with OmniPrep abrasive (Weaver & Co), skin conductance electrodes were attached onto the palmar side of the second phalanx of the third and fourth

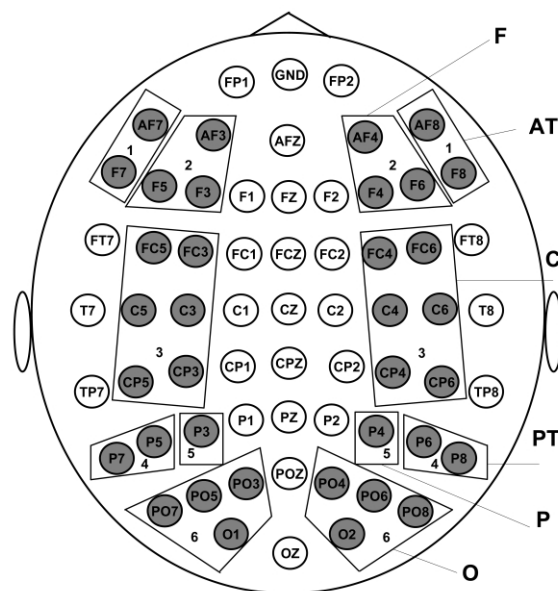


Fig. 1. The electrocap layout and 12 regional means (six for each hemisphere) used for analyses (see text for details).

fingers of both the left and right hands using Sensormedics Ag/AgCl electrodes. Ten20 gel (Weaver & Co) was used as an electrolyte. The left and right signals were acquired with two Coulbourn S71-22 skin conductance couplers, which provided a constant 0.5 V across the electrodes. The couplers were calibrated prior to each session. The calibration values were used off-line to convert the digitized raw signals to skin conductance values in μ S. SCR data were fed into high-voltage inputs of the third SynAmps of the ESI-128.

2.3.3. Electrocardiogram (ECG)

ECGs were recorded using the third SynAmps of the ESI-128, Ag/AgCl electrodes and pre-cordial bipolar lead, as recommended by Mulder (1992).

All peripheral activities were digitized at 500 Hz throughout the entire 12-s trial period.²

¹ The following pictures formed five categories: *NeutLA*: 7002, 7004, 7006, 7009, 7010, 7020, 7150 and 7175; *PosMA*: 2010, 2345, 2501, 2530, 2540, 5200, 5760 and 5780; *NegMA*: 1930, 2205, 3300, 9008, 9340, 9421, 9911 and 9920; *PosHA*: 1440, 1460, 1722, 1920, 4658, 4659, 4660 and 4669; *NegHA*: 2800, 3080, 3150, 3170, 3261, 9040, 9405 and 9410.

² For technical reasons, high-quality physiological responses (both SCR and ECG) were retained only in 13 recorded Ss.

2.4. Procedure

Ss were seated in a comfortable armchair and the light in the room was dimmed. The experiment began with four 60-s eyes open/eyes closed baselines that will not be reported here. A single experimental trial had the following sequence: a blank screen was replaced by a small cross presented in the center of the screen for 4 s, and followed by presentation of a picture for 6 s. The total length of EEG epoch recorded was 12 s (5 s before and 7 s after picture onset). After the picture offset, three affective dimensions of pleasure, arousal and dominance (in a nine-point scale for each dimension) were assessed using computerized Self-Assessment Manikin (SAM) (Bradley and Lang, 1994). Upon the completion of SAM ratings, the stimulation program started the next trial with a randomly determined interval of 1–3 s. In the preceding training procedure, Ss were confronted with six examples including neutral and affective stimuli that were not a part of the main experimental set. In this training procedure, Ss learned to maintain gaze on the center of the screen avoiding explorative eye movements, as well as to respond to SAM scales. Overall, there were 80 experimental trials. Each stimulus was exposed twice in a block-randomized fashion, distributed over two blocks of 40 trials. Because the affective feature of a particular stimulus was not necessarily in the center of the picture, stimuli were mirrored for a second block of presentations. In both blocks, the order of stimuli was pseudo-randomized under the restriction that trains of three pictures belonging to the same subset should not occur. There was a break of 5 min between two blocks of presentations.

2.5. Data analysis

2.5.1. EEG analysis

Contributions from the horizontal and vertical EOGs to the EEG were eliminated off-line by submitting the data to the SCAN 4.1 eye movement correction algorithm (Semlitsch et al., 1986). In addition, individual EEG traces were visually inspected for any remaining eye movement, EMG,

or movement-related artifacts. Only valid trials were retained for analyses. There were no significant differences in the number of valid trials per category (NeutLA: $M = 12.85$, $S.D. = 2.01$, $\text{min.} = 10$; PosMA: $M = 12.80$, $S.D. = 2.39$, $\text{min.} = 9$; NegMA: $M = 12.75$, $S.D. = 1.88$, $\text{min.} = 8$; PosHA: $M = 12.15$, $S.D. = 2.20$, $\text{min.} = 8$; and NegHA: $M = 11.90$, $S.D. = 2.42$, $\text{min.} = 8$).

Changes in band power were defined as the percentage of decrease (ERD) or increase (ERS) in band power during the test interval (here 6000 ms post-stimulus) as compared to the reference interval (here –3000 to –1000 ms before picture onset) (Pfurtscheller and Aranibar, 1977). Frequency bands were individually defined in relation to the individual alpha frequency (IAF), which was used as the cut-off point for the lower and upper alpha band. The bandwidth was also individually determined and was calculated as the percentage (20%) of IAF (Doppelmayr et al., 1998a). The frequency bands obtained by this method are termed: theta, $(IAF \times 0.4) - (IAF \times 0.6)$; alpha-1, $(IAF \times 0.6) - (IAF \times 0.8)$; alpha-2, $(IAF \times 0.8) - (IAF \times 1.0)$; and alpha-3, $(IAF \times 1.0) - (IAF \times 1.2)$. Averaged over the entire sample of 20 subjects, the IAF was 10.44 Hz and the following cut-off points were obtained: theta, 4.10–6.21; alpha-1, 6.21–8.28; alpha-2, 8.28–10.35; and alpha-3, 10.35–12.46 Hz. For each subject, after band-pass filtering (96 dB/octave roll-off, warm-up filter left, trim left and right of 1000 ms) ERD/ERS was calculated within these bands with a time resolution of 100 ms (Pfurtscheller and Aranibar, 1977; Doppelmayr et al., 1998a) and averaged according to the five categories.

2.5.2. ERD / ERS data reduction

With respect to spatial sampling points, electrodes were collapsed into 12 electrode clusters (Fig. 1). This procedure resulted in six regional means for each hemisphere: anterior temporal (AT); frontal (F); central (C); parietotemporal (PT); parietal (P); and occipital (O). The average ERD/ERS values across the respective electrode sites were calculated for these regional means for each time interval of 100 ms and each arousal category.

2.6. Skin conductance response

The skin conductance signals were downsampled to 10 samples/s for analyses. For stimulus presentation periods, skin conductance responses from the left hand were scored as responses occurring between 0.9 and 5 s after picture onset and exceeding $0.01 \mu\text{S}$ (e.g. Prokasy and Raskin, 1973). Log-transformation ($\log[\text{SCR} + 1]$) was used to normalize the amplitude data.

2.7. Heart rate (HR)

The electrocardiogram (ECG) output channel was converted into HR/0.5 s. For the 6-s viewing period, mean values of HR/0.5 s were used to construct a mean change score waveform (mean HR/0.5 s post-stimulus minus mean HR for the last 0.5-s pre-stimulus) for editing and detection of acceleratory and deceleratory peaks and nadirs, respectively. The largest deceleratory values were selected (Roedema and Simons, 1999).

2.8. Statistical analyses

Before statistical analyses in order to obtain ERD/ERS values of moderate and high emotional arousal, prompted by equal amounts of positive and negative stimuli, the following transformations were performed. ERD/ERS data on positive and negative pictures with moderate arousal (see Section 2.2) were averaged to form

the moderate arousal category (MA), whereas data on high-arousal positive and negative stimuli were averaged into the high arousal category (HA). As a result, three stimulus categories (low, moderate and high arousal pictures) were obtained instead of five.³ The SAM, SCR and HR data were treated in the same manner.

Separate one-way repeated-measures ANOVAs (ARO 3: low, moderate and high arousal) were performed for individual SAM ratings, SCR (probability and amplitude) and HR deceleration data. For each EEG frequency band, ERS/ERD data were analyzed in four-way repeated-measures ANOVAs with the following factors: arousal (ARO 3: low, moderate, high) \times hemisphere (HEM 2: left, right) \times localization (LOC 6: AT, F, C, PT, P and O) \times time (TIME 6: 1, 2, 3, 4, 5 and 6 s post-stimulus). Additionally applied ANOVAs

³ As is evident from the above, three levels of arousal and emotionality were not orthogonally combined. Instead, neutral stimuli were used for low arousal category, whereas both positive and negative pictures were used to form medium- and high-arousal categories. Orthogonality was sacrificed for two reasons. Due to existing quadratic relationships between valence and arousal, extremely high arousal values involve extreme valence scores, and vice versa (Bradley and Lang, 1994). In this respect, the psychophysiological meaning of positive and negative emotionality of low arousal stimuli seems rather confusing. Another reason was related to the experimental set-up. Additional low-arousal stimuli would extend the experimental procedure in time, thereby enhancing risks for interfering influences of fatigue.

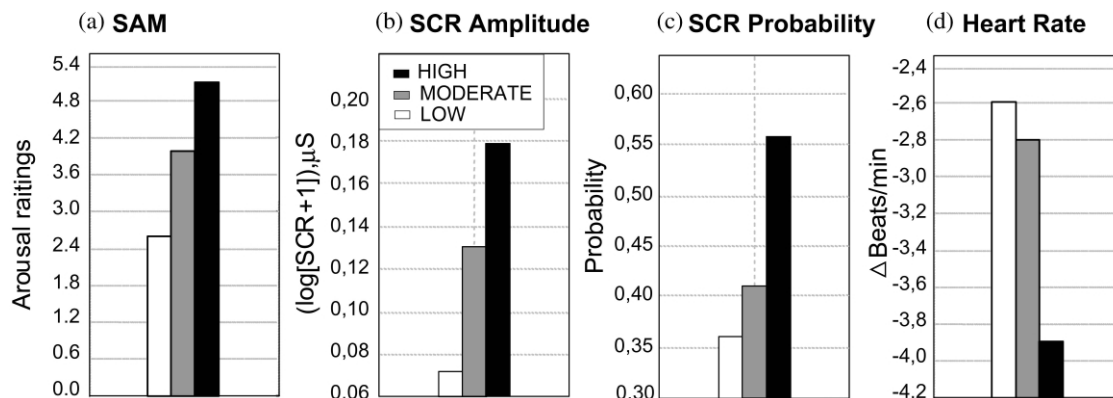


Fig. 2. (a) SAM ratings; (b) SCR amplitude; (c) SCR probability; and (d) heart rate deceleration in beats/min as a function of arousal.

depended on the time course and topography of effects revealed involving the arousal factor (see Section 3).

For all the analyses, degrees of freedom were Greenhouse–Geisser-corrected where appropriate. All the post hoc comparisons were evaluated by means of the Scheffe test.

3. Results

3.1. SAM ratings

The mean arousal ratings for all the subcategories are presented in Fig. 2a. Pictures varied robustly in arousal level [$F(2,44) = 60.85$, $P < 0.000$], which was rated significantly higher for moderate ($M = 3.92$) and high ($M = 5.03$) as compared to low ($M = 2.50$) arousal pictures. In turn, high arousal stimuli were rated significantly higher than moderate arousal pictures (all post hoc at $P < 0.01$).

3.2. Skin conductance

As expected, skin conductance activity was higher in the response to affectively salient vs. neutral stimuli (Fig. 2b,c). This is demonstrated by significant effects of the ARO factor for SCR amplitude and probability [$F(2,24) = 10.65$, $P < 0.007$ and $F(2,24) = 15.69$, $P < 0.000$, respectively]. Both skin conductance amplitude and probability values were larger for HA vs. LA stimuli. Furthermore, HA when compared to MA stimuli prompted higher SCR probability (Fig. 2b,c) (all post hoc at $P < 0.01$).

3.3. Heart rate

As Fig. 2d illustrates, there was a significant main effect of arousal [ARO: $F(2,24) = 8.45$, $P < 0.006$], indicating the largest deceleratory activity for HA, intermediate for MA and the lowest for LA stimuli (post hoc at $P < 0.01$).

3.4. ERD / ERS measures

3.4.1. Theta band

ANOVA for the whole test interval and all the loci resulted in the robust effect of hemisphere,

indicating a greater extent of ERS over the right hemisphere overall (Table 1). The highly significant effect of the arousal factor shows higher theta production in response to both moderate ($M = -30.99$) and high ($M = -36.28$) when compared to low ($M = -18.32$) arousal stimuli overall (Table 1). As may be inferred from the significant interaction $ARO \times LOC$ presented in Fig. 3a, all stimuli yielded topographically larger ERS values over posterior than anterior sites and this effect was more pronounced for the pictures with elevated arousal content. According to post hoc comparisons, when compared to the LA, HA stimuli produced significantly larger ERS over parietotemporal, parietal and occipital loci, whereas MA pictures prompted larger ERS only over occipital leads (post hoc at $P < 0.01$). As supported by significant interactions for $ARO \times HEM \times LOC$ and $ARO \times LOC \times TIME$ (Table 1), the theta band also revealed effects of arousal discrimination, associated with the time factor and hemispheric asymmetries in the anterior–posterior direction of the cortical plane. In an effort to substantiate the essence of these effects, the additional four-way repeated-measures ANOVA including the anterior and posterior regions as a caudality factor was performed: arousal (ARO 3: LA, MA, HA) \times caudality (CAUD 2: AT, F, C vs. PT, P, O) \times hemisphere (HEM 2: left, right) \times time (TIME 6: 1, 2, 3, 4, 5 and 6 s post-stimulus). Because the resulting two-way interaction of $ARO \times CAUD$ [$F(2,38) = 9.53$; $P < 0.001$] is included in the three-way interaction $ARO \times CAUD \times HEM$ [$F(2,38) = 4.53$; $P < 0.024$], only this higher-order interaction is plotted in Fig. 4a. Analysis of this interaction clearly demonstrates that over the left anterior regions, both MA and HA stimuli induce larger ERS than LA pictures. This is supported by the significant interaction $ARO \times HEM$ [$F(2,38) = 4.96$; $P < 0.016$] in separate ANOVA for anterior leads and post hoc comparisons at $P < 0.01$. In turn, theta power was significantly larger on right vs. left hemisphere anterior electrodes only for the LA stimuli [HEM: $F(1,19) = 8.26$; $P < 0.010$] and there were no hemispheric asymmetries for MA and HA stimuli (Fig. 4a, left panel). Separate ANOVAs for posterior leads exhibit robust overall effects of greater

Table 1

ANOVA [ARO(3) \times HEM(2) \times LOC(6) \times TIME(6)] results (F , d.f. and probability) of main effects, along with two- and three-way interactions for theta, alpha-1, alpha-2, and alpha-3 bands

Effect	d.f.	Theta	Alpha-1	Alpha-2	Alpha-3
ARO	2, 38	12.11 $P < 0.000$	4.23 $P < 0.027$	NS	NS
HEM	1, 19	12.91 $P < 0.002$	6.94 $P < 0.016$	NS	NS
LOC	5, 95	21.61 $P < 0.000$	15.94 $P < 0.000$	3.59 $P < 0.041$	44.23 $P < 0.000$
TIME	5, 95	103.57 $P < 0.000$	33.21 $P < 0.000$	5.25 $P < 0.019$	7.04 $P < 0.005$
ARO \times HEM	2, 38	NS	NS	NS	3.34 $P < 0.046$
ARO \times LOC	10, 190	6.92 $P < 0.000$	7.26 $P < 0.000$	4.45 $P < 0.000$	2.35 $P < 0.030$
ARO \times TIME	10, 190	2.54 $P < 0.024$	NS	NS	2.77 $P < 0.018$
ARO \times HEM \times LOC	10, 190	3.11 $P < 0.029$	NS	NS	NS
ARO \times LOC \times TIME	50, 950	2.04 $P < 0.035$	NS	NS	NS

ARO, arousal; HEM, hemisphere; LOC, localization (AT, F, C, PT, P, O); TIME (6 by 1000 ms after stimulus onset). Only significant two- and three-way interactions associated with the arousal factor are reported.

ERS over the right hemisphere [overall HEM in separate ANOVA: $F(1,19) = 14.82$; $P < 0.001$] and demonstrate that affectively salient vs. neutral stimuli bilaterally induce significantly larger theta power (all post hoc at $P < 0.01$; Fig. 4a, right panel). Finally, the significant interaction ARO \times CAUD \times TIME [$F(10,190) = 2.33$; $P < 0.034$] further indicates that all affective vs. low arousal pictures induce a greater amount of the theta ERS over posterior regions in the early post-stimulus period of 1 s, whereas high arousal stimuli reveal the second power increase at 4 s post-stimulus (Fig. 4b, right panel, post hoc at $P < 0.01$).

For a better understanding of the early temporal effects of arousal over posterior leads, separate repeated-measures ANOVAs for PT, P, and O regions with higher time resolution were performed [ARO(3) \times HEM(2) \times LOC(3) \times TIME(7: 100, 200, 300, 400, 500, 600 and 700 ms post-stimulus)]. The emerging significant interaction ARO \times TIME [$F(12,228) = 3.52$; $P < 0.013$] demonstrated (Fig. 5a) that HA vs. LA stimuli pro-

duce larger ERS in the 200–700-ms time window post-stimulus, whereas MA vs. LA pictures are discriminated somewhat later and in the shorter time period of 300–500 ms (post hoc at $P < 0.01$). All the other interactions involving arousal factor were not or only marginally significant.

3.4.2. Alpha-1 frequency band

The significant main effect of hemisphere (Table 1) revealed overall greater alpha synchronization over the right hemisphere. The main effect of the arousal factor, along with respective means, indicates the largest extent of synchronization for the moderate ($M = -14.47$), intermediate for high ($M = -12.01$), and faint power increase in response to the low arousal ($M = -3.06$) stimuli overall. The two-way interaction ARO \times LOC (Table 1, Fig. 3b) further clarifies that when compared to the LA, both MA and HA stimuli prompted greater ERS only over occipital leads (post hoc at $P < 0.01$). Finally, additional ANOVA for occipital leads at the early post-stimulus phase [ARO(3) \times HEM(2) \times TIME(6:

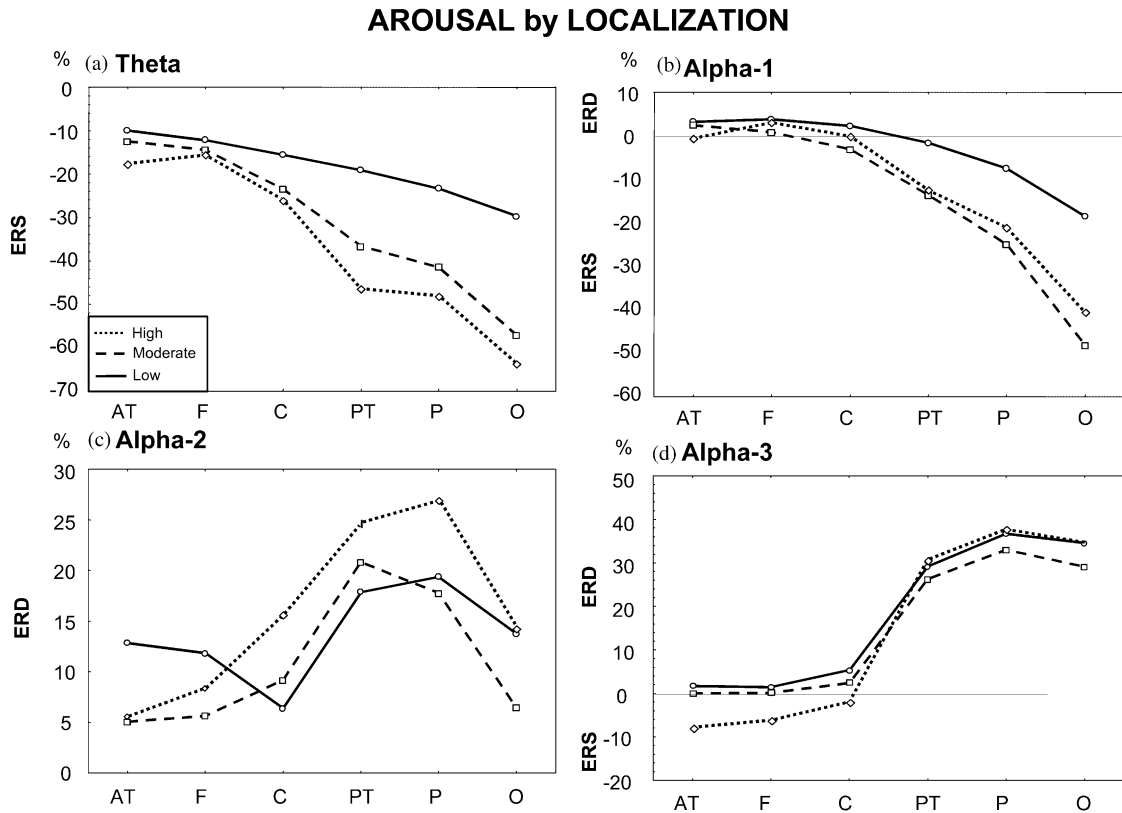


Fig. 3. Two-way arousal \times localization interactions in: (a) theta; (b) alpha-1; (c) alpha-2 and (d) alpha-3 bands for all the three picture categories in the 6-s test interval (ERS goes down, ERD goes up).

200, 400, 600, 800, 1000 and 1200 ms post-stimulus)] resulted in the significant interaction ARO \times TIME [$F(10,190) = 2.95$; $P < 0.027$, Fig. 5b), according to which MA vs. LA pictures induce greater ERS starting at 400–600 ms post-stimulus. The emerging difference reaches significance at 1200 ms (post hoc at $P < 0.01$). During this period, the HA pictures yielded intermediate ERS values.

3.4.3. Alpha-2 band

Although in the alpha-2 band ERD/ERS values exhibited great inter-individual variability, particularly over anterior leads, inspection of respective means of the only significant effect, associated with the arousal factor (i.e. two-way interaction ARO \times LOC) indicates that HA vs. both MA and LA stimuli exhibited tendencies to in-

duce greater ERS over parietal sites (Table 1, Fig. 3c). The more pronounced effect of affective stimuli over posterior leads is also supported by significant effects of LOC for both HA [$F(5,95) = 5.80$; $P < 0.000$] and MA [$F(5,95) = 4.36$; $P < 0.001$], along with an insignificant effect for LA [$F(5,95) = 1.47$; $P < 0.205$] stimuli in separate ANOVAs for each category.

3.4.4. Alpha-3 band

According to preliminary analyses, overall in the alpha-3 frequency band, anterior temporal, frontal and central regions exhibited short-lasting significant synchronization within the first 1200 ms post-stimulus, whereas posterior loci exhibited significant desynchronization that started on average from 200 to 400 ms post-stimulus and persisted throughout the whole test interval of

THETA

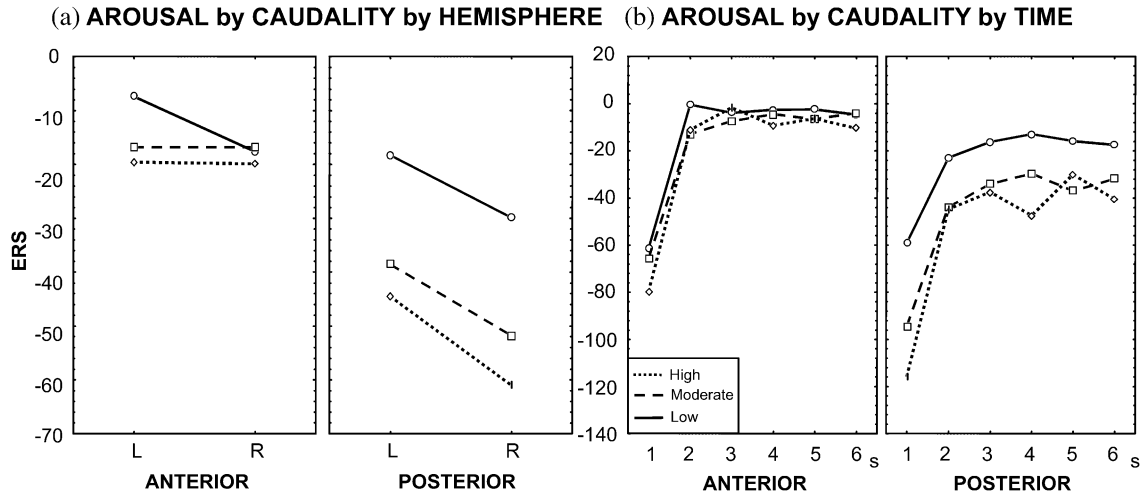


Fig. 4. (a) Three-way arousal \times caudality \times hemisphere and (b) arousal \times caudality \times time interactions in theta band for all the three picture categories in the 6-s test interval; L, left, and R, right, hemisphere.

0–6000 ms. For the whole test interval, the arousal factor was involved in the only interaction ARO \times LOC (Table 1), presented in Fig. 3d. According to this interaction, HA vs. LA stimuli induced larger ERS over anterior leads whereas over posterior sites all the three picture categories prompted about equal extent of desynchronization. The additional ANOVA for the early test

period and anterior leads [ARO(3) \times HEM(2) \times LOC(3: AT, F and C) \times TIME(6: 200, 400, 600, 800, 1000 and 1200 ms post-stimulus)] revealed a significant interaction for ARO \times TIME [$F(10,190) = 2.81$; $P < 0.013$] embedded in the three-way interaction ARO \times HEM \times TIME [$F(10,190) = 2.91$; $P < 0.021$] (Fig. 6). Inspection of respective means of the last interaction indi-

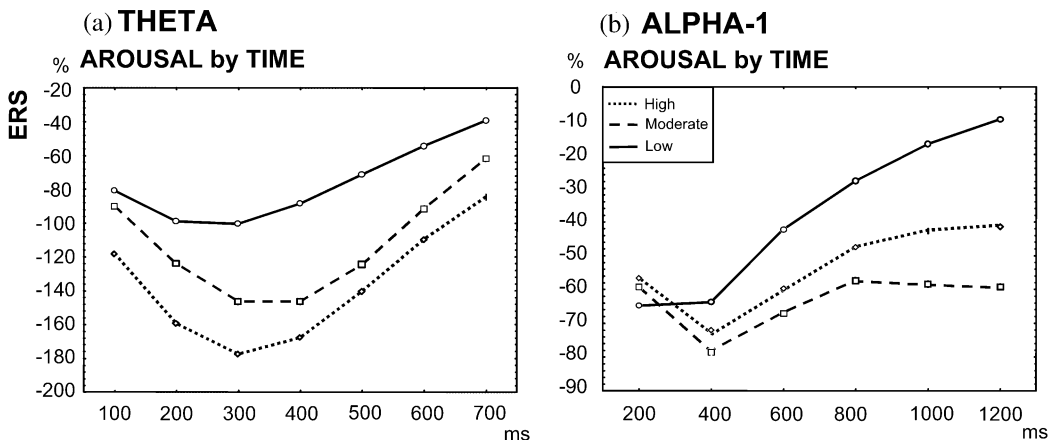


Fig. 5. (a) Two-way arousal \times time interactions for parietal, parietotemporal and occipital leads in theta and (b) occipital leads in alpha-1 bands as a function of arousal.

cates that HA stimuli induce a time-dependent increase in power, lateralized to left anterior leads: in the range 800–1200 ms post-stimulus in response to HA stimuli, alpha-3 ERS achieves significantly larger values than for LA pictures (Fig. 6). Of special note is the fact that the time-dependent asymmetry observed is manifested against the background of the overall larger right-hemisphere ERS over anterior cortical sites [HEM: $F(1,19) = 15.34$; $P < 0.000$].

Summing up, event-related band power was modulated by picture arousal content. Of the four frequency bands, theta, alpha-1 and alpha-3 bands exhibited effects of arousal discrimination. Theta and alpha-3 bands exhibited association with hemispheric asymmetries in the anterior–posterior direction of the cortical plane. The time course of developing affective reactions demonstrates that theta had a substantial lead before alpha-1 and alpha-3 bands in identifying the affective salience of incoming stimuli.

4. Discussion

Segregated into arousal categories, self-report and SCR data (amplitude and probability) were

related to arousal, reliably supporting findings from other studies incorporating the SAM and SCR measures with IAPS stimuli (e.g. Lang et al., 1993). In addition, heart rate deceleration, which is a characteristic of orienting or attention to input (Graham, 1979), was the largest in response to high arousal category and may be interpreted as indicative of greater attention allocated to the more arousing stimuli (Detenber et al., 1997; Roedema and Simons, 1999). The consistency of subjective and physiological data produced in this paradigm is rather impressive and gives additional credence to the ERD/ERS effects revealed.

In the theta frequency band, both moderate and high vs. low arousal stimuli induced greater synchronization over left anterior regions and bilaterally over posterior regions. Nowadays, event-related theta oscillations can be considered as important building blocks of functional signaling in the nervous system related to cognitive processing and cortico-hippocampal interaction (for review see Basar et al., 1999, 2001). Previous research suggests that higher theta activity within the anterior cortical regions is best interpreted as an electrophysiological manifestation of higher activation. This interpretation relies on observations of increased theta activity during stimulus

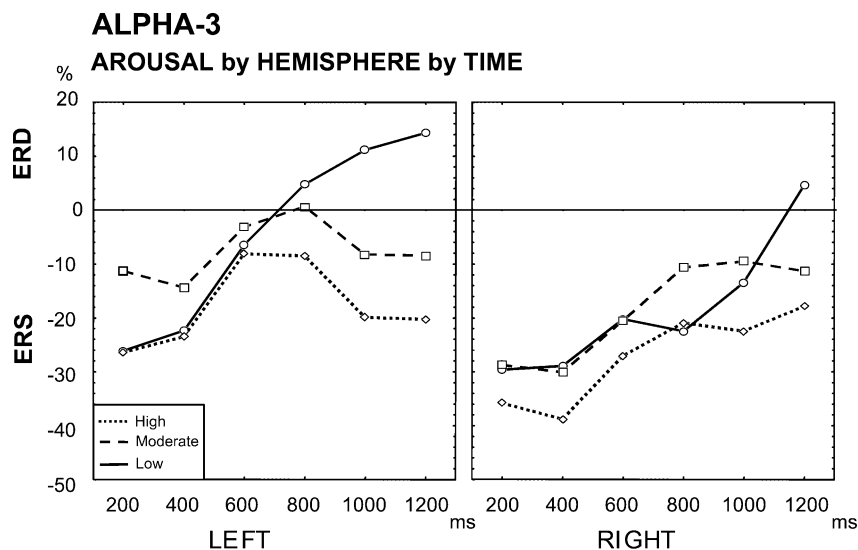


Fig. 6. Three-way arousal \times hemisphere \times time interaction over anterior temporal, frontal and central leads in alpha-3 band.

expectancy and focused attention (Basar-Eroglu et al., 1992), successful encoding of new information (reviewed by Klimesch, 1999), concentrated task performance (Sasaki et al., 1996) and affective processing (Aftanas et al., 2001; Aftanas and Golocheikine, 2001). As indexed by enhanced theta synchronization, moderate and high arousing stimuli increased activation of the left anterior region. In the current experimental set-up, the moderate- and high-arousal picture categories were formed in such a manner that they included equal amounts of positive and negative stimuli (see Section 2). Thus, according to existing models of anterior affective asymmetries (Davidson et al., 2000a,b), effects of positive and negative stimuli would cancel each other and no hemispheric asymmetries would be expected.⁴ The possible way to resolve this issue consists of the partial separation of motivational tendencies and emotional appraisal from experiencing emotion. A growing body of literature is converging on the idea that two fundamental systems exist, which underlie approach- and withdrawal-related emotion and motivation, or certain forms of positive and negative affect. Certain regions within the left prefrontal cortex are part of a circuit that implements approach-related behavior, while symmetrical regions of the right prefrontal cortex are part of a circuit that implements withdrawal-related behavior. These cortical regions are held to interact with several subcortical structures (including the left and right amygdala as important members) in the elaboration of different components of emotional response (Cacioppo and Gardner, 1999; Davidson et al., 2000a,b). By demonstrating in EEG studies that dispositional anger (an emotion involving a negatively valenced ap-

proach tendency) is positively associated with left- and negatively with right-anterior cortical activity, it was suggested that the anterior asymmetry in cortical activity may more clearly tap motivational direction than affective valence (Harmon-Jones and Allen, 1998). It may be suggested that increased anterior left-hemisphere activity reflects an enhanced appetitive motivational tendency to learn more about the potential value (pleasure or threat) or importance of survival stimuli. These tendencies may promote such inherent left hemisphere strategies as analytical, detail-oriented, focused processing (see e.g. Heller, 1994). In turn, the clearly defined theta synchronization increase over posterior cortical sites in response to affective challenge, silhouetted against the overall right hemisphere dominance in theta production, may reflect processing of affective stimulus significance. Considering that increased task demands give rise to marked theta enhancement in ERP components (Basar et al., 1999; Spencer and Polich, 1999), investigations of 'emotional ERPs' indicating that affective (both negative and positive) vs. neutral stimuli induce larger amplitudes of the P3 component and late positivity and exhibit greater impact on posterior regions of the right hemisphere (Johnston et al., 1986; Diedrich et al., 1997; Cacioppo et al., 1996; Kayser et al., 1997, 2000) may be congruent with this suggestion.

In contrast to several other studies (reviewed in Klimesch, 1999), the frequency band which was termed as lower alpha (i.e. alpha-1), has not shown a clear pattern of event-related decrease, which would be typical for alpha. Instead, rather unexpectedly, both moderate and high vs. low arousing stimuli yielded a pronounced increase in power (typical for theta). Lower-alpha increase (within approx. 600 ms post-stimulus) was also observed in a recent ERD/ERS investigation of episodic memory (Klimesch et al., 2001). Although there is accumulating evidence that not only the alpha-blocking, but also alpha-synchronizing responses to mental tasks may be considered as markers of the activation of functionally involved brain areas, reflecting specific operations of higher brain functioning (see e.g. Pfurtscheller et al., 1996; Niedermayer, 1997; Basar et al., 1999; Kolev et al.,

⁴ Additional three-way ANOVA of valence dimension with neutral and strong emotional stimuli for AT regions and theta band (VAL: NeutLA, PosHA, NegHA) \times HEM(2) \times TIME(7:7 by 100 ms poststimulus) revealed significant VAL \times HEM interaction [$F(2,38) = 6.65$, $P < 0.007$]. This is a replication of our pilot findings, indicating greater right than left ERS for negative and greater left than right ERS for positive stimuli. However, when contrasted with neutral, both positive and negative picture categories induced larger ERS over the left anterior region (Aftanas et al., 2001).

1999), at this early phase, the findings on alpha-1 synchronization must be regarded as indicative. Future investigations will be necessary to determine the factors responsible for the different event-related responses in the fast theta or slow alpha frequency range of approximately 6–8 Hz.

In the medium alpha, suggestively reflecting attentional processes such as expectancy (Klimesch et al., 1998a), high arousal pictures tended to produce more salient desynchronization over parietal leads. Because expectancy plays a role during the pre-stimulus period, differences in expectancy engagement would be expected in the reference interval. The additional analyses of the reference intervals revealed no significant differences among arousal picture categories.⁵ If so, the desynchronization observed may point to other effects of affective processing, not related to expectancy.

In the ‘cognitive’ upper alpha band (Klimesch et al., 1998a), high vs. low arousal stimuli exhibited significantly greater synchronization over anterior leads, accompanied by category-independent desynchronization over posterior leads. It is noteworthy that during some cognitive tasks, posterior cortical areas manifest ERD, while at the same time, the alpha activity in anterior regions is synchronized (e.g. Pfurtscheller and Klimesch, 1992). Increased ERS over anterior sites could reflect their deactivation due to enhanced activation of posterior sites, which are involved in the analysis of the meaning of the pictures. This interpretation would be plausible only if at least some posterior sites showed larger ERD due to higher arousal. However, since separate analyses for parietal, parietotemporal and occipital regions have not revealed any differences among picture categories, anterior synchronization may be regarded as an active process, reflecting greater cognitive involvement during processing of emotionally arousing stimuli. Furthermore, emerging larger left- than right-hemisphere involvement in

response to affective challenge indicates that high arousing information accesses the processing capacity of the left hemisphere, invoking additional, more detailed analyses of importance for survival information.

In light of affective chronometry (Davidson, 1998), the significant arousal \times time interaction for posterior theta clearly indicates that discrimination of affective stimuli from neutral ones has already started at 100–200 ms post-stimulus, whereas for posterior lower and anterior upper alpha, this process is delayed by up to 800–1200 ms. Findings on the early discriminative properties of the theta synchronization are congruent with a recent ERPs study of emotion, according to which selective discrimination of emotionally arousing stimuli from less affective content occurs in the 150–260-ms time window post-stimulus (Junghofer et al., 2001). This time is sufficient for re-entrant projections from cingulate or amygdala to activate motivational systems and to set in motion the first stage of conceptual stimulus processing of the hypothetical, very short-term, conceptual memory system, in which stimuli reach meaningful representation rapidly, but consolidation is transient (Potter, 1999; Junghofer et al., 2001). Overall, discriminative properties of theta synchronization were observed in the time period of 100–700 ms post-stimulus. Considering that this is the time period when time-locked theta is associated with orienting, selective attention, stimulus decoding and memory processes (Basar et al., 1999), arousal-related time-dependent changes of anterior and posterior theta synchronization may reflect evaluation of emotional stimulus significance rather than peculiarity of emotional experience. In the alpha-1 and alpha-3 bands, discriminative process was delayed by up to 800–1200 ms. Due to the vague nature of alpha-1 synchronization, correct interpretation of the dynamic of affective response revealed is problematic for this band. As for the upper alpha, in line with the prediction, the greatest differences among arousal categories in the ‘cognitive’ upper alpha emerged at 800–1200 ms post-stimulus, i.e. by the time when the stimulus type is recognized and mechanisms of extended cognitive analysis start to function.

⁵ The three-way ANOVAs [ARO(3) \times HEM(2) \times LOC(6)] for the reference intervals did not yield either main effect of arousal or any significant interactions with this factor for theta, alpha-1, alpha-2 and alpha-3 frequency bands.

In summary, the arousal-related hemispheric asymmetries revealed support Heller's model outcome (e.g. Heller, 1993; Heller et al., 1997) relating to the proposal that posterior regions of the right hemisphere are involved in the modulation of emotion-related arousal (theta and alpha-3 bands), and also point to recruitment of anterior regions of the left hemisphere (theta and alpha-3 bands) in affect analysis beyond valence dimension. As for the frequency domain, along with earlier observations on EEG correlates of affective processing (Crawford et al., 1996; Aftanas et al., 1996a, 1998; Muller et al., 1999; Krause et al., 2000), the findings challenge the notion that emotion-related anterior and posterior hemispheric asymmetries are mainly sensitive to a wide alpha frequency band. Affective processing seems to be frequency-dependent, revealing that among the four bands analyzed, the theta oscillating networks were the fastest in affect discrimination. Furthermore, the findings reported emphasize a clearly defined time-dependence of hemispheric asymmetries induced by affective processing. We should also stress the value of employing adjunct psychophysiological measures in studies of brain mapping and emotion. The skin conductance and heart rate data provided important support that picture differences are attributable to emotional arousal.

We should also briefly note some limitations of the present findings, which suggest directions for future research. The first limitation deals with EEG phenomena putatively induced by IAPS stimulus sets. Picture exploration may be accompanied by sharp transients in the form of positive (upward) triangular waves, termed lambda waves. These transients occur bilaterally over the occipital regions of waking subjects and may represent generation of a singular visually evoked potential. The main energy of lambda waves could contribute to the posterior power increase reported for theta and alpha-1 bands (Niedermeyer and Lopes da Silva, 1999). In the present experiment, the clearly defined larger theta and alpha-1 synchronization increase over posterior cortical sites in response to affective vs. neutral stimulation was silhouetted against the overall right-hemi-

sphere dominance in theta and alpha-1 production. Hence, it is unlikely that the subjects would systematically produce larger right-hemisphere lambda transients that are bilateral in nature. However, the overall contribution of lambda transients to posterior theta and alpha-1 increases cannot be fully excluded. Another limitation is related to the traditional measures of event-related band power that are composed of evoked (phase-locked) and induced (non-phase-locked) components (Pfurtscheller and Aranibar, 1977; Klimesch et al., 1998b). In line with recent findings, rhythms induced in narrow frequency bands may be modulated by stimuli and/or events in a non-phase-locked way (e.g. Klimesch et al., 1998b; Doppelmayr et al., 1998b, 2000). Because it is well known that different components of ERPs are also sensitive to affective processing (e.g. Diedrich et al., 1997; Kayser et al., 1997, 2000), future investigations should clarify whether event-related band-power increases observed in the first 0.5 s after stimulus onset in the theta and alpha-1 bands is due to ERP components.

Overall, the findings obtained, along with the earlier ERD/ERS data on affective processing (Aftanas et al., 1996a,b, 2001; Krause et al., 2000), substantiate the notion that, as stated by Basar et al. (1999), unique rhythm- or event-related oscillations cannot be the only processor for a given function — complex functions, such as affect analysis, are certainly interwoven with several oscillations that occur in combination.

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