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ORIGINAL PAPER

First Valence, Then Arousal: The Temporal Dynamics of Brain Electric Activity Evoked by Emotional Stimuli

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Abstract The temporal dynamics of the neural activity that implements the dimensions valence and arousal during processing of emotional stimuli were studied in two multichannel ERP experiments that used visually presented emotional words (experiment 1) and emotional pictures (experiment 2) as stimulus material. Thirty-two healthy subjects participated (mean age 26.8 ± 6.4 years, 24 women). The stimuli in both experiments were selected on the basis of verbal reports in such a way that we were able to map the temporal dynamics of one dimension while controlling for the other one. Words (pictures) were centrally presented for 450 (600) ms with interstimulus intervals of 1,550 (1,400) ms. ERP microstate analysis of the entire epochs of stimulus presentations parsed the data into sequential steps of information processing. The results revealed that in several microstates of both experiments, processing of pleasant and unpleasant valence (experiment 1, microstate #3: 118–162 ms, #6: 218–238 ms, #7: 238–266 ms, #8: 266–294 ms; experiment 2, microstate #5: 142–178 ms, #6: 178–226 ms, #7: 226–246 ms, #9: 262–302 ms, #10: 302–330 ms) as well as of low and high arousal (experiment 1, microstate #8: 266–294 ms, #9: 294–346 ms; experiment 2, microstate #10: 302–330 ms, #15: 562–600 ms) involved different neural assemblies. The results revealed also that in both experiments, information about valence was extracted before information about arousal. The last microstate of valence extraction was identical with the first microstate of arousal extraction.

Keywords Emotional processing · ERP · Microstate analysis · Valence · Arousal · Temporal dynamics

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Introduction

The detection of emotional salient stimuli is a fundamental skill that plays an important role in successful behavior [12]. In order to be useful in ongoing interactions with the environment, salient features of emotional stimuli must be recognized rapidly and appropriately.

Emotional information was hypothesized to span various basic dimensions. Multivariate studies have consistently shown that the principal variance in the categorization of emotional stimuli is accounted for by two predominant dimensions, arousal and valence (e.g., [31, 37]). Arousal refers to a continuum that varies from calm to excited, whereas valence refers to a continuum that varies from pleasant to unpleasant. These two dimensions correlated with different peripheral, physiological responses: for example, startle reflex amplitude increased with reported negative valence and decreased with positive valence (e.g., [1, 9, 47]). On the other hand, the amplitude of the skin conductance responses correlated positively with arousal: skin conductance increased with increasing stimulus intensity (e.g., [1, 3, 8, 10]).

A series of fMRI studies showed the existence of two distinct neural systems for the processing of valence and arousal. Summarizing the results of these fMRI studies that have exclusively focused on the amygdala or the prefrontal cortex (but see [1, 23]) who also examined activity in other

regions), it is suggested that amygdala responds to emotional stimuli in a arousal-based manner (i.e., only high arousal stimuli, independent of their valence, activate the amygdala; e.g., [2, 23, 24]), whereas valence-dependent responses occur in the prefrontal cortex. For the valence-dependent activity of the prefrontal cortex, two lines of evidence were proposed: (1) the valence-dependent laterality (i.e., left prefrontal cortex plays a crucial role in the processing of positive stimuli, and right prefrontal cortex plays a crucial role in the processing of negative stimuli, e.g., [6, 15], but see [19], who challenged such an over-simplification, for a critical review of this issue), and (2) the lateral orbital prefrontal cortex regions respond mainly to negative stimuli, whereas ventromedial prefrontal cortex regions respond mainly to positive stimuli (e.g., [34, 35]).

Successful real-time interaction with the environment evidently requires rapid decisions that involve perception and evaluation of emotional information in the sub-second range. Brain electric or magnetic data offer time resolution in the millisecond range and thereby make it possible to describe physiological correlates of such very rapid processing.

Event-related potential (ERP) studies that focused on the arousal dimension of emotional stimuli consistently demonstrated a so-called 'arousal effect', i.e., a larger late positive ERP wave in response to high-arousing stimuli compared to low-arousing stimuli; this wave developed around 300–400 ms after stimulus onset and lasted for several hundred milliseconds [8, 11, 13, 14, 21]. In the motivational model, this effect has been linked to the concept of motivated attention which proposes that motivationally significant stimuli are selectively processed because they naturally engage attentional resources [4, 26]. Additionally, in two ERP studies that used a short exposure presentation (120–300 ms), differences between high- and low-arousing stimuli were shown in ERP components starting as early as 100–200 ms after stimulus onset [20, 43], thus also demonstrating that the observed latencies clearly depended on stimulus duration.

The ERP studies that focused on the valence dimension of emotional stimuli demonstrated that the 'valence effect' modulates ERP components starting as early as 100 ms after stimulus onset (e.g., [16, 21, 36, 39, 40, 44, 45]).

We are aware of only three ERP studies that examined arousal and valence effects in a combined design: Dolcos and Cabeza [14] reported valence as well as arousal effects in a time period between 500 and 800 ms post-stimulus, followed by a time window lasting until 1,200 ms post-stimulus during which ERPs were modulated only by the arousal dimension of the stimuli. Keil et al. [21] found valence effects in an early component from 120 to 150 ms post-stimulus and reported arousal effects in late components from 300 to 900 ms post-stimulus. Finally, Delplanque et al. [13] used an oddball paradigm and focused their attention to the P3a (333–384 ms) and the P3b (439–630 ms) components; they found valence effects in both components and an arousal effect in the P3b component. These three ERP studies used the comparison of emotional versus non-emotional stimuli (i.e., neutral stimuli) to study the arousal effect. This means that the two classes of stimuli, high- versus low-arousal stimuli were not matched for the valence dimension. For the present analysis, we selected only emotional stimuli in such a way that valence and arousal effects were studied with exactly the same stimulus material. Moreover, the three ERP studies reviewed above had analyzed pre-defined ERP components. Contrary to this procedure, the present analysis used the microstate approach [29] that allows for a comprehensive, bottom-up analysis of the entire data without an a priori selection of pre-defined ERP components. It was shown that the topography, sequence and duration of ERP microstates reflects steps and types of information processing (e.g., [5, 25, 32]). The microstate approach eliminates effects of signal magnitude while exclusively recognizing differences in potential topography, thereby addressing the question whether over time, the same or different neuronal populations are active and not the question whether the same populations are more or less active.

Current Study

The current work studied the temporal dynamics of the cortical extraction of information about valence and arousal from emotional stimuli.

Two classes of visually presented stimuli were used: emotional words [18] and emotional pictures from the International Affective Picture System (IAPS, [27]). In order to study both dimensions in the same paradigm, we created four sets of stimuli: high-arousing pleasant stimuli, low-arousing pleasant stimuli, high-arousing unpleasant stimuli and low-arousing unpleasant stimuli. Stimuli were classified based on verbal reports of their valence and arousal values. Crucially, the high-arousing stimuli of both valences (pleasant and unpleasant) compared to the low-arousing stimuli of both valences differed significantly in their arousing dimension but were matched in their valence dimension. In a similar way, the pleasant stimuli of both arousal extremes (high and low) compared to the unpleasant stimuli of both arousal extremes differed significantly in their valence dimension but were matched in their arousal dimension. With the same stimulus material we were thus able to map the temporal dynamics of one dimension, controlling for the other one and vice versa.

In view of the recent fMRI results that showed different neural networks processing high versus low arousal and

processing pleasant versus unpleasant aspects of an incoming emotional stimulus, we hypothesized that the brain electric field information with its high temporal resolution offers the possibility to specify the temporal dynamics of these separate neural networks. As information processing in the brain generally has a quasi step-wise temporal structure, we asked in which of these sequential steps (microstates) valence and/or arousal was treated by different active neural networks. We examined whether the latencies reported in ERP component magnitude studies for processing the arousal and valence dimensions of emotional stimuli correspond to the temporal dynamics of different networks that can be established in ERP microstate analysis. Based on the above reviewed ERP literature, we hypothesized that the valence aspect of an incoming emotional stimulus is processed before its arousal characteristics. Our study also includes the question whether the putative temporal dynamics in emotional processing is similar for linguistic and pictorial input.

Methods

Participants

Thirty-two right-handed German or Swiss–German native speakers (mean age 26.8 ± 6.4 years, range: 21–46 years, 24 women) participated in the study, most of them students of psychology. They all had normal or corrected-to-normal vision. Prior to the experiment, participants were given questionnaires about their handedness [7] and to check that they had no history of neurological or psychiatric disorder, or alcohol or drug abuse. The study was approved by the Ethics Committee of the University Hospital Zurich, and subjects gave their written, informed consent for participation. Subjects were remunerated with CHF 40. The 32 subjects took part to both experiments, but for technical reasons, the data of four subjects in the word experiment and of three other subjects in the picture experiment could not be used.

Stimuli and Task

Word Experiment

The 74 words of the word list in Gianotti et al. [18] were rated by an independent group of 71 subjects (mean age 23.9 ± 2.2 years, 38 women) on the two dimensions of valence and arousal. The valence scale ranged from unpleasant ("one", very unpleasant) to pleasant ("seven", very pleasant), and the arousal scale ranged from low ("one", very relaxing) to high ("seven", very exciting).

Based on the rating results of the 71 subjects, the 74 words were split into two packs that differed maximally in valence. Then, the same words were assigned to two packs that differed maximally in arousal. Statistics showed as expected that pleasant and unpleasant words differed strongly in arousal, and vice versa, that high and low arousal words differed strongly in valence.

Subsequent pruning steps that omitted single words aimed at optimizing the two competing goals: the same words assigned to the first two packs should differ significantly in valence while not differing in arousal, and when assigned to the second two packs should differ significantly in arousal while not differing in valence. In addition, the assignments should produce packs of near-equal number of words. In parallel, the paired packs had to be matched for word length (measured in number of letters, number of syllables and length on the PC screen), for frequency of occurrence in German texts [41] and for imagery propensity [18].

Interactive statistics evaluated the result of each pruning step. Eventually, the optimal result yielded 40 words that were assigned to the sub-packs of 11 "pleasant and high arousing" words, nine "pleasant and low arousing" words, eight "unpleasant and high arousing" words and 12 "unpleasant and low arousing" words. Thus, from the 40 words, we obtained two packs with 20 pleasant and 20 unpleasant words on one side, and 19 high and 21 low arousal words on the other side that showed the desired characteristics. The statistical details are shown in Table 1.

In addition, a pack of 20 neutral words [18] was included in the stimulus material; these data were not included in the present analysis.

Examples of the utilized words are: pleasant and high arousing: Spass (fun), Glück (luck); pleasant and low arousing: Rose (rose), Wärme (warmth); unpleasant and high arousing: Mord (murder), Hass (hatred); unpleasant and low arousing: Armut (poverty), Tadel (reproach); neutral: Format (format), Phase (phase). The complete list of the German stimulus words with their English translations is available upon request.

The words extended a visual angle of 3.7 (±0.7)° at the center of a PC screen. They were sequentially presented for 450 ms followed by an interval of 1,550 ms during which a fixation cross was displayed at the screen center.

The 60 words were used repeatedly as stimuli, in six runs, for a total of 360 word presentations for each subject. In order to maintain some surprise in stimulus appearance while limiting the persistence of a given emotion, we chose a pseudo-random sequence of presentation where no more than two successive stimuli of the same valence category followed each other. For each subject and for each run, different pseudo-random sequences of the 60 words were used. About 18–24 stimuli, inserted at random, were

Table 1 Characteristics of the word stimuli

	Valence rating	Arousal rating	Number of letters	Number of syllables	Length on PC screen (°)	Frequency of occurrence	Imaginability rating
Pleasant ($n = 20$)	6.1 ± 0.5	4.8 ± 1.1	4.7 ± 0.7	1.6 ± 0.5	3.7 ± 0.7	10,078 ± 9,747	5.1 ± 1.6
Unpleasant ($n = 20$)	2.0 ± 0.5	4.4 ± 1.3	5.1 ± 0.9	1.5 ± 0.5	3.7 ± 0.6	9,084 ± 9,401	4.6 ± 0.8
P-value	<0.00001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
High-arousing ($n = 19$)	4.4 ± 2.4	5.7 ± 0.5	5.1 ± 0.8	1.4 ± 0.5	3.8 ± 0.6	10,209 ± 9,270	5.1 ± 1.2
Low-arousing ($n = 21$)	3.7 ± 1.7	3.6 ± 0.7	4.7 ± 0.8	1.6 ± 0.5	3.6 ± 0.7	9,012 ± 9,831	4.6 ± 1.3
P-value	n.s.	<0.00001	n.s.	n.s.	n.s.	n.s.	n.s.

question marks. Words, fixation points and question marks were displayed in white on a dark grey background. Between runs, there was a 1 min intermission.

Picture Experiment

Pictures were taken from the IAPS according to their reported scores on the valence and arousal dimensions for males and females [27].

For the selection of the pictures, a similar strategy was used as for the selection of words. Subsequent pruning steps that omitted single pictures aimed at optimizing the two competing goals: the same pictures assigned to the first two packs should differ significantly in valence while not differing in arousal, and when assigned to the second two packs should differ significantly in arousal while not differing in valence. In addition, the assignments should produce packs of near-equal number of pictures.

Interactive statistics evaluated the result of each pruning step. Eventually, the optimal result yielded 90 pictures that were assigned to the sub-packs of 20 "pleasant and high arousing pictures", 25 "pleasant and low arousing pictures", 24 "unpleasant and high arousing pictures" and 21 "unpleasant and low arousing pictures". Thus, among the 90 pictures we obtained two packs with 45 pleasant and 45 unpleasant pictures on one side, and 44 high and 46 low arousal pictures on the other side that showed the desired characteristics. The statistical details are shown in Table 2.

Table 2 Characteristics of the picture stimuli

	Valence rating	Arousal rating
Pleasant ($n = 45$)	7.6	5.4
Unpleasant ($n = 45$)	2.7	5.4
P-value	<0.00001	n.s.
High-arousing ($n = 44$)	4.9	6.1
Low-arousing ($n = 46$)	5.4	4.8
P-value	n.s.	<0.00001

An additional pack of 20 neutral pictures was also used for stimulus presentation; these data were not included in the present analysis. The IAPS identification numbers of all 110 pictures eventually used in the experiment are shown in Note 1.[1]

The pictures were displayed in randomized sequence on the computer screen, each for 600 ms, followed by a fixed interval (black screen) of 1,400 ms.

The 110 pictures were presented in two blocks of 37 pictures and one block of 36 pictures. The blocks were separated by brief rest periods. This was repeated twice so that eventually each picture was shown three times during the experiment.

For each subject, three individual pseudo-random sequences were generated where no more than two successive pictures of the same valence category followed each other.

Procedure

Subjects were seated in a comfortable chair in a sound, light, and electrically shielded EEG recording chamber. The experimenter in the adjacent recording room was in contact with the subject via intercom. During recording, the subject's head was placed in a forehead–chin rest so that the distance between eyes and PC screen was constant (100 cm) and head movements were minimized.

[1] Note 1: The IAPS identification numbers are the following: Pleasant-high: 4,220, 4,680, 5,260, 5,270, 5,470, 5,480, 5,621, 5,910, 7,230, 8,030, 8,080, 8,170, 8,185, 8,190, 8,200, 8,210, 8,370, 8,470, 8,501, 8,502. Pleasant-low: 1,440, 1,460, 1,463, 1,721, 1,811, 1,920, 1,999, 2,057, 2,058, 2,160, 2,165, 2,311, 2,550, 2,650, 2,660, 4,610, 5,600, 5,660, 5,820, 5,831, 5,982, 7,330, 7,580, 8,510, 8,540. Unpleasant-high: 2,691, 2,710, 6,210, 6,212, 6,242, 6,243, 6,250, 6,312, 6,360, 6,530, 6,560, 6,570, 6,571, 6,821, 6,834, 9,120, 9,160, 9,560, 9,600, 9,621, 9,622, 9,630, 9,911, 9,920. Unpleasant-low: 1,111, 1,274, 2,700, 2,751, 2,900, 3,300, 6,561, 7,361, 9,000, 9,001, 9,041, 9,181, 9,220, 9,280, 9,290, 9,330, 9,340, 9,417, 9,421, 9,530, 9,830. Neutral: 2,383, 2,575, 5,395, 5,531, 5,731, 5,740, 7,002, 7,009, 7,035, 7,090, 7,100, 7,130, 7,140, 7,150, 7,170, 7,185, 7,211, 7,233, 7,705, 7,710.

Stimuli (pictures and words) were presented using the software "Presentation" (Neurobehavioral Systems, Albany, CA, USA, Version 9.20, 2005).

For the word experiment, subjects were instructed to fixate the cross at the center of the screen and to read the words silently but attentively. When the question mark appeared, the subject had to repeat loudly the last word that was presented before the question mark (one-back-task). For the picture experiment, subjects were asked to look attentively at the images. In either case, the instructions targeted attention and memory aspects, and were intended to divert the subjects' attention from the emotional content of the stimuli; the inclusion of irrelevant neutral stimuli in the presentations also aimed at this goal. Indeed, unstructured post-experiment debriefing revealed that none of the subjects suspected emotion as topic of the study.

The entire ERP recording lasted about 25 min.

Data Acquisition and Preprocessing

About 58 electrodes were placed using the "Easy Cap System" (FMS Falk Minow Services, Herrsching-Breitbrunn, Germany) according to the 10/10 international system [33] at the positions Fp1/2, AF7/8, AF3/4, AFz, F7/8, F5/6, F3/4, F1/2, Fz, FT7/8, FC5/6, FC3/4, FCz, T7/8, C5/6, C3/4, C1/2, Cz, TP7/8, CP5/6, CP3/4, CP1/2, CPz, P7/8, P5/6, P3/4, P1/2, Pz, PO7/8, PO3/4, POz, O1/2, Oz, using Cz as recording reference. Horizontal and vertical eye movements were recorded with electrodes at the left and right outer canthi and left infraorbital. Impedances were kept below 10 kΩ. The signals were amplified (bandpass 0.5–125 Hz) and digitized (250 samples/s) using a 64-channel EEG/ERP system (hardware: M & I Ltd., Prague, Czech Republic; software: Easys221, Neuroscience Technology Research Ltd., Prague, Czech Republic).

For both experiments, all data epochs, starting at the onset of stimulus presentation and covering the entire stimulus presentation from onset to offset were displayed off line on a PC screen and carefully examined for artifacts (muscle, eye and head movements, eye blinks, electrode artifacts); no artifact correction was used; epochs with artifacts were excluded from further processing. For the word experiment, the data epochs started at the onset of word presentation up to 113 timeframes later (=448 ms), and for the picture experiment the data epochs started at the onset of picture presentation up to 151 timeframes (=600 ms). The number of artifact-free data epochs that were eventually available on the average from each subject was 137.7 ± 42.9 for the word experiment and 171.3 ± 49.7 for the picture experiment.

Separately for the two experiments, for each subject and channel, all available ERP data epochs were averaged separately for the stimuli of pleasant and of unpleasant valence; and likewise, all available data epochs were averaged separately for the stimuli of high and of low arousal, thereby yielding an averaged ERP waveshape for each of the four stimulus conditions of each subject.

For each subject, the average ERP waveshapes (4 × 58) were FFT-filtered (2–20 Hz, mean-value zero padding, boxcar window) and recomputed against average reference. Thus, for each of the two stimulus dimensions (valence and arousal), an original ERP waveshape was computed for both levels (pleasant and unpleasant, or high and low arousing, respectively).

In order to recognize steps of information processing, not intensities of processing, we set out to test the ERP data over time for differences of electric landscape (of spatial distribution), not for differences of strength. Accordingly, the original ERP waveshape data were transformed into series of momentary potential distribution maps. For the word experiment, each original 58-channel ERP waveshape resulted in 113 momentary potential distribution maps, and in the picture experiment, each original 58-channel ERP waveshape resulted in 151 momentary potential distribution maps.

The strength of the individual potential distributions was removed by normalizing all maps: Global Field Power (GFP, [29]) for each map was set to one by dividing the voltages at all electrodes by the GFP value of that map. The rational is that only differences in landscape of the potential distribution, not differences in strength of the distribution must have been caused by a different intracerebral spatial distribution of neural activity [17].

The four normalized ERP map series were averaged across subjects into four grandmean 58-channel ERP map series. For each experiment, a grand–grandmean ERP map series was computed across the four stimulus conditions, producing 113 maps for the word experiment and 151 maps for the picture experiment of which representative samples are illustrated in Fig. 1 for the word experiment and in Fig. 2 for the picture experiment. A cursory inspection of these two figures shows that the mapped potential landscapes change in a non-steady manner: For example, in Fig. 1, the sequence of posterior negative potential maps from 0 to 56 ms reverts to anterior negative maps from 72 to 112 ms, then changes again within 16 ms to posterior negative maps at 128 ms. Similar drastic and quasi step-wise discontinuities of sequential map landscapes are also very obvious in Fig. 2. Microstate analysis formalizes the identification of such landscape changes.

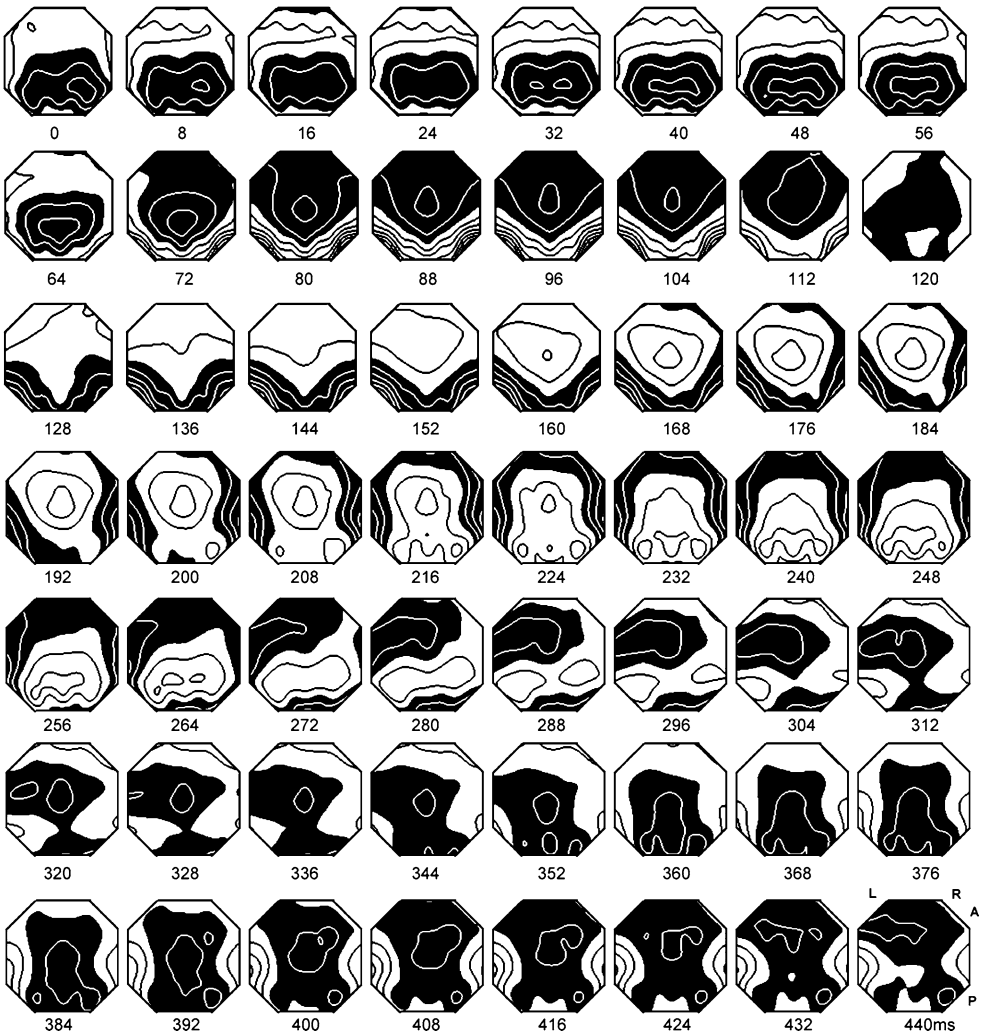

Fig. 1 The ERP grand–grandmean map series of the word experiment (56 maps at 8 ms intervals), averaged across the four stimulus conditions and the 28 subjects. Head seen from above, nose up, left ear left; L/R = left/right, A/P = anterior/posterior. Isopotential levels in arbitrary units. White = positive, black = negative potential versus average reference. Latencies in ms after stimulus onset

Data Reduction and Analysis

Microstate Analysis

The following procedure was applied and separately executed for the two experiments:

The grand–grandmean ERP map series were parsed into temporal microstates. Microstates are defined as brief sequences of successive momentary ERP maps with quasi-stable potential landscape [29]. For microstate analysis, the global clustering approach [38] was employed; this strategy uses Global Map Dissimilarity [29] as a measure of 'landscape distance' between any two maps to produce clusters of maps where each cluster contains member maps of closely related landscapes. The settings for the utilized analysis program (by R.D. P.-M.) were: 20 random initializations with maximal 50 iterations computing between 2 and 20 clusters of different map landscapes. A subsequent cross-validation analysis determined the optimal number of map clusters for the treated dataset. This analysis step identified map clusters by the maps' spatial configuration. Multiplying all electrodes in a given map (of some given spatial configuration) by (−1) will reverse its polarity but of course keep its spatial configuration. The recognition of the polarity of each map configuration is done in the subsequent step of the analysis.

Next, each map of the grand–grandmean ERP map series was recognized as member of one of the obtained map clusters, or of the map cluster with the same spatial configuration but with reversed polarity. All sequential maps assigned to the same cluster with the same polarity were then recognized as one microstate. The membership and polarity thus established the start and end times of the microstates. Note that each of the clusters could occur more than once during the analysis period and with the same or with the opposite polarity so that there can be more microstates than map clusters.

Within the four normalized ERP map series of each subject all maps that belonged to a given microstate were averaged. This resulted in a single 'microstate map' for

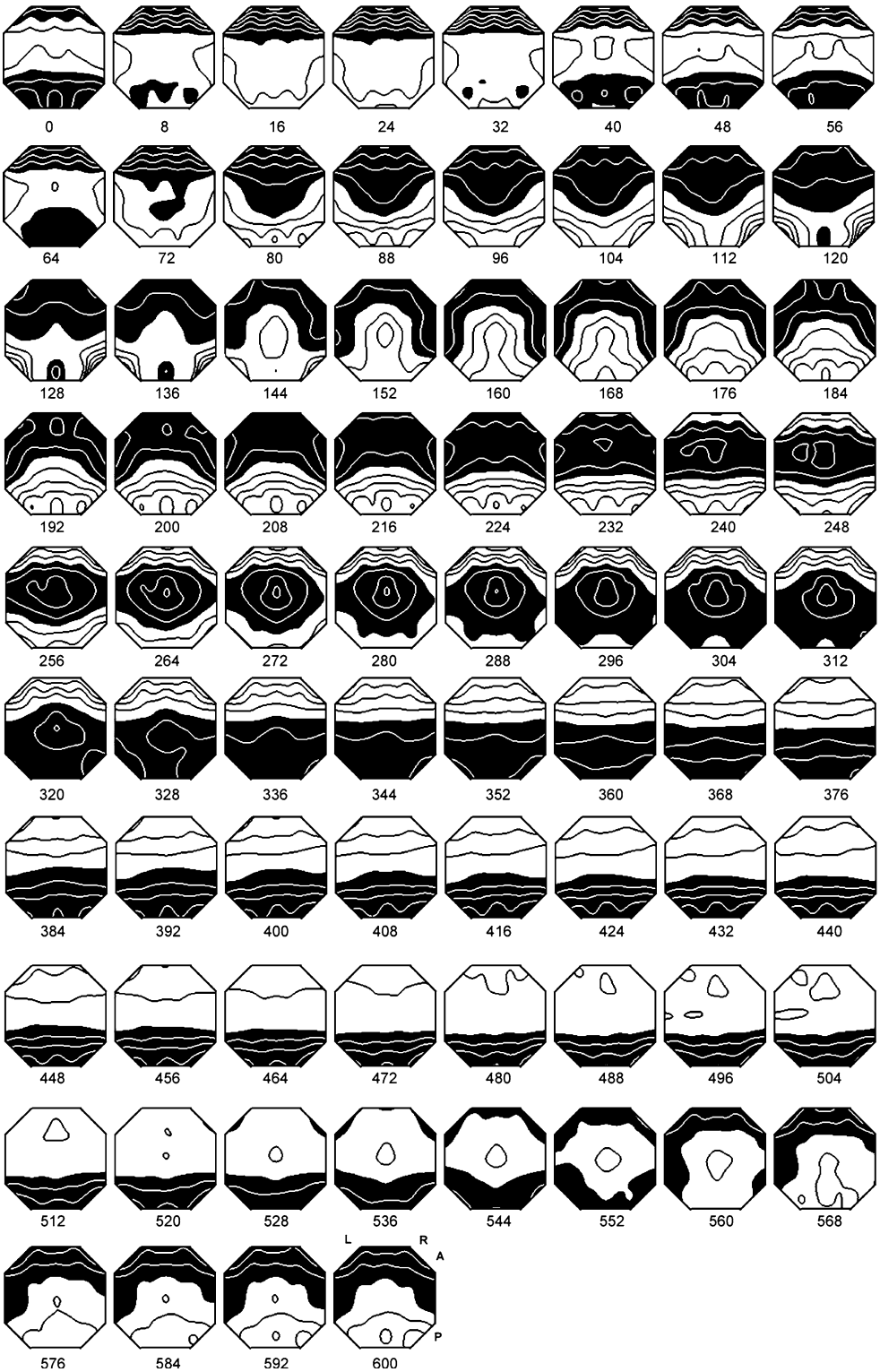

Fig. 2 The ERP grand–grandmean map series of the picture experiment (76 maps at 8 ms intervals), averaged across the four stimulus conditions and the 29 subjects. Head seen from above, nose up, left ear left; L/R = left/right, A/P = anterior/posterior. Isopotential levels in arbitrary units. White = positive, black = negative potential versus average reference. Latencies in ms after stimulus onset

each microstate of each of the four stimulus conditions per subject.

The results of this analysis established the mean behavior of the microstates during the four stimulus conditions. In order to assure that there was no latency effect of the microstate start (end) times between conditions, the microstate analysis was also done separately for the four stimulus conditions applying the number of clusters that was determined by the crossvalidation of the grand–grandmean analysis. The microstate start (end) times

obtained with the four stimulus conditions in both experiments were then compared with the corresponding times of the grand–grandmean microstate analyses.

Statistical Analysis

For each microstate, the difference in global map landscape between microstate maps evoked by pleasant and by unpleasant stimuli, as well as that evoked by high arousing and by low arousing stimuli was tested across subjects using topographic analysis of variance (TANOVA). TANOVA employs Global Map Dissimilarity and a statistical randomization procedure to establish the exact probability of the observed 'distance' between map landscapes with additional correction for multiple testing (see [46]).

If the TANOVA yielded $P < 0.10$, follow-up tests compared the local values at all 58 electrodes between conditions (pleasant versus unpleasant valence, and high versus low arousal) using *t*-statistics across subjects.

Two tail values $P < 0.10$ are reported.

Results

Word Experiment

Behavioral Results

All subjects gave 100% correct answers after the 18–24 times in random order appearance of the question marks. The perfect accomplishment of the one-back-task ensured that all subjects were paying attention to the words through the whole experiment.

ERP Results

Microstate Analysis. The microstate analysis identified 11 sequential microstates. The microstate maps across all subjects and conditions were averaged for each microstate. The latency and duration of the 11 microstates with their mean topography across subjects is illustrated in Fig. 3a, b. The mean duration of all microstates was 41 ms (range = 20–66 ms, SD = 15).

Table 3 shows that the separate microstate analyses for the four stimulus conditions revealed start (end) times of the 11 microstates that were almost identical to the start (end) times obtained with the grand–grandmean microstate analyses. Across the 10 start (end) points of the 11 microstates, the average deviation from the start (end) points of the grand–grandmean was for pleasant valence 0.40 (SD = 3.98), for unpleasant valence 1.20 (SD = 2.70), for high arousal 0.00 (SD = 5.33) and for low arousal 0.40 (SD = 2.95) ms. This supports the application of microstate start (end) times of the grand–grandmean ERP map series to all four stimulus conditions.

Global Topographical Differences between Microstate Maps of Compared Conditions. Figure 3c, d illustrate the microstate mean maps for the four conditions. TANOVA identified the microstates that differed at $P < 0.10$ between conditions. As indicated by the dotted frames in Fig 3c, d, four of the eleven microstates were different for pleasant versus unpleasant words (microstate #3 at 118–162 ms, $P = 0.08$; microstate #6 at 218–238 ms, $P = 0.05$; microstate #7 at 238–266 ms, $P = 0.02$; and microstate #8 at 266–294 ms, $P = 0.04$). Two of the eleven microstates were different for high versus low arousing words (microstate #8 at 266–294 ms, $P = 0.03$; and microstate #9 at 294–346 ms, $P < 0.001$). Three of the four valence-sensitive microstates occurred before the two arousal-sensitive microstates; the fourth valence-sensitive microstate was identical with the first arousal-sensitive microstate.

Local Topographical Differences between Microstate Maps of Compared Conditions. The results of the electrode-wise post-hoc tests of the four valence-sensitive and the two arousal-sensitive microstates are displayed as statistical difference maps below the grandmean maps that were compared in the tests. Of the 58 tested electrode locations, between 7 and 38 yielded $P < 0.10$ in the six difference maps; on average across the four valence-sensitive difference maps, there were 13.5 (SD = 5.4) such cases, and 27.5 (SD = 14.8) across the two arousal-sensitive difference maps. These plotted locations evidently were not randomly distributed over the electrode array but clearly packed into at most three clusters in a given difference map. Naturally, decreasing distance between electrodes tends to increasingly correlated signals, but it is of interest to note that more than one spatial pack of similar differences in the electrode array indicates that more than one neural population contributed to the observed global difference. The topographies of the differences differed between microstates: for example, more amplitude for unpleasant than pleasant was detected in microstate #7 in right posterior areas, but in microstate #8 in left central areas.

Picture Experiment

ERP Results

Microstate Analysis. The microstate analysis identified 15 sequential microstates. The microstate maps across all subjects and conditions were averaged for each microstate. The latency and duration of the 15 microstates with their

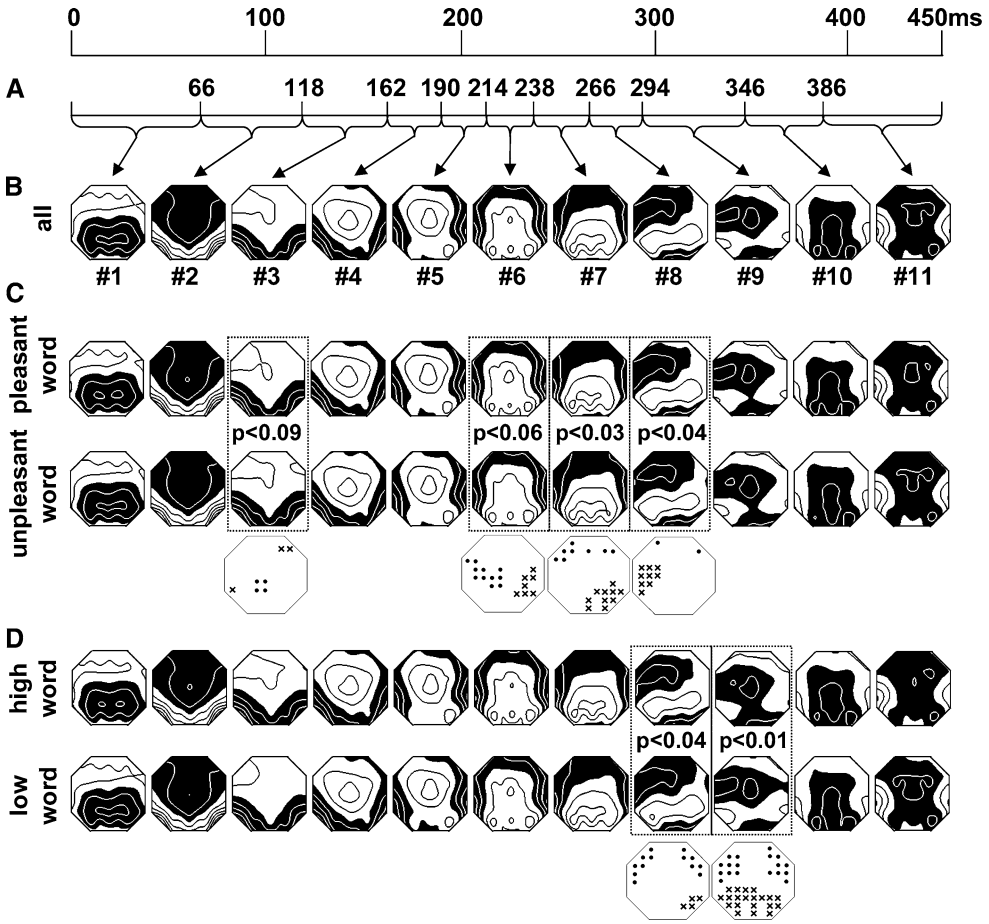

Fig. 3 Word experiment: (**a**) latencies start (end) times, and (**b**) topographical maps of the 11 microstates of the grand–grandmean map series; (**c** and **d**) the 11 grandmean microstate maps as separate averages for pleasant and unpleasant valence words, and for high and low arousal words. Framed microstates differed between conditions in the global tests at $P < 0.10$; the P-values are indicated between the grandmean maps; these were the microstates #3, #6, #7, and #8 for valence, and #8 and #9 for arousal. For these microstates, the topography of the difference between the compared grandmean maps is displayed as electrode-wise post-hoc test results below the framed microstate [dots = pleasant (high arousal) had higher amplitude at $P < 0.10$ than unpleasant (low arousal), respectively; crosses = pleasant (high arousal) had lower amplitude at $P < 0.10$ than unpleasant (low arousal), respectively]. Head seen from above, nose up, left ear left; isopotential levels in arbitrary units; white = positive, black = negative potential versus average reference

Table 3 Microstate start (end) times in ms for the grand–grandmean microstate analysis and for the four separate grandmean (condition) analyses of the word experiment

Microstate	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11
Grand–grandmean	66	118	162	190	214	238	266	294	346	386 ms	
Pleasant	66	122	162	190	210	238	262	302	350	382	
Unpleasant	66	118	158	190	218	242	266	294	350	390	
High arousal	62	118	158	194	214	238	258	306	346	386	
Low arousal	70	122	162	190	214	238	262	298	346	382	
Mean	66	120	160	191	214	239	262	300	348	385	
SD	3.3	2.3	2.3	2.0	3.3	2.0	3.3	5.2	2.3	3.8	

mean topography across subjects is illustrated in Fig. 4a, b. The mean duration of all microstates was 40 ms (range = 16–88 ms, SD = 20).

Table 4 shows that the separate microstate analyses for the four stimulus conditions revealed start (end) times of the 15 microstates that were almost identical to the start

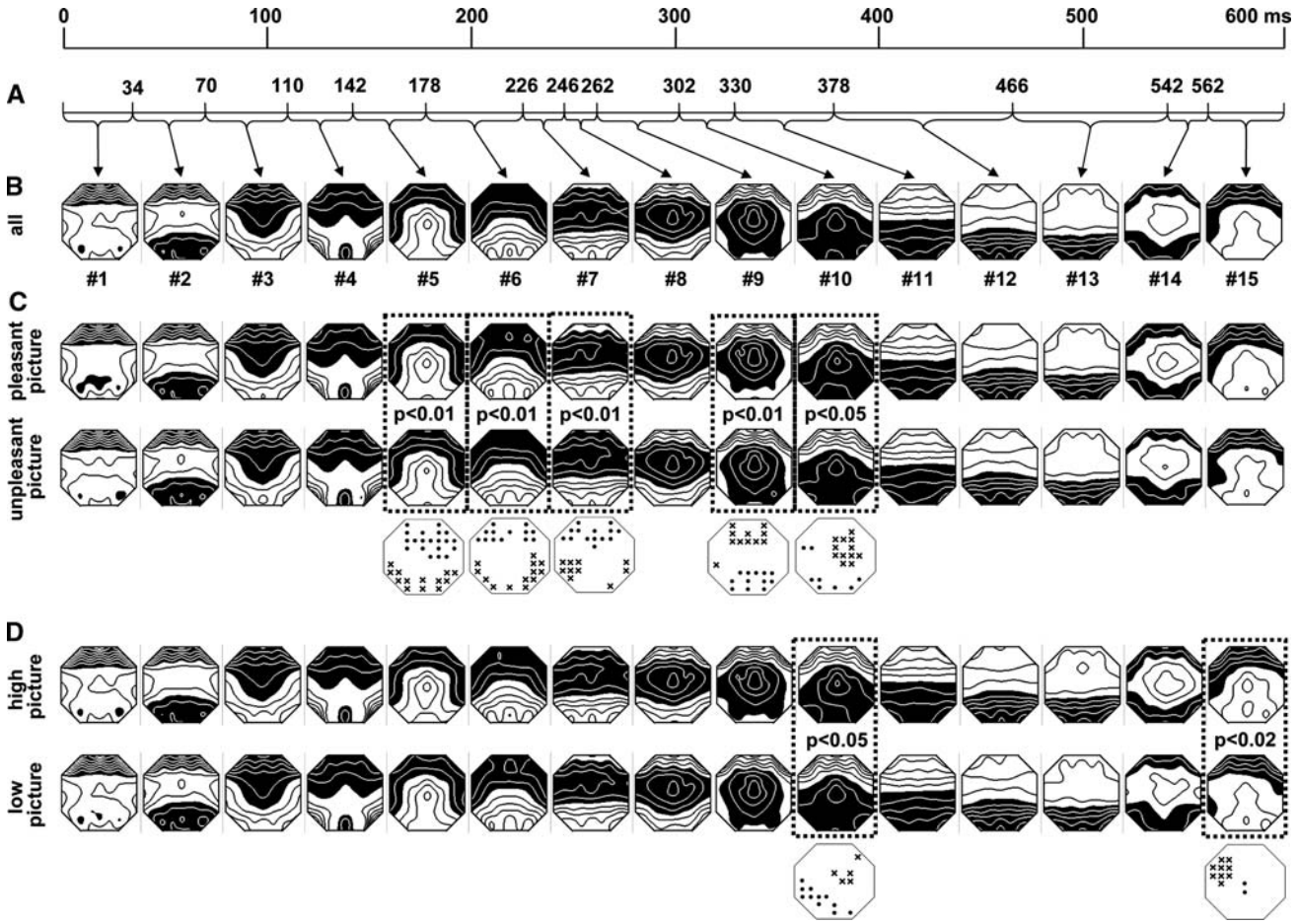

Fig. 4 Picture experiment: (**a**) latencies start (end) times, and (**b**) topographical maps of the 15 microstates of the grand–grandmean map series; (**c** and **d**) the 15 grandmean microstate maps as separate averages for pleasant and unpleasant valence pictures, and for high and low arousal pictures. Framed microstates differed between conditions in the global tests at $P < 0.10$; the *P*-values are indicated between the grandmean maps; these were the microstates #5, #6, #7, #9 and #10 for valence, and #10 and #15 for arousal. For these microstates, the topography of the difference between the compared grandmean maps is displayed as electrode-wise post-hoc test results below the framed microstate [dots = pleasant (high arousal) had higher amplitude at $P < 0.10$ than unpleasant (low arousal), respectively; crosses = pleasant (high arousal) had lower amplitude at $P < 0.10$ than unpleasant (low arousal), respectively]. Head seen from above, nose up, left ear left; isopotential levels in arbitrary units; white = positive, black = negative potential *versus* average reference

(end) times obtained with the grand–grandmean microstate analyses. Across the 14 start (end) points of the 15 microstates, the average deviation from the start (end) points of the grand–grandmean was for pleasant valence −0.29 (SD = 2.92), for unpleasant valence −0.29 (SD = 5.31), for high arousal 0.29 (SD = 4.83) and for low arousal −0.86 (SD = 3.21) ms. This supports the application of microstate start (end) times of the grand–grandmean ERP map series to all four stimulus conditions.

Global Topographical Differences Between Microstate Maps of Compared Conditions. Figure 4c, d illustrate the microstate mean maps for the four conditions. TANOVA identified the microstates that differed at $P < 0.10$ between conditions. As indicated by the dotted frames in Fig. 4c, d, five of the fifteen microstates were different for pleasant versus unpleasant pictures (microstate #5 at 142–178 ms, $P = 0.001$; microstate #6 at 178–226 ms, $P < .0001$; microstate #7 at 226–246 ms, $P = 0.007$; microstate #9 at 262–302 ms, $P = 0.008$; and microstate #10 at 302–330 ms, $P = 0.045$). Two of the fifteen microstates were different for high versus low arousing pictures (microstate #10 at 302–330 ms, $P = 0.046$; and microstate #15 at 562–600 ms, $P = 0.013$). Four of the five valence-sensitive microstates occurred before the two arousal-sensitive microstates; the fifth valence-sensitive microstate was identical with the first arousal-sensitive microstate.

Local Topographical Differences between Microstate Maps of Compared Conditions. The results of the electrode-wise post-hoc tests of the four valence-sensitive and the two arousal-sensitive microstates are displayed as statistical difference maps below the grandmean maps that were compared in the tests. Of the 58 tested electrode

Table 4 Microstate start (end) times in ms for the grand–grandmean microstate analysis and for the four separate grandmean (condition) analyses of the picture experiment

Microstate	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	#12	#13	#14	#15
Grand–grandmean	34	70	110	142	178	226	246	262	302	330	378	466	542	562 ms	
Pleasant	38	70	110	142	178	222	246	266	306	330	374	466	538	558	
Unpleasant	34	70	110	142	170	218	250	270	310	330	370	470	542	558	
High arousal	34	70	114	142	174	222	250	270	306	326	370	474	542	558	
Low arousal	38	70	110	142	178	222	238	266	302	330	374	466	542	558	
Mean	36	70	111	142	175	221	246	268	306	329	372	469	541	558	
SD	2.3	0.0	2.0	0.0	3.8	2.0	5.7	2.3	3.3	2.0	2.3	3.8	2.0	0.0	

locations, between 11 and 33 yielded $P < 0.10$ in the seven difference maps; on average across the five valence-sensitive difference maps, there were 25.2 (SD = 4.9) such cases, and 13.5 (SD = 3.5) across the two arousal-sensitive difference maps. These plotted locations evidently were not randomly distributed over the electrode array but clearly packed into at most three clusters in a given difference map. Naturally, decreasing distance between electrodes tends to increasingly correlated signals, but it is of interest to note that more than one spatial pack of similar differences in the electrode array indicates that more than one neural population contributed to the observed global difference. The topographies of the differences differed between microstates: for example, more amplitude for unpleasant than pleasant was detected in microstate #7 bilateral over posterior areas, but in microstate #9 over anterior areas, and more amplitude for low than high arousal was detected in microstate #10 over right anterior areas, but in microstate #15 over left anterior areas.

Discussion

The present study investigated the temporal dynamics of the brain electric mechanisms that are responsible for the implementation of the dimensions valence and arousal during the processing of emotional stimuli. The visually presented stimuli were words in the first and pictures in the second experiment; they were chosen according to verbally reported valence and arousal.

ERP microstate analysis revealed that the processing of the two dimensions of the incoming emotional stimuli is implemented in several distinct microstates. Because different microstates must have been generated by differently active neural populations, we conclude that processing of valence and of arousal involved different neural assemblies. This result corroborates previous functional neuroimaging studies that reported a dissociated neural representation of the two dimensions (e.g., [2, 22, 23]).

As to our first hypothesis, the results clearly showed that the high temporal resolution in the range of milliseconds of the applied ERP analysis allowed us to describe the temporal dynamics of the partly dissociated neural networks. We found that the extraction of valence information started at around 100 ms after stimulus onset-precisely at 118 ms in the word experiment and at 142 ms in the picture experiment. Extraction of the arousal information occurred in a later step, starting at 266 ms in the word experiment and at 302 ms in the picture experiment. In sum, in both our experiments, a clear dynamical temporal pattern appeared, indicating that information about valence of an incoming stimulus is extracted before information about arousal, thus validating our second hypothesis. This observed temporal succession of the extraction of the two emotional dimensions is supported by separate literature reports of earlier ERP signs of valence effects, starting at about 100 ms [16, 36, 39, 40, 44, 45], and of later ERP signs of arousal effects, starting at about 300–400 ms [8, 11]. Two ERP studies [20, 43] that used shorter stimulus presentations (333 and 120 ms, respectively) found arousal effects as early as 150 ms after stimulus onset. It seems thus that the observed latencies for arousal effects might depend on stimulus duration. Consequently, experiments that aim at the study of the temporal dynamics in the processing of emotional stimuli should use the same paradigm for valence as well as arousal effects.

Two studies that analyzed the two dimensions in the same experiment [13, 21] likewise identified earlier ERP components for valence than arousal.

A central finding in both our experiments was that the last microstate of valence extraction was identical with the first microstate of arousal extraction; thus, the results showed a ‘common step’ for extraction of valence and arousal. In a series of reaction time experiments with IAPS pictures and with emotional words, Robinson et al. [42] observed a significant interaction between the two dimensions of valence and arousal when subjects evaluated emotional stimuli: evaluation latencies were faster if an

unpleasant stimulus was high in arousal or if a pleasant stimulus was low in arousal. Based on this report, one might speculate that our 'common step' represents the time period where the two dimensions of valence and arousal interact in the evaluative processing of the incoming stimulus. Dolcos and Cabeza [14] and Delplanque et al. [13] reported an ERP component after 450 ms that was affected by both dimensions, but the authors did not further discuss this interesting point. In our word experiment, the 'common step' lasted from 266 to 294 ms, whereas in the picture experiment the 'common step' lasted from 302 to 330 ms after stimulus onset. Thus, our 'common steps' occurred much earlier than the 500–600 ms latency reported by Dolcos and Cabeza [14] and Delplanque et al. [13]. What are the reasons for this discrepancy in latency? There are at least three important differences between these two studies and ours. Firstly, our paradigm did not include an emotional task. Our one-back task is related to memory functions and was introduced to divert the subjects' attention from possible emotional aspects. Our subjects were naïve in regard to the aim of the study, emotions, and in fact, the debriefing after the ERP recording confirmed that none of the subjects suspected it. On the contrary, the subjects of Dolcos and Cabeza [14] were instructed to experience the feelings elicited by the pictures, and the subjects of Delplanque et al. [13] had to categorize as fast as possible the target stimuli as to their emotional valence. That means that in both of these studies, 'emotion' was an overt issue. Secondly, for the comparison between high versus low arousing stimuli, Dolcos and Cabeza [14] and Delplanque et al. [13] used pleasant as well as unpleasant stimuli for the high arousing condition and neutral stimuli for the low arousing condition. But, when using neutral stimuli, the valence dimension between the two categories high versus low arousal cannot be matched and therefore valence might become a confounding variable. Thirdly, our analysis approach, the microstate analysis, is a bottom-up, data-driven, comprehensive approach that does not require a priori assumptions about putative ERP components. Our approach takes full advantage of the high temporal resolution of the electromagnetic measurements: each datapoint (i.e. at 4 ms intervals) is analyzed, giving us a complete temporal overview of the stimulus processing. Preselection of ERP component epochs might omit time periods where information about valence and/or arousal is extracted.

Given the parallel findings of the temporal dynamics during the processing of emotional pictures and words, our results cannot be due to the stimuli's verbal or pictorial nature. Rather, a general principle appears to be operative that privileges valence information, then provides processing interaction between valence and arousal information, and eventually handles the arousal aspects. We note that EEG data predominantly reflect the cortical activity of the brain. Therefore we cannot exclude the possibility that subcortical areas such as the amygdala or thalamus that are well known to play a crucial role in the processing of emotional stimuli might show different temporal dynamics than the presently analyzed data.

In an fMRI study, Kensinger and Schacter [23] found that the extraction of valence information from pictorial stimuli activated a wider neural network compared to the extraction from linguistic stimuli. This might be seen as parallel to our observation that the number of valence-distinguishing topographical locations (panel d in Figs. 3 and 4) was on average larger for pictorial compared to linguistic stimuli.

A caveat is to be mentioned here: The interpretation of the topographic differences between microstate maps in terms of intracortical source localization is not directly available. Brain electric sources cannot be assumed to be located perpendicularly under the scalp location of maximal or minimal potential; computational approaches are needed for intracortical source modeling.

A second caveat is that we did not examine gender differences because of the limited number of our subjects, but we note that 75% of the subjects were women and that the results might be skewed accordingly. A future study on a larger population should provide the opportunity to test for putative gender differences.

A final issue is the observation that the extraction of valence and of arousal information is implemented in many different, separate microstates. In other words, there are multiple microstates that apparently implement the same process, i.e. the extraction or evaluation of valence and/or arousal. Some of these microstates are directly concatenated (i.e. immediately successive) but others are temporally separated by microstates that are not involved in the extraction of the two dimensions. Why should our brain repeat the same process on the same information? The process 'evaluation of pleasant or unpleasant valence' for example is implemented in four (word experiment) or five (picture experiment), topographically different microstates. Different topographies (i.e. different brain potential landscapes) on the head must have been generated by differently active neural populations, and it appears reasonable to assume that different active neural populations implement different functions [28, 30]. Based on this rational we suggest that the process of 'evaluation of pleasant or unpleasant valence' plays a crucial role in different brain functions as for instance perception, attention, updating of working memory, etc. Inspection of panel d of Figs. 3 and 4 clearly shows that the microstates that process the evaluation of valence and/or arousal implement this evaluation in different neural assemblies. Hence it appears that function-specific subsidiary networks become active for this evaluation. As mentioned above, the cortical localizations of these networks based on the scalp-recorded potential

distributions need to be determined by computational source modeling.

Future studies should aim at clarifying the functional significance of the relevant microstates by adequate experimental designs, as well as aim at establishing the cortical localization of their active neural networks by the application of computational source modeling.

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