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Faces and emotions: brain electric field sources during covert emotional processing

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Abstract—Covert brain activity related to task-free, spontaneous (i.e. unrequested), emotional evaluation of human face images was analysed in 27-channel averaged event-related potential (ERP) map series recorded from 18 healthy subjects while observing random sequences of face images without further instructions. After recording, subjects self-rated each face image on a scale from "liked" to "disliked". These ratings were used to dichotomize the face images into the affective evaluation categories of "liked" and "disliked" for each subject and the subjects into the affective attitudes of "philanthropists" and "misanthropists" (depending on their mean rating across images). Event-related map series were averaged for "liked" and "disliked" face images and for "philanthropists" and "misanthropists". The spatial configuration (landscape) of the electric field maps was assessed numerically by the electric gravity center, a conservative estimate of the mean location of all intracerebral, active, electric sources. Differences in electric gravity center location indicate activity of different neuronal populations. The electric gravity center locations of all event-related maps were averaged over the entire stimulus-on time (450 ms). The mean electric gravity center for disliked faces was located (significant across subjects) more to the right and somewhat more posterior than for liked faces. Similar differences were found between the mean electric gravity centers of misanthropists (more right and posterior) and philanthropists. Our neurophysiological findings are in line with neuropsychological findings, revealing visual emotional processing to depend on affective evaluation category and affective attitude, and extending the conclusions to a paradigm without directed task. © 1998 Elsevier Science Ltd. All rights reserved.

Key Words: brain mapping; evoked potentials; facial expression; laterality; personality; source localization.

Introduction

Facial expressions as stimuli have been used to study the spatial organization of brain mechanisms of emotions in the human brain. In neuropsychological investigations, behavioural changes were observed when the evaluation or generation of facial emotion was supposed to be predominantly generated by the left or the right hemisphere [25, 40, 41, 43, 51]. Using event-related potential (ERP) measurements, electrophysiological correlates of the outcome of forced emotional classification of faces were reported [12, 29, 32, 34, 53] but their localizing interpretations lacked methodological validation. Employing a non-ambiguous method to estimate the center location of brain activity, we investigated whether the effect of different emotional meaning on the spatial organization of brain activity also occurs spontaneously, i.e. when no emotional decision is required and it occurs automatically and when the information is available to both hemispheres.

One of the hypotheses suggested by the neuropsychological assessment of normal subjects and brain-damaged patients was that the right hemisphere is generally more efficient than the left hemisphere in the processing of emotional stimuli [3, 23]. In particular, right hemisphere advantage was observed in the perception and/or expression of facial emotion in normals (perception: [39, 41, 43, 60]; expression: [5, 43, 44]). Similarly, deficits in the perception and/or expression of facial emotion have been found more frequently in right than left hemisphere damage (perception: [2, 6, 16, 18, 40]; expression: [11, 55]). These results led to the suggestion that "the right hemisphere may contain a lexicon/representation of facial emotions" ([7], p. 2603).

This view has been challenged by the hypothesis that the quality of emotion alters hemispheric contribution [58]. Support for this assumption arose from reports on

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left hemispheric contributions to the recognition of faces and to the discrimination of facial expression [14, 25, 51, 59], thus suggesting that the left hemisphere is considerably involved in emotion [63]. In particular, some studies suggested right-hemisphere dominance for negative emotions and either left-hemisphere or bilateral involvement for positive emotions: Normals tended to prefer faces presented to the right visual field/left hemisphere and to disfavour faces presented to the left visual field/right hemisphere [45, 47–51]. Right brain damage impaired the perception of negative facial expressions but not of positive expressions [4, 13]. Conversely, when attributing emotions to neutral faces, left hemisphere damaged patients attributed sadness significantly more often and happiness significantly less often than right hemisphere damaged patients [40], suggesting that left hemisphere-damaged patients may show a bias towards negative emotions. Indeed, "catastrophic reactions" (i.e. outbursts of tears, anxiety) were more frequent in patients with left hemispheric lesions whereas "indifference reaction" (i.e. tendency to joke, anosognosia, inappropriate cheerfulness) were predominant with right hemispheric lesions [19, 20, 57]. In stroke patients, indifference reportedly was related to right anterior lesions, depression to left anterior lesions [52].

Neuropsychological methods traditionally explored the capacities of brain information processing by assuming that contributions from brain regions involved in a task usually increase processing capacities and thus lead to an improved performance in terms of speed and accuracy. In order to elucidate the contribution of different brain regions, this approach must analyse the reduction of processing capacities while processing contributions are constrained in some regions; this is achieved by unilateral stimulus presentation in normals or by the presence of localized brain lesions in patients. In order to reduce needed constraints in the experimental design, the event-related field topography might be recorded because this is the direct electrical manifestation of the neural activity. Different configurations of the brain electric field must originate from differences in geometry of the active neural elements and thus are assumed to subserve different brain functions [35, 37, 38]. Brain electric field-based conclusions about the neural processes that constitute perceptual, emotional and cognitive processing can be drawn even during covert processing, i.e. when the subjects are not required to produce an overt response to the stimulus [8, 24, 30]. Avoiding directed, specific tasks offers the additional advantage that powerful brain mechanisms needed for task execution, *per se*, are not activated. If active, such mechanisms may overlay and conceal more subtle cognitive-emotional processes.

In a variety of tasks, differences in ERP waves were recorded for emotional vs neutral faces as stimuli [12, 27, 29, 32, 34, 53, 65]. Emotion-related processing tended to produce more ERP wave differences on the right side of the scalp. ERP amplitude or latency differences between positively and negatively evaluated faces were reported by some groups [29, 32] but no spatial organization could be described. Other studies failed to find ERP wave differences between these two conditions [27, 34, 65].

Our criticism of the ERP literature in this field is that conclusions about the spatial organization of emotions in the brain have been based on the assumption that the brain location of the processing site is identical to the scalp location of differences of EEG and ERP waveshapes. This is, however, only the case if the generators are oriented perpendicular to the scalp surface [9], an assumption that is unlikely, has never been validated and is proven to be wrong by the mere existence of magnetoencephalographic (MEG) measurements which can record only sources tangential to the surface. This issue is illustrated by the well-known ERP component P100 which often shows maximal scalp voltage values at locations contralateral to the active hemisphere [10, 26]. In order to obtain conclusive results about differences in neuronal activity, spatial descriptors of the brain electric field are required that offer an unambiguous distinction between the activity of different neural populations [36, 38, 42]. In particular, conclusions about changes of the location of active neuronal elements may only be drawn if they are based on adequate source modeling.

The aim of this study was to assess ERP map differences related to differences in spontaneous, covert emotional evaluation of images of human faces presented to normal subjects. These differences were assessed as a function of the subjects' affective evaluation of the single face images ("liked" vs "disliked") and as a function of the subjects' general affective attitude towards the entire set of face images (in line with the vernacular "misanthropists" vs "philanthropists"). In order to describe the most basic features of these processes, a paradigm without any directed task was used. Thus, possible interferences due to task execution were minimized by having the subjects merely look at the face images. To avoid ambiguities in the interpretation of the results, the brain electric field data were evaluated using the location of the point of gravity of the entire neuronal activity as a conservative localization approach.

Method

Subjects

Seven female and 11 male healthy volunteers (mean age 29.4, range 22–37) with normal or corrected-to-normal vision were recruited via campus advertisements and gave their informed consent to serve as subjects. No subject had any history of psychiatric disorder, alcohol or drug abuse. The subjects were informed about the experimental design (i.e. that they were going to see face images during the recordings), but not about the specific aim of the study. Handedness was assessed with the Edinburgh Handedness Inventory [46]; all were right-handed; the mean laterality index was 80.5 (S.D. = 20).

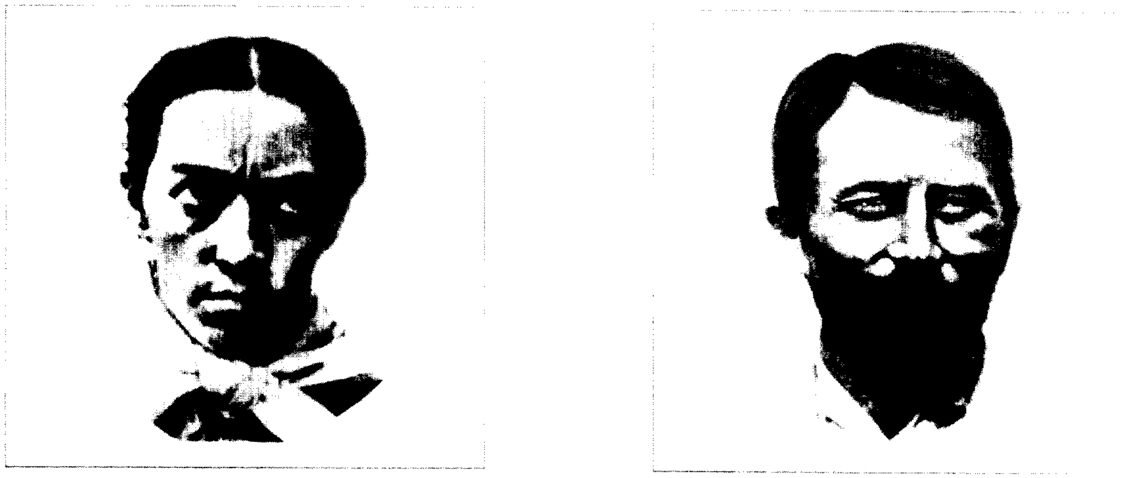

Fig. 1. Examples of the face images [61] used as stimuli. The image on the left was on average across subjects the most disliked face, the image on the right the most liked face. (By permission of Huber Verlag, Bern.)

Stimulus material and experimental procedure

To obtain affect-associated stimuli, we chose 32 photographs of psychiatric patients' faces from the Szondi-Test [61]. The Szondi face stimuli generate a wide range of emotions and therefore are particularly suited to elicit emotional decisions, i.e. both approach- and withdrawal-related judgments [47–49]. The black and white photographs were digitized and adjusted for size, brightness and contrast (Fig. 1). The subjects were comfortably seated in a sound, light and electrically shielded recording room where an intercom system provided the possibility to interact with the experimenter if needed.

Before the main experimental recording started, the subjects' average evoked potential map series were recorded during a control condition for visual input. The subjects passively observed emotionally neutral, visual checkerboard-reversal stimuli on a computer screen [26], a standard paradigm in neurological diagnostics.

After this control recording, the subjects were instructed to look at the center of the permanently visible frame on the screen and to observe passively the face images which were to appear in the frame at regular intervals. No other task was given so that cognitive-emotional and input-dependent sensorimotor tasks were excluded. In other words, the subjects had not been given constraints or requests on what they should or might think about while watching the face images.

The face stimuli were presented on light gray background on a computer screen 100 cm in front of the subject. Each face image covered an area of about 8 × 11 cm surrounded by the frame of 12.8 × 12.5 cm. The face stimuli were presented binocularly for 450 ms at intervals of 2000 ms. The presentation of the entire set of faces was repeated 20 times with pauses of 1 min in-between. For each repetition, the face sequence was newly randomized.

Data acquisition

Twenty-seven channel ERP map series were recorded while subjects observed the random sequences of face images. Electrodes were attached at scalp positions Fpz, Fp 1/2, Fz, F3/4, F7/8, FC1/2, Cz, C3/4, T7/8, CP1/2, Pz, P3/4, P7/8, PO3/4, Oz and O1/O2 of the international 10–10 system [1]. Fpz was the recording reference. Eye movements were recorded with an electrode at the outer left canthus vs Fpz. Impedances were kept below 5 Kohms. The data were amplified (0.3–70 Hz) and digitized (256 samples/sec) with a 31-channel BioLogic Ceegraph System. Two channels of the system recorded the stimulus codes through an optocoupling device.

Subjective rating

After recording, the subjects self-rated the face stimuli for affective appeal on a visual-analog scale. Each face image was printed on a separate 15 × 21 cm sheet with a vertical 10 cm line on the right margin as rating scale. The sheets were presented in random sequence. The upper end of the scale was labeled (in German) "sympathisch" ("liked face") and the lower "unsympathisch" ("disliked face") or vice versa and randomized within each subject to keep the subjects' attention engaged. Subjects indicated with a tick mark how much they liked/disliked the face.

Analysis and data reduction

Using the ratings, the 16 personally most liked and the 16 most disliked face images were determined for each subject. We also computed the mean rating of all face images for each subject so that subjects could be dichotomized into a group of "philanthropists" (the 9 subjects with highest mean ratings) and a group of "misanthropists" (the 9 subjects with lowest mean ratings). Table 1 shows the results of the post-recording rating of the face stimuli for their affective appeal. Means and standard deviations for each subject are separately reported for disliked and liked faces (affective evaluation categories) as well as for all face images (affective attitude). Misanthropists and philanthropists differed in their affective attitudes to the face images (t-test, $P < 0.0001$) which ranged between 1.68 and 4.59 for misanthropists ($M = 3.89 \pm 0.89$) and between 4.72 and 5.83 for philanthropists ($M = 5.34 \pm 0.36$), but did not differ in age (misanthropists: 29.7 ± 6.1 years, philanthropists: 29.2 ± 4.3) and mean laterality index (misanthropists: 79.1 ± 22.4, philanthropists: 81.2 ± 18.6). Dichotomising both the face images and the subjects, allowed us to include all the collected data in the analysis.

Data epochs containing eye and muscle artifacts were edited out in an off-line visual screening procedure of the raw data. The analysis covered the entire stimulus on-time, up to 450 msec after stimulus onset. For each subject, three average ERP

Table 1. Post-recording ratings of the face stimuli for affective appeal by the 18 subjects

	Affective Attitudes	Affective Evaluation Categories	
Rating:	All faces Mean (S.D.)	Disliked faces Mean (S.D.)	Liked faces Mean (S.D.)
Misanthropists ($n = 9$)	1.68 (1.46)	0.84 (0.27)	2.53 (1.67)
	3.66 (2.93)	1.31 (0.93)	6.01 (2.29)
	3.68 (2.46)	1.89 (0.58)	5.46 (2.31)
	3.95 (2.57)	1.84 (1.01)	6.05 (1.79)
	4.22 (3.10)	1.66 (1.91)	6.77 (1.51)
	4.31 (3.34)	1.36 (1.42)	7.27 (1.57)
	4.37 (3.25)	1.65 (1.49)	7.08 (1.98)
	4.54 (2.95)	2.16 (1.49)	6.91 (1.92)
	4.59 (3.20)	1.86 (1.62)	7.33 (1.59)
Mean (S.D.)	3.89 (0.89)	1.62 (0.39)	6.16 (1.50)
Philanthropists ($n = 9$)	4.72 (3.51)	1.62 (1.04)	7.82 (1.97)
	5.05 (2.80)	2.85 (1.92)	7.26 (1.47)
	5.13 (2.06)	3.36 (1.07)	6.90 (0.98)
	5.24 (2.50)	3.26 (1.63)	7.23 (1.36)
	5.26 (2.79)	2.89 (1.41)	7.63 (1.45)
	5.45 (3.35)	2.53 (1.74)	8.38 (1.43)
	5.64 (3.32)	2.82 (1.55)	8.46 (1.86)
	5.77 (2.27)	3.92 (1.52)	7.61 (1.04)
	5.83 (2.77)	3.46 (1.69)	8.21 (0.97)
Mean (S.D.)	5.34 (0.36)	2.97 (0.66)	7.72 (0.55)

Means and standard deviations for individually disliked and liked faces (affective evaluation categories) and for all face images (affective attitude) are tabulated. The values are in cm of the utilized visual-analog scale ranging from "disliked" = 0 to "liked" = 10.

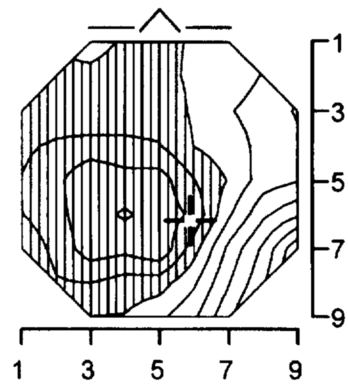

Fig. 2. Example of spatial feature extraction from a scalp field map. The head is seen from above, nose up, left ear left. The numbers identify the electrode positions of the international 10–10 system as rows (vertical, from anterior to posterior) and columns (horizontal, from left to right). Equipotential lines are linearly interpolated in steps of 1 microV; hatched areas are negative, white areas positive, relative to the average reference. The cross indicates the location of the electric gravity center (point of gravity of the absolute map voltages); the spatial configuration of a momentary field map is thus numerically assessed by two co-ordinate values.

map series were averaged, each across the 20 repetitions, using: (1) the 16 most "liked" stimuli, (2) the 16 most "disliked" stimuli and (3) all 32 stimuli. Spatial DC removal (so called average reference computation) and a digital 1.5–30 Hz temporal band pass filter was applied to all map series. Across subjects, the map series were averaged for disliked and liked faces (both, $n = 18$), and for philanthropists and misanthropists (both, $n = 9$). In addition, the map series for disliked and liked faces were averaged separately across philanthropists and across misanthropists (all 4 series, $n = 9$).

The topography of each ERP map landscape was reduced to the location of the point of gravity of the absolute voltages within the map. This value is a conservative estimate of the mean location of all active, electric, intracerebral sources in two-dimensional space, and from now on will be called "electric gravity center". (This electric gravity center is the mean location between the locations of the centroids of the positive and negative map areas which were used for the numerical assessment of map landscapes in previous studies, e.g. [9, 30, 66]). Thus, the spatial configuration of a momentary field configuration was numerically expressed by two spatial co-ordinate values (Fig. 2). The average location of the electric gravity center over all maps during the entire analysis time (0–450 ms post-stimulus) was computed for each ERP map series; these locations of the electric gravity centers were used for further analysis.

In a second approach, the described analyses were repeated using only the extreme cases, i.e. the six most misanthropic and the six most philanthropic subjects of all 18 (now to be called "extreme subjects").

Thirdly, in order to test for possible changes of observed effects over time due to the repetition of the stimuli, the stimulus sequence was divided into blocks. For differences between philanthropists and misanthropists, five equal blocks each consisting of 4 stimulus runs were used (4×32 stimuli per block). For differences between liked and disliked face images, two equal blocks were used (10×16 stimuli per block), because the reduced number of stimuli available after block partitioning limited the number of possible blocks. The analyses were done for all blocks.

Analysis and data reduction of the control recordings during the visual checkerboard-reversal stimulation was done using the same methodology. For all stimuli, the electric gravity center location was computed for each subject.

Comparisons and statistics

The difference between subjective affective categories was established in each subject as the difference of the electric gravity center location for liked stimuli and for disliked stimuli. From these differences, the mean difference over subjects was computed. As differences of electric gravity center location are two-dimensional vectors and include length and direction, statistics had to take into account how much the single subject's electric gravity center locations went into the direction of the corresponding mean electric gravity center location. Thus, the single subjects electric gravity center difference vectors were projected onto the mean difference vector and the lengths of these projections were compared between categories (liked vs disliked faces) using a standard paired t-test. In a first step, the electric gravity center differences between liked and disliked faces were tested over all subjects; the second step of analysis consisted of separate comparisons between categories in philanthropists and misanthropists.

The assessment of the effect of subjective affective attitude was similar to the comparison of subjective affective categories: The electric gravity center location of all philanthropists and all misanthropists were separately averaged and the mean difference vector between the two groups was established. Then, the single subjects' electric gravity centers were projected onto this difference vector and the positions of these projections on the mean vector were compared between attitudes (philanthropists vs misanthropists) using a unpaired t-test. The difference of attitude was evaluated on a first level by comparing the philanthropists and misanthropists electric gravity center locations obtained from the evoked potentials that included all stimuli; on a second level, the difference between philanthropists and misanthropists was separately tested for liked and disliked faces. Two-tailed P values are reported.

Results

Disliked vs liked faces: effect of subjective, affective evaluation categories

The comparison within subjects showed that the electric gravity center location for disliked faces was significantly different from that of liked faces at $P = 0.027$ (d.f. = 17); the former was located more to the right and more posterior. Figure 3A and Table 2A show that the difference on the left–right axis was roughly twice the size of the difference on the anterior–posterior axis.

Misanthropists vs philanthropists: effect of affective attitude

The comparison between subject groups showed that the electric gravity center location of the misanthropists was significantly different from that of the philanthropists at $P = 0.005$ (d.f. = 16). It was located more to the right and more posterior for misanthropists, but the left–right difference was much larger than the anterior–posterior difference (Fig. 3B and Table 2B).

Effect of subjective, affective evaluation categories and affective attitude

On the level of the affective evaluation categories, differences between liked and disliked faces were present in the group of philanthropists ($P = 0.038$, d.f. = 8) as well as in the group of misanthropists ($P = 0.081$, d.f. = 8). As illustrated in Fig. 3C and Table 2C, both groups showed a right-shift for disliked faces; the posteriorization was observed only in the group of misanthropists.

On the level of affective attitude, a significant shift of the electric gravity center in right-posterior direction (Fig. 3C and Table 2C) was present when misanthropists were compared to philanthropists using disliked faces ($P = 0.008$, d.f. = 16) as well as using liked faces ($P = 0.036$, d.f. = 16).

The mean gravity center locations as shown in Fig. 3 and Table 2 were all to the right from the midline. In fact, the mean location over all subjects (philanthropists and misanthropists) differed highly significantly from the midline ($P = 0.0004$, d.f. = 16).

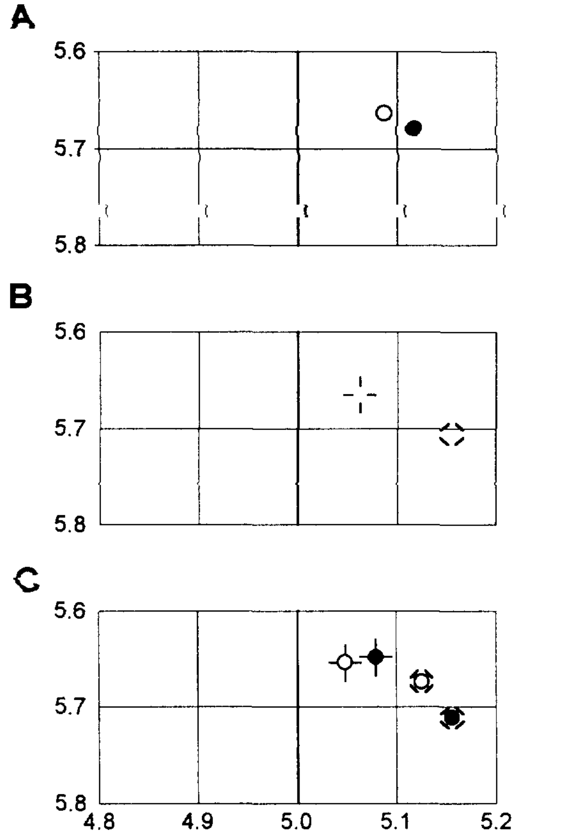

Fig. 3. Locations of the brain's electric gravity centers (means across subjects) during the spontaneous evaluation of the face images. (A) Effect of subjective, affective evaluation categories: liked and disliked face images. (B) Effect of affective attitudes: philanthropists and misanthropists. (C) Combinations of affective evaluation categories (liked and disliked face images) and affective attitudes (philanthropists and misanthropists). The frames (imagine a head seen from above, anterior is up) illustrate an area near the vertex, around the sagittal midline (heavy vertical line), extending from electrode position 5.6 to 5.8 on the anterior-posterior axis (vertical) and from position 4.8 to 5.2 on the left-right axis (horizontal), using the position numbering of Fig. 2. Open circles (mean location across subjects 5, 11, S.D. = 0.12; $P = 0.001$), liked faces; black dots = disliked faces; star symbols = philanthropists; square symbols = misanthropists.

The results of the control condition for visual input (the emotionally neutral, visual checkerboard-reversal stimuli) across subjects showed a significant displacement of the locations of the electric gravity centers to the right from the midline. Further, these locations evoked by the control stimuli showed no significant differences from the corresponding locations evoked by the mean of all liked and disliked face image stimuli.

Extreme subjects

When we repeated the analysis using only the extreme six misanthropic and six philanthropic subjects of all 18,

Table 2. Mean locations of the brain electric gravity centers; position numbering as in Fig. 2

A			Affective Evaluation Categories			
			Disliked faces	Liked faces	Difference	Vector[a]
		L-R	5.11 (0.10)	5.08 (0.11)	0.034	0.038**
		A-P	5.67 (0.13)	5.65 (0.13)	0.016	
B			Affective Attitudes			
			Misanthropists	Philanthropists	Difference	Vector[b]
		L–R	5.16 (0.07)	5.05 (0.10)	0.112	0.131***
		A–P	5.71 (0.14)	5.64 (0.14)	0.068	
C			Affective Attitudes			
			Misanthropists	Philanthropists	Difference	Vector[b]
Affective evaluation categories	Disliked	L–R	5.16 (0.09)	5.06 (0.07)	0.101	0.123***
		A–P	5.70 (0.12)	5.63 (0.14)	0.071	
	Liked	L–R	5.13 (0.11)	5.03 (0.10)	0.097	0.106**
		A–P	5.67(0.14)	5.63 (0.12)	0.043	
	Difference	L–R	0.036	0.032		
		A–P	0.031	0.002		
	Vector[a]		0.047*	0.032**		

(A) Effect of subjective, affective evaluation categories: liked and disliked face images. (B) Effect of affective attitudes: philanthropists and misanthropists. (C) Combinations of affective evaluation categories and affective attitudes. [a,b] Two-dimensional vector assessing the differences of the electric gravity center location between [a] affective evaluation categories and between [b] affective attitudes. L–R: Left–Right axis, A–P: Anterior–Posterior axis; *** $P < 0.01$, ** $P < 0.05$, * $P < 0.1$.

the differences between the electric gravity centers became larger than with the dichotomization, as might be expected. Again, a significant shift of the electric gravity center in the right-posterior direction was observed when extreme misanthropists were compared to extreme philanthropists (the length of two-dimensional vector differentiating the two subject groups increased from 0.112 to 0.163; the latter vector was greater than 0 at $P = 0.007$). On the left–right axis, the mean location of the extreme misanthropists was 5.17, whereas that of the extreme philanthropists was 5.01.

Changes due to stimulus repetition

A first analysis of variance was performed on the vectors differentiating between misanthropists and philanthropists with "blocks" as within-subject factor and "affective attitude" as between-subject factor. The 5×2 ANOVA revealed a significant main effect for affective attitude ($F(1,14) = 9.45$; $P = 0.003$). Both the block main effect as well as the interaction block × affective attitude were not significant ($P > 0.1$). *Post-hoc t*-tests revealed significant differences between misanthropists and philanthropists in all 5 blocks (the vector differentiating the two subject groups was always significantly greater than 0: block 1: 0.116, $P = 0.04$; 2: 0.134, $P = 0.005$; 3: 0.163, $P < 0.000\ 1$; 4: 0.168, $P = 0.004$; 5: 0.107, $P = 0.04$); therefore, the electric gravity center was located more to the right and more posterior for misanthropists compared to philanthropists in all five experimental periods.

A second analysis of variance was performed on the vectors differentiating between disliked and liked faces with "blocks" and "affective evaluation category" as within-subject factors. The 2×2 ANOVA showed a significant main effect for affective evaluation category, $F(1,17) = 7.03$, $P = 0.017$. Again the main effect for blocks and the interaction block × affective evaluation category did not reach significance ($P > 0.1$). *Post-hoc t*-tests showed that the electric gravity center was located more to the right and more posterior for disliked compared to liked faces in both experimental periods (the vector differentiating the two category groups tended to be greater than 0 in both blocks: block 1: 0.036, $P = 0.1$; 2: 0.042, $P = 0.063$). Repetition effects interacting with face perception and emotional processing could, therefore, be excluded.

Discussion

In our study, the mean location of brain electric activity evoked by the presentation of face images was consistently related to the subjects' later emotional evaluation of the stimuli. To our knowledge, all previous work on brain electric activity related to emotions and face viewing was based on the comparison of amplitudes and peak latencies of the brain electric field at specific electrode sites. This type of analysis allows no conclusive interpretations in terms of location of active generators because the source is located under the scalp location of maximal amplitude only if it is oriented perpendicular to the scalp surface [9]. The assumption of solely perpendicular orientation however is contradicted by systematic ERP studies on lateralized visual stimulation [10, 26] and by the possibility to perform MEG measurements where only tangentially oriented sources can be detected. The electric gravity center employed in the current study is the most conservative estimate of the mean location of all brain electric activity perpendicularly projected onto the two-dimensional scalp surface; changes of its location in a particular direction can thus directly and unambiguously be interpreted as shifts of neural activity in that direction. Using this conclusive assessment of brain electric source configuration, we found representations both of the specific affective evaluation of single face images and of the subject's general affective attitude.

The chosen assessment of brain activity localization by means of the electric gravity center is supported by the commonly accepted notion that emotional processes are likely to be implemented by the activity of widely distributed brain systems. In our results, this activity most probably consists of activity in both hemispheres, because the absolute differences between the electric gravity centers of subject groups and stimulus categories were relatively small (but very reliable across subjects or cases) and therefore, the respective, actively participating neural elements presumably are in partially overlapping brain areas. However, the results yielded the clear conclusion that it is not the same neuronal population that is active in "disliked vs liked", or in "misanthropists vs philanthropists" conditions. In other words, it is not just more or less activity of the same neuronal population, but it is the activities of at least partially different populations. Further, all electric gravity centers were located right from the midline. Hence, even though the analysis method does not yield information on the extension of the involved brain areas, there is no indication that the opposing evaluations might have been generated exclusively by right or left hemispheric mechanisms.

However, the right-displacement of the mean electric activity in our results cannot serve as direct support for a suspected right-hemisphere preponderance in the processing of face information or of emotion information, since the averaged map series of the control condition that applied emotionally neutral, visual checkerboard-reversal stimuli produced comparable right-displacements. This general right lateralization might well be the result of the visual modality used for stimulation. In fact, when auditory input was used to induce emotions (verbal suggestions during hypnosis: [31]), the EEG model sources significantly differentiating between positive (joy) and negative emotions (sadness, fear, anger) were all located in the left hemisphere; in this latter study, significant differences between source locations occurred in the β EEG frequency band and as in the present results, positive emotion associated activity was located more to the left than the negative emotions-associated activity.

On the level of the affective category, i.e. on the subject's personal liking or disliking of individual face images, significant brain electric correlates of the subjects' different affective preferences were present in the data: The center of gravity of brain electric activity showed a different location during negative compared to positive emotional evaluation; a change to the right constituted the main component of this difference. Apparently, and as expected from large parts of the neuropsychological literature [58], at least partially different neural populations with a left or right preponderance were active when liked and disliked faces were seen.

Only a few ERP studies used face stimuli to distinguish brain activity related to positive and negative emotional evaluation and, to our knowledge, none of these studies used adequate source model estimations. P300-differences were reported between negative and positive facial expression [32]. Larger ERP amplitudes at right hemisphere electrodes were found for emotionally negative stimuli (faces deformed by dermatological diseases) compared to neutral stimuli (normal faces), but significant differences between stimulus condition were detectable only after 510 msec [53]. Using an oddball paradigm, no P300 differences between positive and negative faces were observed, but only a modulation of the P300 effect at right-centroparietal electrodes when emotional vs non-emotional evaluation was required [34].

On the level of general, more positive or more negative affective attitude of the subject towards all face images, we found a neurophysiological basis of the individual differences. These differences in affective attitude were proposed to be intrinsic features of personality and temperament [17, 33, 56, 62, 67], i.e. as dependent not on the stimulus but on the state of the perceiver. Indeed, across all more positive or more negative expressions of the face images, our subjects showed remarkable differences in their general affective attitudes towards the stimuli as shown in Table 1, thus suggesting that the interaction between perceiver and stimulus and not the configuration of the stimulus *per se* was responsible for the observed effects. In our results, the active neural populations had significantly different localizations in subjects who generally showed positive affective attitude for the presented faces compared to those who generally showed negative affective attitude. In those subjects with generally negative affective attitude, the estimated mean source of the brain electric field was shifted to the right, thus paralleling the result of the specific affective evaluation of single faces. We note that the differences between subject groups and between affective evaluation categories were consistent over sub-epochs during the data collection. Moreover, the shift to the right for misanthropists and to the left for philanthropists was accentuated for both groups when considering only the extreme subjects. Taken together, the results support PET (positron-emission tomography) findings of different cerebral blood flow during different mood states [21] and are in line with neuropsychological and neurological studies where disturbances of the processing of negative emotions were associated with right-hemispheric impairments and where positive emotions were disturbed more by left-hemispheric impairments [4, 13, 19, 20, 40, 52, 57]. It also confirms claims in earlier work on emotions and EEG and ERPs, although conclusive evidence for changes of location of active generators cannot be drawn from these studies.

Some groups proposed that differences in temperament, affective reactivity and mood can be predicted by individual differences of asymmetry at frontal [17, 62, 64, 67] or more distributed [28] electrode sites, thus advancing a biological substrate of affective style; in particular, positive emotions and approach-related behaviour was claimed to be associated with EEG effects on the left side, negative emotions and withdrawal-related behaviour with changes at the right side. Greater P300 amplitudes in the odd-ball paradigm, differentiated strongly introverted from strongly extroverted subjects, suggesting a higher cortical arousal level for the introverts [68]. Individual hemispheric differences of EEG α power were reported as stable, task-independent and related to individual differences in perceptual asymmetry assessed by visual half-field stimulation [22]. In a pessimistic mood, subjects showed differently localized N400 and P300 effects than when in an optimistic mood [15].

In agreement with our results, affective decisions, i.e. measures of preference, and cognitive decisions, i.e. measures of accuracy were proposed to be differentially processed by the two hemispheres [49]; for affective decisions, both hemispheres reacted effectively to faces; presenting them to the left hemisphere, they were more often liked; presenting them to the right hemisphere, they were more often disliked. This demonstrated a cerebral asymmetry, but not a hemispheric dominance in making emotional preference judgments [47, 48, 50]. However, this was only the case when presenting the stimuli below the level of conscious perception. On the other hand, accuracy of cognitive decision displayed the well-known pattern of right hemisphere advantage for the recognition of faces, suggesting that "at later stages of processing... affective decisions may be overridden by cognitive decisions" ([49], p. 365).

In our experiment, lateral differences in brain activity were found when the subjects merely looked passively at the faces for 450 ms while they were not aware of the emotion-related purpose of the study and were not required to perform any specific task or to make any conscious, affective decision. Event-related brain electric field maps thus seem to be able to elucidate changes of the spatial organization of brain activity that occur covertly and spontaneously. Such changes might be distorted or obscured when a task is imposed. More generally, the results of our study suggest that both complementary and converging results are available from different methods such as electrophysiology, neuropsychology and more recently also positron-emission tomography (PET), and may thus advance our knowledge of the spatial organization of emotions in the human brain.

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References

1. American Electroencephalographic Society Guidelines for Standard Electrode Position Nomenclature. *Journal of Clinical Neurophysiology*, 1991, **8**, 200–202.
2. Benowitz, L. I., Bear, D. M., Rosenthal, R., Mesulam, M. M., Zaidel, E. and Sperry, R. W., Hemispheric specialization in non-verbal communication. *Cortex*, 1983, **19**, 5–11.
3. Borod, J. C., Interhemispheric and intrahemispheric control of emotion: A focus on unilateral brain damage. *Journal of Consulting and Clinical Psychology*, 1992, **60**, 339–348.
4. Borod, J. C., Koff, E., Perlman Lorch, M. and Nicholas, M., The expression and perception of facial emotion in brain-damaged patients. *Neuropsychologia*, 1986, **24**, 169–180.
5. Borod, J. C., Koff, E. and White, B., Facial asymmetry in posed and spontaneous expressions of emotion. *Brain and Cognition*, 1983, **2**, 165–175.
6. Bowers, D., Bauer, R. M., Coslett, H. B. and Heilman, K. M., Processing of faces by patients with unilateral hemisphere lesions. *Brain and Cognition*, 1985, **4**, 258–272
7. Bowers, D., Blonder, L. X., Feinberg, T. and Heilman, K. M., Differential impact of right and left hemisphere lesions on facial emotion and object imagery. *Brain*, 1991, **114**, 2593–2609.
8. Brandeis, D. and Lehmann, D., ERP mapping: A tool for assessing language disorders? In *Cognitive Electrophysiology*, eds H. J. Heinze, T. F. Münte and G. R. Mangun. Birkhäuser, Boston, 1994, pp. 242–250.
9. Brandeis, D., Lehmann, D., Michel, C. M. and Mingrone, W., Mapping event-related brain potential microstates to sentence endings. *Brain Topography*, 1995, **8**, 145–159.
10. Brigell, M., Rubboli, G. and Celesia, G. G., Identification of the hemisphere activated by hemifield visual stimulation using a single equivalent dipole model. *Electroencephalography & Clinical Neurophysiology*, 1993, **87**, 291–299.
11. Buck, R. and Duffy, R. J. Non-verbal communication of affect in brain damaged subjects. *Cortex*, 1980, **16**, 351–362.
12. Carretie, L. and Iglesias, J., An ERP study on the specificity of facial expression processing. *Inter-*

national Journal of Psychophysiology, 1995, **19**, 183–192.

13. Chavoix, C., Desi, M. and de Bonis, M., Relationship between mood state and information processing of negative versus positive emotional stimuli in brain-damaged patients. *Psychopathology*, 1985, **20**, 34–41.
14. Christen, L., Landis, T. and Regard, M., Left hemispheric functional compensation in prosopagnosia? A tachistoscopic study with unilaterally lesioned patients. *Human Neurobiology*, 1985, **4**, 9–14.
15. Chung, G., Tucker, D. M., West, P., Potts, G. F., Liotti, M., Luu, P. and Hartry, A. L., Emotional expectancy: Brain electrical activity associated with an emotional bias in interpreting life events. *Psychophysiology*, 1996, **33**, 218–233.
16. Cicone, M., Wapner, W. and Gardner, H., Sensitivity to emotional expressions and situations in organic patients. *Cortex*, 1980, **16**, 145–158.
17. Davidson, R. J., Anterior cerebral asymmetry and the nature of emotion. *Brain and Cognition*, 1992, **20**, 125–151.
18. Etcoff, N. L., Perceptual and conceptual organisation of facial emotions: Hemispheric differences. *Brain and Cognition*, 1984, **3**, 385–412.
19. Flor-Henry, P., On certain aspects of the localization of the cerebral systems regulating and determining emotion. *Biological Psychiatry*, 1979, **14**, 677–698.
20. Gainotti, G., Emotional behavior and hemispheric side of the lesion. *Cortex*, 1972, **8**, 41–55.
21. George, M. S., Ketter, T. A., Parekh, P. I., Horwitz, B., Herscovitch, P. and Post, R. M., Brain activity during transient sadness and happiness in healthy women. *American Journal of Psychiatry*, 1995, **152**, 341–351.
22. Green, J., Morris, R. D., Epstein, C. M., West, P. D. and Engler, H. F., Assessment of the relationship of cerebral hemisphere arousal asymmetry to perceptual asymmetry. *Brain and Cognition*, 1992, **20**, 264–279.
23. Heilman, K. M. and Satz, P. *Neuropsychology of Human Emotion*. Guilford, New York, 1983.
24. Heine, A., Roth, N., Koenig, T. and Knye, M., Effects of auditory priming and word frequency upon ERP and task performance during word recognition. In *New Developments in Event-Related Potentials*, eds H. J. Heinze, T. F. Münte, and G. R. Mangun. Birkhäuser, Boston, 1994, pp. 61–70.
25. Hirschman, R. S. and Safer, M. A., Hemisphere differences in perceiving positive and negative emotions. *Cortex*, 1982. **18**, 569–580.
26. Hoffman, K., Skrandies, W., Lehmann, D., Witte, H. and Strobel, J., Instantaneous frequency maps, dipole models and potential distributions of pattern reversal-evoked potential fields for correct recognition of stimulated hemiretinae. *Electroencephalography & Clinical Neurophysiology*, 1996, **100**, 569–578.
27. Johnston, V. S., Miller, D. R. and Burleson, M., H. Multiple P300s to emotional stimuli and their theoretical significance. *Psychophysiology*, 1986, **23**, 684–694.
28. Jones, N. A. and Fox, N. A. Electroencephalogram asymmetry during emotionally evocative films and its relation to positive and negative affectivity. *Brain and Cognition*, 1992, **20**, 280–299.
29. Kestenbaum, R. and Nelson, C. A., Neural and behavioral correlates of emotion recognition in children and adults. *Journal of Experimental Child Psychology*, 1992, **54**, 1–18.
30. Koenig, T. and Lehmann, D., Microstates in language-related brain potential maps show noun-verb differences. *Brain and Language*, 1996, **53**, 169–182.
31. Koenig, T., Revenstorf, D., Kochi, K., Kondakor, I., Frei, E. and Lehmann, D., Hypnotic induction of different emotional states alters the location of single dipole models in the frequency domain. *Psychiatry Research Neuroimaging*, 1997, **68**, 169.
32. Lang, S. F., Nelson, C. A. and Collins, P. F., Event-related potentials to emotional and neutral stimuli. *Journal of Clinical and Experimental Neuropsychology*, 1990, **12**, 946–958.
33. Larsen, R. J. and Ketelaar, T., Personality and susceptibility to positive and negative emotional states. *Journal of Personality and Social Psychology*, 1991, **61**, 132–140.
34. Laurian, S., Bader, M., Lanares, J. and Oros, L., Topography of event-related potentials elicited by visual emotional stimuli. *International Journal of Psychophysiology*, 1991, **10**, 231–238.
35. Lehmann, D., EEG assessment of brain activity: Spatial aspects, segmentation and imaging. *International Journal of Psychophysiology*,1984, **1**, 267–276.
36. Lehmann, D., Principles of spatial analysis. In *Methods of Analysis of Brain Electrical and Magnetic Signals. Handbook of electroencephalography and Clinical Neurophysiology, revised series*, Vol. 1, eds A. S. Gevins and A. Remond. Elsevier, Amsterdam, 1987, pp. 309–354.
37. Lehmann, D., Brain electric microstates and cognition: The atoms of thought. In *Machinery of the Mind*, ed. E. R. John. Birkhäuser, Boston, 1990, pp. 209–224.
38. Lehmann, D. and Skrandies, W., Spatial analysis of evoked potentials in man. A review. *Progress in Neurobiology*, 1984, **23**, 227–250.
39. Ley, R. G. and Bryden, M. P., Hemispheric differences in processing emotions and faces. *Brain and Language*, 1979, **7**, 127–138.
40. Mandal, M. K., Mohanty, A. and Pandey, R., Emotion-specific processing deficit in focal brain-damaged patients. *International Journal of Neuroscience*, 1996, **84**, 87–95.
41. McLaren, J. and Bryson, S. E., Hemispheric asymmetries in the perception of emotional and neutral faces. *Cortex*, 1987, **23**, 645–654.
42. Michel, C. M., Henggeler, B., and Lehmann, D. 42-channel potential map series to visual contrast and stereo stimuli: Perceptual and cognitive event-related segments. *International Journal of Psychophysiology*, 1992, **12**, 133–145.
43. Moreno, C. R., Borod, J. C., Welkowitz, J. and Alpert, M. Lateralization for the expression and perception of facial emotion as a function of age. *Neuropsychologia*, 1990, **28**, 199–209.
44. Moscovitch, M. and Olds, J., Asymmetries in spon-

taneous facial expression and their possible relation to hemispheric specialization. *Neuropsychologia*, 1982, **20,** 71–81.
45. Natale, M., Gur, R. E. and Gur, R. C., Hemispheric asymmetries in processing emotional expressions. *Neuropsychologia*, 1983, **21,** 555–565.
46. Oldfield, R. C., The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 1971, **9,** 97–113.
47. Regard, M., *The Perception and Control of Emotion: Hemispheric Differences and the Role of the Frontal Lobes.* Habilitationsschrift, University of Zurich, 1991.
48. Regard, M., Cajöri, M. and Landis, T., Opposite hemispheric superiorities for sympathy and antipathy: A tachistoscopic study with the Szondi faces. *Journal of Clinical and Experimental Neuropsychology*, 1987, **9,** 21.
49. Regard, M. and Landis, T., Affective and cognitive decisions on faces in normals. In *Aspects of Face Processing*, eds H. D. Ellis, M. A. Jeeves, F. Newcombe and A. Young. NATO ASI Series, Martinus Nijhoff, Dordrecht, 1986 pp. 363–369.
50. Regard, M. and Landis, T., Beauty may differ in each half of the eye of the beholder. In *Beauty and the Brain: Biological Aspects of Aesthetics*, eds I. Rentschler, B. Herzberger and D. Epstein. Birkhäuser, Basel, 1988, pp. 243–257.
51. Reuter-Lorenz, P. and Davidson, R. J., Differential contributions of the two cerebral hemispheres to the perception of happy and sad faces. *Neuropsychologia*, 1981, **19,** 609–613.
52. Robinson, R. G., Kubos, K. L., Starr, L. B., Rao, K. and Price, T. R., Mood disorders in stroke patients. Importance of location of lesion. *Brain*, 1984, **107,** 81–93.
53. Roschmann, R. and Wittling, W., Topographic brain mapping of emotion-related hemisphere asymmetries. *International Journal of Neuroscience*, 1992, **63,** 5–16.
54. Ross, E. D., Right hemisphere's role in language, affective behavior and emotion. *Trends in Neuroscience*, 1981, **7,** 342–346.
55. Ross, E. D. and Mesulam, M. M., Dominant language functions in the right hemisphere? *Archives of Neurology*, 1979, **36,** 144–148.
56. Rothbart M. K. and Derryberry, D., Development of individual differences in temperament. In *Advances in Developmental Psychology*, Vol. 1, eds M. E. Lamb and A. L. Brown. Hillsdale, NJ, Erlbaum, 1981, pp. 37–86.
57. Sackeim, H. A., Greenberg, M., Weiman, A., Gur, R. C., Hungerbuhler, J. P and Geschwind, N., Hemispheric asymmetry in the expression of positive and negative emotions: Neurological evidence. *Archives of Neurology*, 1982, **39,** 210–218.
58. Silberman, E. K. and Weingartner, H., Hemispheric lateralization of functions related to emotion. *Brain and Cognition*, 1986, **5,** 322–353.
59. Stone, V. E., Nisenson, L., Eliassen, J. C. and Gazzaniga, M. S., Left hemisphere representations of emotional facial expressions. *Neuropsychologia*, 1996, **34,** 23–29.
60. Strauss, E. and Moscovitch, M., Perception of facial expressions. *Brain and Language*, 1981, **13,** 308–332.
61. Szondi, L., *Lehrbuch der experimentellen Triebdiagnostik*. Huber, Bem, 1960.
62. Tomarken, A. J., Davidson, R. J. and Henriques, J. B., Resting frontal brain asymmetry predicts affective responses to films. *Journal of Personality and Social Psychology*, 1990, **59,** 791–801.
63. Tucker, D. M., Lateral brain function, emotion, and conceptualization. *Psychological Bulletin*, 1981, **89,** 19–46.
64. Tucker, D. M., Stenslie, C. E., Roth, R. S. and Shearer, S. L., Right frontal lobe activation and right hemisphere performance. *Archives of General Psychiatry*, 1981, **38,** 169–174.
65. Vanderploeg, R. D., Brown, W. S. and Marsh, J. T., Judgments of emotion in words and faces: ERP correlates. *International Journal of Psychophysiology*, 1987, **5,** 193–205.
66. Wackermann, J., Lehmann, D., Michel, C. M., and Strik, W. K., Adaptive segmentation of spontaneous EEG map series into spatially defined microstates. *International Journal of Psychophysiology*, 1993, **14,** 269–283.
67. Wheeler, R. E., Davidson, R. J. and Tomarken, A. J., Frontal brain asymmetry and emotional reactivity: A biological substrate of affective style. *Psychophysiology*, 1993, **30,** 82–89.
68. Wilson, M. A. and Languis, M. L., A topographic study of differences in the P300 between introverts and extraverts. *Brain Topography*, 1990, **2,** 269–274.