Emotional Cognition without Awareness after Unilateral Temporal Lobectomy in Humans

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To investigate the function of the amygdala in human emotional cognition, we investigated the electrodermal activity (EDA) in response to masked (unseen) visual stimuli. Six epileptic subjects were investigated after unilateral temporal lobectomy. Emotionally valenced photographic slides (10 negative, 10 neutral) from the International Affective Picture System were presented to their unilateral visual fields under either subliminal or supraliminal conditions. An interaction between hemispheres and emotional valences was found only under the subliminal conditions; greater EDA responses to negative stimuli compared with neutral ones were observed when stimuli were presented to the intact hemispheres. The findings suggest that nonconscious emotional processing is reflected in EDA in a different manner from conscious emotional processing. Medial temporal structures, including the amygdala, thus appear to play a critical role in the neural substrates for this automatic processing.

Key words: amygdala; unilateral temporal lobectomy; emotion; emotional visual stimuli; backward masking; awareness; EDA

Animal studies have revealed the crucial role of the amygdala in processing emotionally significant stimuli (Weiskrantz, 1956; Geschwind, 1965; Nishijo et al., 1988; Gaffan et al., 1989; Brothers et al., 1990; LeDoux et al., 1990; Nakamura et al., 1992; Goldstein et al., 1996). Lesion and functional imaging studies in human have shown the critical role of the amygdala in recognizing emotional facial expressions, notably negative ones (Adolph et al., 1994, 1995, 1999; Young et al., 1995; Calder et al., 1996; Morris et al., 1996; Breiter et al., 1996; Broks et al., 1998; Hamann and Adolph, 1999).

Recently, functional imaging studies of normal subjects have demonstrated the involvement of the amygdala in subliminal processing of visual stimuli, i.e., processing below the level of awareness (Morris et al., 1998; Whalen et al., 1998). Activation of the amygdala was observed during the presentation of stimuli with high emotional significance such as an angry face, even in the absence of explicit knowledge in the subjects that such stimuli were presented. The results suggest that emotional valence is processed at the subconscious level and that the amygdala plays a crucial role in this process.

Electrodermal activity (EDA) is a measure of autonomic nervous system (ANS) activity frequently used to index complex CNS processes such as emotion (Boucsein, 1992). More specifically, EDA is often used as a monitor of subconscious neural processing of psychologically significant stimuli, as in studies demonstrating that prosopagnosics display normal EDA responses to familiar faces which they cannot identify (Bauer, 1984; Tranel and Damasio, 1988). Recent cerebral stimulation and neuroimaging studies have shown an association between amygdala activation and EDA (Mangina et al., 1996; Furmark et al., 1997). It has also been reported that amygdala lesions in humans caused an impairment in EDA, especially during aversive conditioning and reward-related feedback (Bechara et al., 1995, 1999; LaBar et al., 1995). Thus, EDA could be regarded as an appropriate method for investigating amygdala function in emotional processing below the level of awareness.

In the present study, using patients after unilateral temporal lobectomy as subjects, EDA was measured during visual presentation of emotionally valenced stimuli both under either conditions of subliminal or supraliminal presentation. Backward masking was applied to realize the subconscious presentation of visual stimuli (Esteves and Öhman, 1993). Visual stimuli were presented to each unilateral visual field (i.e., input to the hemisphere contralateral to the visual field of stimuli presentation), and EDA responses were compared within a subject regarding the stimulated side of the hemisphere (intact side vs lesion side) and emotional valence of the presented stimuli. The present study is, to our knowledge, the first lesion study conducted in human subjects using a subliminal emotional cognition paradigm.

MATERIALS AND METHODS

Subjects

Initially, nine subjects who had previously undergone unilateral temporal lobectomies for pharmacologically intractable seizures were investigated. One of these initial subjects was excluded because of a visual fields deficit (see Materials and Methods), and two were excluded because of poor control of seizure and unstable mental state during measurement. Consequently, six patients were selected for data analysis (two males and four females, ages 22–53). They were all right-handed. These patients had

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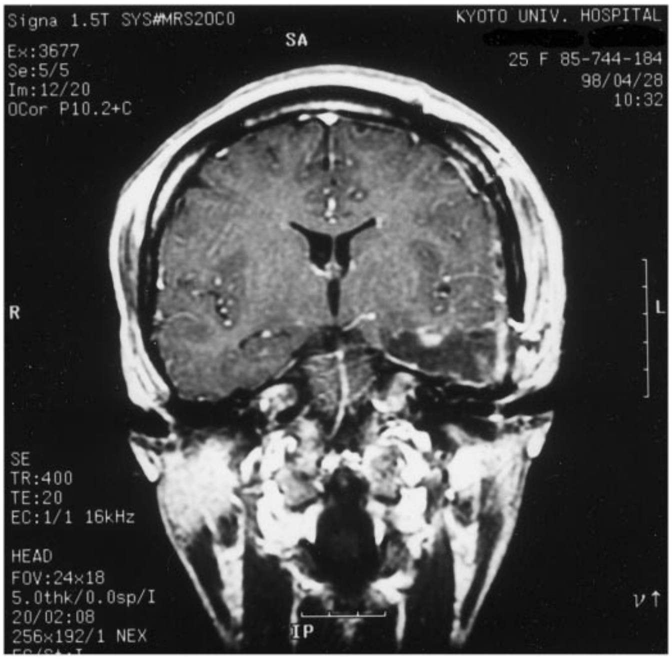

Figure 1. An example of T1-weighted MRI scan in one of the patients after unilateral temporal lobectomy.

undergone standard anterior temporal lobectomy; four patients underwent left temporal lobectomy, and two underwent right temporal lobectomy. The extent of the temporal resection was 4–5 cm posterior to the temporal pole. The superior temporal gyrus was preserved except for in one patient who underwent additional partial superior temporal gyrectomy. Postsurgical magnetic resonance imagings (MRIs) were obtained in all patients to reexamine the extent of the resection, which confirmed that substantial portions of amygdala was removed in them. Damages to hippocampal formation and surrounding cortices were also found. An example of MRI in one of the patients is shown (Fig. 1). All of these six patients were being maintained on one or more antiepileptic medications and were seizure-free after surgery. The mean score of the Weschler Adult Intelligence Scale-Revised after surgery was 74.4 (61–88). All of the subjects gave written informed consent to participate in this study after the procedure was fully explained.

Stimulus materials

A set of negative (10 items) and neutral (10 items) slides were selected from the International Affective Picture System (IAPS) (Lang et al., 1995). Negative slides included themes such as frightening animals, human violence, mutilated bodies, etc. Neutral slides consisted of inanimate objects, people with neutral facial expressions, natural landscapes, etc. All subjects were naive to these picture stimuli. A mask of mosaic patterns made of the fragments of these slides was applied in a backward masking procedure.

Apparatus and response measurement

Picture stimuli were presented on a flat type CRT monitor (Sony GDM-F400). The presentation of stimuli was controlled using an NEC personal computer with SuperLab (Cedrus) software. The time lag of presentation in this system was estimated to be within 8 msec. The monitor was located ~57.3 cm in front of the subject, and the size of visual stimuli on the monitor corresponded to 5.0 (horizontal) × 8.0° (vertical) of visual angle. To examine emotional processing in the lesion side and the intact side hemisphere separately, EDA responses were compared within a subject with regard to the visual field to which the stimuli were presented. We used a within-subject approach to avoid a problem associated with large between-subject variability of EDA, which is the major limitation of this measurement technique (Yokota et al., 1991; Claus and Schondorf, 1999). Sympathetic skin response (SSR) was used as the measure of EDA (Claus and Schondorf, 1999). SSR was recorded bilaterally with Ag/AgCl electrodes attached to the hypothenar eminences of both hands. Eye movements were also monitored using EOG to confirm that stimuli had been presented only to unilateral visual fields. Physiological signals were digitized at 200 Hz and recorded for off-line analyses using an NEC digital encephalograph (SYNAFIT 5000). The lower frequency limit was 0.15 Hz, and the upper limit was 15 Hz.

Procedure

The subjects, with arm electrodes attached, were seated in an armchair in a dark, quiet room at normal ambient temperatures and instructed to look at the monitor situated in front of them.

Assessment session

Visual field deficit. An assessment of possible visual field deficit because of temporal lobectomy was conducted using the same monitor. Subjects were instructed to look at a fixation point in the center of the monitor, and a target stimulus (2 × 2° of visual angle) was presented for 200 msec in one of the corners. Then subjects were asked to point to the place where the target appeared.

Baseline of SSR. SSR was recorded for 5 min in the resting condition. This measure was regarded as the baseline activity for each subject.

The upper limit of SOA for subliminal presentation. Esteves and Öhman (1993) demonstrated that whether the stimulus onset asynchrony (SOA; i.e., the interval between the onset of the target and the mask) was sufficiently brief, the subjects were not aware of the target stimuli. To assess the upper limit of SOA for subliminal presentation in each subject, five stimuli were presented, and the subject was instructed to describe what they had seen (these stimuli were not used in the following trial session). The stimuli were presented at random to each unilateral visual field using backward masking. The duration of slide presentation was fixed at 30 msec in all subjects and that of mask presentation was 100 msec. Starting from 60 msec, SOA was prolonged by 10 msec increments. For each length of SOA, five stimuli were presented. If the subject was aware of at least one of the five stimuli, the corresponding SOA was regarded as the lower limit of conscious recognition for that subject, and an interval 10 msec shorter than that limit was used in the trial session.

Trial session

Forty successive trials of slide presentation were performed (10 negative, 10 neutral × left, right visual fields) under subliminal conditions. After a short break, another 40 trials under supraliminal conditions were performed. The order of slide presentation was varied systematically across the subjects. For subliminal conditions, the duration of presentation was fixed at 30 msec in all subjects. SOA was adjusted for each subject, and the mask was presented after that interval. For supraliminal conditions, the presentation period was fixed at 200 msec in all subjects and there was no masking. The interval between each slide presentation was 30 sec, and during that period the monitor was blacked out. The subjects were instructed to relax between each of these periods.

A trial consisted of the following phases: (1) A white screen appeared on the monitor and the target (black, cross mark) was presented at the center. (2) The cue sound was delivered 1 sec before the slide presentation. The subject was instructed to look at the target after hearing the cue sound. (3) A photographic slide was presented either to the left or the right side of the target (3° of visual angle from the centerline). (4) SSR was recorded for 10 sec after the presentation of a slide. (5) After the recordings, two questions ("Negative/Neutral?", "What?") were presented on the monitor and subjects were asked to describe how they felt and what they saw during slide presentation phase. This verbal assessment provided a measure of subjective emotional judgement and declarative knowledge of the slide contents.

Data analysis

The first five trials were not included in the data analysis to minimize the effect of nonrelaxation. Any SSR deflection with a peak latency <1 sec or >8 sec was rejected as an artifact. Magnitudes of SSR were used as the measures for subsequent analyses. SSR responses from both left and right hands were scored, and the scorer was blind to the types of affective stimuli and to which hemisphere the stimuli were inputted.

Under subliminal conditions, 2.08% of the stimuli were correctly identified. These data were excluded from subsequent analysis. As to affective judgment, three subjects judged all the slides as "Neutral" and one subject judged all as "Negative" under subliminal conditions, and two subjects judged all as Neutral under supraliminal conditions. Because of small subject size and the relatively large number of these inappropriate responses, we did not include the data of subjective affective judgement in the following analysis. The mean SSR magnitudes were calculated for each of the six subjects in eight conditions (arm × hemisphere × emotional content), rejecting any data larger than mean + 2 SD as artifacts. Subsequently, 93% of the total data were used, and all the data were log-transformed.

Statistical analysis

Under both subliminal and supraliminal conditions, the SSR data were analyzed using a 2 × 2 × 2 repeated-measures ANOVA performed on the mean magnitude in each subject with arm (lesion side/intact side), hemisphere (lesion side/intact side), and emotional content (negative/neutral) as within-subject factors. Results were considered as significant whether the p value was <0.05.

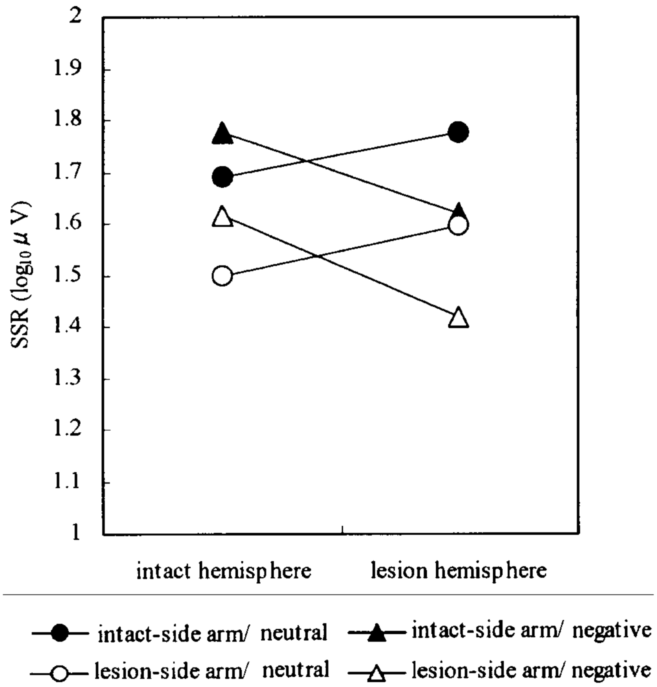

Figure 2. SSR magnitude under subliminal conditions. Mean of SSR magnitudes ($\log_{10}$ μV) in six subjects in the case of intact hemisphere stimulation (*left side*) or in the case of lesion hemisphere stimulation (*right side*), recorded from intact-side arm (*black marker*) or lesion-side arm (*white marker*), in response to negative stimuli (*circle marker*) or neutral stimuli (*triangle marker*).

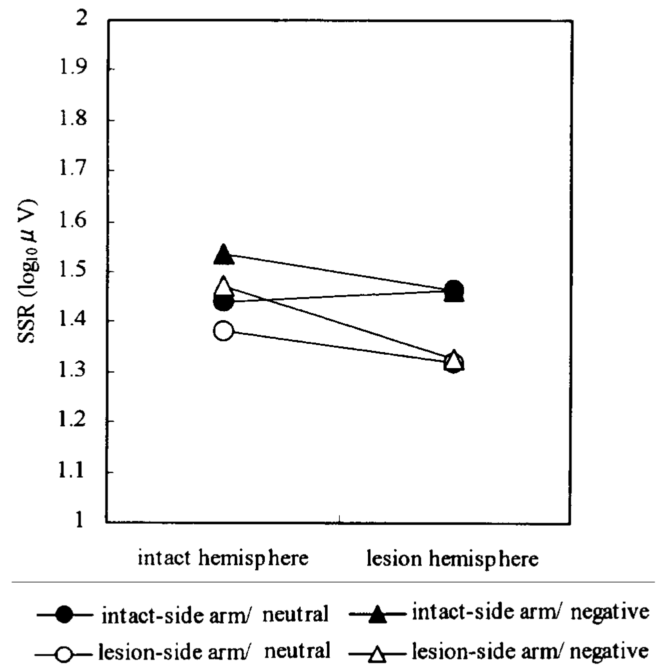

Figure 3. SSR magnitude under supraliminal conditions. Mean of SSR magnitudes ($\log_{10}$ μV) in six subjects in the case of intact hemisphere stimulation (*left side*) or in the case of lesion hemisphere stimulation (*right side*), recorded from intact-side arm (*black marker*) or lesion-side arm (*white marker*), in response to negative stimuli (*circle marker*) or neutral stimuli (*triangle marker*).

RESULTS

SSR magnitude

Under subliminal conditions, the main effect was found with the factor of arm. The magnitude of SSR from the intact-side arm was significantly greater than that from the lesion-side arm ($F_{(1,5)}$ = 13.7; p = 0.014) (Fig. 2). A significant interaction was found between stimulated hemisphere and emotional content ($F_{(1,5)}$ = 8.07; p = 0.036), indicating that in the case of stimulation of the intact hemisphere (i.e., the presentation of stimuli to the visual field contralateral to the operated side), the SSR response to negative stimuli was greater than that to neutral stimuli. Under supraliminal conditions, there were no significant differences (Fig. 3).

DISCUSSION

Amygdala and subliminal emotional processing

During intact hemisphere stimulation, higher EDAs were observed in response to negative slides than to neutral slides under the subliminal condition. In the case of the lesion hemisphere stimulation, no significant difference of EDA was observed between stimuli with different affective valence. On the other hand, no such discrepancy between the intact and lesion hemisphere stimulation was found under the supraliminal condition. These findings suggest that nonconscious emotional processing is reflected in EDA in a different manner from conscious emotional processing. The medial temporal structures, including the amygdala, thus appeared to play an important role in the neural substrates for such automatic emotional processing. To our knowledge, the present study is the first study in humans showing that unilateral medial temporal lesions have crucial effects on nonconscious emotional processing. These data are consistent with the proposal of LeDoux (1996) that the amygdala responds to early, crude representations of external stimuli. A recent neuroimaging study suggested that a subcortical pathway to the amygdala via the midbrain and thalamus provides a route for processing masked (unseen) emotional stimuli (Morris et al., 1999). Our results are also consistent with the hypothesis that the amygdala might receive stimuli information directly from the thalamus (LeDoux et al., 1985), although the present study does not address this issue directly. However, it should be noted that the extent of lesion in our subjects was not restricted to the amygdala. There is a possibility that the present findings might be attributable not only to amygdala lesion but also to extra-amygdala damage.

Backward masking of emotional visual stimuli resulted in a characteristic pattern of EDA responses reflecting the unilateral medial temporal lesion. This is consistent with the functional imaging study in normal subjects by Whalen et al. (1998) that demonstrated the isolation of the amygdala activation in response to masked fearful face versus masked happy face targets. Under the condition without masking, no significant differences of EDA were observed. This might be because emotional processing with awareness is a highly complex cognitive process, involving not only the amygdala but also other neocortical neural connections. Whereas a role for the amygdala in emotion is crucial, it can be compensated for by other structures in the case of supraliminal processing even with an amygdala lesion. This does not exclude the possibility that the amygdala is involved in supraliminal processing, but the lesion effect might become relatively small in the above case. Our view is that the function of the amygdala in human emotional cognition would be much more specifically reflected in EDA in the case of subliminal processing.

Two different modes of emotional cognition

The present demonstration of automaticity in emotional processing casts light on the question of the amygdala function in highly complex emotional behavior in humans, the elucidation of which has been hampered by the rarity of cases with selective bilateral amygdala lesions. Notably, the literature does not provide satisfying data on the relationships between ANS activity and amygdala functioning (for review, see Aggleton, 1992). Recent case studies in which electrophysiological measurement was performed are not unanimous as to the EDA responses to visual emotional stimuli. A decrease of EDA after bilateral amygdalectomy was reported by Lee et al. (1988). In contrast, normal EDA in response to emotional visual stimuli has been reported in patients with bilateral amygdala damage due either to Urbach-Wiethe disease (Tranel and Hyman, 1990) or to encephalitis (Tranel and Damasio, 1989). Studies in subjects after temporal lobectomy that were specifically designed to assess hemispheric asymmetries noted that EDA responses while subjects were viewing emotional stimuli were unrevealing (Davidson et al., 1992). These studies did not use a subliminal cognition paradigm. Thus, the results might have been obscured by EDA responses reflecting activation of various brain structures other than the amygdala.

Our subjects showed a considerable number of unusual responses on the affective rating of the stimuli both under subliminal and under supraliminal conditions. The rating under subliminal conditions were considered to be unreliable because the subjects could not identify the stimuli. Nevertheless, our subjects, under subliminal conditions, showed EDA responses that were congruent with the emotional valence of the stimuli. On the other hand, typical EDA responses to the emotional stimuli were not obtained under supraliminal conditions, which may suggest a influence of the affective judgement on EDA under these conditions. Therefore, there is a possibility that EDA under supraliminal conditions may be confounded with cortical influences associated with conscious processing of the stimuli. This is in accordance with our view above mentioned and might account for the failure to find impaired EDA in patients with amygdala lesions in previous studies.

From our present findings, we postulate that there exist two different, probably hybrid systems of emotional cognition in humans: (1) Preconscious processing: performed in the medial temporal circuitry of the unilateral side; the amygdala probably plays a key role in it. This process is closely related to body ANS activities and may parallel or be situated on the way to emotional processing with awareness. (2) Conscious processing: further complex information processing which involves sensory cortices and higher-order association cortices. The latter process might be related to other higher brain functions such as memory of personal experiences or social value judgements.

Interarm differences

Higher EDAs from the arm ipsilateral to the intact amygdala were observed only under subliminal conditions. The tendency was observed regardless of the affective valence of the stimulus, suggesting that the amygdala also plays an important role in the control of the unilateral output of EDA. A recent study of intracerebral stimulation showed that limbic structures, including the amygdala, were related to ipsilateral electrodermal control (Mangina and Beuzeron-Mangina, 1996). This is in line with our finding that a unilateral amygdala lesion has an effect on the ipsilateral output of EDA. Boucsein (1992) proposed that there are two neural pathways mediating EDA: (1) Ipsilateral hypothalamic influences on EDA with facilitary influences stemming from the amygdala, and (2) Contralateral influences from the basal ganglia together with premotor cortical areas. This hypothesis leads to the inference that the ipsilateral pathway is probably mainly related to emotional processing without awareness. Our finding that the effect of the amygdala lesion was observed only under subliminal conditions was in accord with the above-described hypothesis. A recent functional magnetic resonance imaging (fMRI) study investigated the cortical basis of the EDA, and it was reported that areas implicated in emotion, particularly ventromedial prefrontal regions, are differently involved in generation and representation of EDA (Critchley et al., 2000). Further studies are needed to investigate the role of the amygdala in EDA control in humans, and we believe that the subliminal cognition paradigm applied in the present study is potentially important for providing directions for future research.

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