

The role of the amygdala in facial emotional expression during a discrimination task

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A total of 50 patients with temporal lobe epilepsy with unilateral resection of the hippocampus and the amygdala were studied: —27 with left lobectomy (LTL group) and 23 with right lobectomy (RTL group)—; and 28 healthy control participants (HC group). The task consisted of identifying the dissimilar photograph from a group of photographs of the same face. The difference could correspond to the identity of the model or the facial expression (happiness, anger, sadness and fear). The results showed that when the difference in the photograph resided in the identity of the model, the RTL group made more mistakes than the HC group. When the facial expression was the distinguishing feature, mean response latency was longer in the LTL group than in the HC group. Comparison of the emotions revealed that the greatest differences were obtained with the fear expression, in all three participant groups. The dissociation of neural circuits responsible for processing facial expressions is discussed and, especially, the role of the left amygdala to discriminate between facial expressions.

El papel de la amígdala en una tarea de discriminación de expresiones emocionales. Se evaluaron 50 pacientes con epilepsia del lóbulo temporal con resección unilateral del hipocampo y la amígdala — 27 con lobectomía izquierda (grupo LTL) y 23 con lobectomía derecha (grupo RTL)— y a 28 participantes controles (grupo HC). La tarea consistió en identificar cuál era la fotografía de la cara diferente entre un conjunto de fotografías de caras iguales. La diferencia podía corresponder a la identidad o a la expresión facial (alegría, ira, tristeza y miedo). Los resultados indicaron que cuando la fotografía difería en la identidad, el grupo RTL cometió más errores que el grupo HC. Cuando la fotografía difería en la expresión, la latencia media de respuesta fue superior en el grupo LTL que en el grupo HC. Al comparar entre emociones, las diferencias principales fueron para la expresión de miedo en los tres grupos de participantes. Se discute la disociación de los circuitos neurales responsables del procesamiento de la cara y, particularmente, el papel de la amígdala izquierda en la discriminación de expresiones faciales.

The ability to express and recognise emotions is an essential adaptive response in human social behaviour. The facial expression of emotions is the main support for language in the job of communicating with others. Its value for survival is reflected by the fact that our perceptual system is highly effective at detecting human faces from the first few months of life (Carvajal & Iglesias, 2002; Purcell & Stewart, 1981; Schwartz, Izard, & Ansul, 1985).

Emotion can also facilitate processes such as perception, memory and behaviour in response to emotional events. The stimuli receive prioritized information which improves their processing (Anderson & Phelps, 2001; Davis & Whalen, 2001; Dolan, 2002; Fox, 2000; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). However, emotions have also been

associated with psychological disorders. A possible role for emotional learning has been proposed in the formation of traumatic memories, phobias and anxiety disorders.

Given the importance of emotions as regulators of an individual's cognitive and behavioural function, in recent years numerous studies have been published which, using neuropsychological studies or functional neuroimaging techniques, have attempted to establish which neural and physiological mechanisms are involved in emotional behaviour (Labar & Cabeza, 2006).

The structures most studied in relation to information about emotions correspond to the amygdala. These have traditionally been assigned an essential role in emotional processing, especially for fear (Aggleton & Young, 2000; Davis & Whalen, 2001). The amygdala are located in the anterior portion of the temporal lobe and present extensive connections with cortical and subcortical regions, including the visual cortex, hippocampus, fusiform gyrus, anterior paracingulate cortex, superior temporal sulcus and prefrontal cortex, making them potential modulators of different cognitive processes (Adolphs, 2002; Ishai, Schmidt & Boesiger, 2005; Kilpatrick & Cahill, 2003; McDonald, 1998; Sarter & Markowitsch, 1985).

The importance of the amygdala in emotional processing has been demonstrated from studies on patients with acquired brain damage and from research conducted in animal models such as the rat and non-human primates. Experiments with rodents have also demonstrated the important role of the amygdala in fear conditioning. Lesions of the central and basolateral nuclei of the amygdala prevent fear acquisition, conditioned by discrete cues and environmental contexts (Phillips & LeDoux, 1992). In humans, organic syndromes rarely selectively affect the amygdala alone. Moreover, only few studies have been carried out on patients with selective conditions that affect the amygdala bilaterally, such as Urbach-Wiethe syndrome, since these are quite rare. Most of the studies carried out have used patients with a medial temporal lobe damaged by epilepsy. A damaged amygdala in humans seems to diminish the ability to recognise expressions of fear or fear conditioning (Adolphs, Traver, Damasio, & Damasio, 1995; Labar LeDoux, Spencer, & Phelps, 1995).

One of the best known roles of the amygdala, established by experimental data and most known for its functional relevance, is its role in memory modulation. This brain structure directly mediates aspects of emotional learning, focuses the attention and facilitates memory operations in other regions, including the hippocampus (Dolcos, Labar, & Cabeza, 2004; Richardson, Strange, & Dolan, 2004). Attentional focalization consists in salient features of a complex event being preferentially retained in the memory, which confers evolutionary advantages. It has recently been suggested that functional interaction between the amygdala and the memory system of the medial temporal lobe is not limited to the coding and consolidation process, but also concerns the retention of remote emotional memories (Dolcos, Labar, & Cabeza, 2005).

On the other hand, another of their functions is to emotionally evaluate the sensorial stimuli we perceive (Zald, 2003). Vuilleumier et al. (2004) using fMRI, have shown that, in control subjects, the amygdala increases bilateral activation in the fusiform cortex and the extrastriated cortices in response to facial expressions of fear compared to neutral expressions, consisting in an improvement in the visual processing of emotional stimuli. Sclerosis of the amygdala cancels out this improved neural response in this group of patients.

Most of the experiments carried out to date have focused on demonstrating the involvement of the amygdala in processing stimuli associated mainly with anger and fear. However, few studies have attempted to explore the possibility that this structure participates in evaluating other types of basic emotions, also important for social communication and a correct theory of mind, such as sadness and happiness. Our aim in this work is to establish whether the amygdala are involved in the perception of the four main emotions expressed by the human face (happiness, sadness, anger, fear). If the amygdalinal complex does appear to be involved, we also aim to establish whether it presents any type of hemispherical specialisation as suggested by some authors (Markowitsch, 1999).

The purpose of this experiment was to study patients with epilepsy and unilateral surgical resection of the right or left medial temporal lobe. Since the brain damage extends to the medial temporal lobe adjacent to the amygdala, the patient's learning abilities can be impaired, which could interfere in the study of emotional processing. As described in previous works, some

patients even have impaired memory with unilateral lesions of the hippocampus and surrounding regions (Martín, Maestú, & García-Sola, 2002). This deficit also depends on the hemispherical location of the damage. Hence, patients with surgical resection of the left hippocampus present more difficulties in verbal memory, while those with a lesioned right hippocampus present impaired spatial memory. However, these patients do not present altered perception or attention.

In this work, a task was used in which the subjects make decisions about emotional stimuli (faces with different expressions) or about facial identity (faces of two different models) while they are watching the stimuli. The aim of this approach is to study the facial processing without the data being affected by the patient's possible memory alterations. The experimental design used in this study, which was designed and used previously by our research team in a study on university students (Carvajal, Vidriales, Rubio, & Martín, 2004), dissociates the influence of emotional expression and facial identity on perception and attention. Memory modulation can also be ruled out since the task does not require retention of the visualized material.

In several works carried out by different authors, these stimuli present, independently, in a sporadic manner. One way in which the perception of stimuli can have a greater ecological value, is to simultaneously present different faces with different facial expressions to determine whether attention tends to fall on the most salient emotional stimuli (Vuilleumier et al., 2004). Therefore, in the present experiment the stimuli are presented in matrices combining the expressions two at a time, or the facial identity of pairs of models. With this process, we aim to assess the mediator role of the amygdala in the perception of different emotions, in an ecological situation, without the interference of memory processes.

Method

Participants

Fifty patients with temporal lobe epilepsy participated in the study. All of them had received surgical interventions for histories of medication-refractory complex partial seizures. Twenty-seven of them (14 men and 13 women) had undergone a left temporal lobectomy (LTL group) and the remaining twenty-three (11 men and 12 women), a right temporal lobectomy (RTL group). In all cases, the lobectomy included resection of the hippocampus and amygdala, and restricted regions of the periamygdalinal cortex, the size of which depended on the clinical characteristics of each patient.

The patients had been operated in the Surgical Service for Epilepsy of the Hospital Universitario Princesa de Madrid and, after the operation, continued with pharmacological treatment with complete control of the seizure. All patients had an intelligence within the normal range, according to the WAIS-III and their ages ranged from 21 to 65 years (in the LTL group $M=36.2$, $Sx=10.1$ and in the RTL group $M=36.3$, $Sx=12.2$).

In addition to these 50 patients, twenty-eight healthy control subjects (HC group) participated in the study (14 men and 14 women) with ages between 19 and 61 years ($M=37.3$, $Sx=12.6$). Most of these control subjects were relatives of the patients and the rest were matched according to sociocultural level.

Stimuli

Considering studies about selective attention (Ballesteros, Reales, García, & Carrasco, 2005; Pacheco, Flores, González, Canales, & Carpio, 2005) stimuli were constructed using the paradigm «a face-in-the-crowd effect» proposed by Hansen and Hansen (1988). Specifically, 40 crowds were constructed, each comprised of 32 photographs of a single female face in each, arranged in 4 rows and 8 columns. The photographs were in black and white and were taken from the Florida Affect Battery-FAB- (Bowers, Blonder, & Heilman, 1991).

Three types of crowds were used (shown in Table 1):

- Ten crowds in which the 32 photographs were all the same. All the photographs were of the same model, who had a happy facial expression in two crowds, an angry expression in two, expression of fear in two, sadness in another two, and in the last two a neutral expression.
- Twenty crowds in which one photograph had a different facial expression from the others: the 32 photographs corresponded to the same model who had the same facial expression in 31 photographs and a different facial expression in one photograph. In this case, in four of the crowds happiness was the predominant expression (background) while the target expression corresponded in one case to anger, in another fear, then, sadness and, finally neutral. Another four crowds were predominated by the anger expression (background) while the target expression corresponded, in turn, to the four remaining expressions. In another four crowds the background expression was fear, in another sadness and the final four corresponded to a neutral expression.
- Ten crowds in which the facial identity of one photograph differed from the rest: in this case, 31 of the photographs were of the same model who posed with a happy expression in two crowds, an angry one in two, fear in two, sadness in

two and neutral in the final two. The target corresponded to the other model in all cases (always the same one). On one occasion, the model expressed the same emotion as the model appearing in the crowd and on another occasion a different emotion.

It is important to note that the model who appeared in the 10 crowds in which all the photographs were the same and in the 30 crowds in which one photograph differed from the rest (either in facial expression or identity of the model) was always the same.

Procedure

A computer screen was used to present all the crowd stimuli. Participants were told that on some of the screens all the photographs they would see would be the same and that others would show the same model who expressed one emotion in 31 photographs («the same expression» or «they felt the same way») and in one of them a different emotion and, the third possibility, was that 31 of the photographs would be of the same model and one of a different model. Participants had to indicate if all the photographs in the crowd were the same, or if one of them was different, pressing the space bar when they had the correct answer. The time taken to respond was recorded by the computer.

Since it had already been demonstrated in a previous study (Carvajal et al., 2004) that the position of the different photograph does not affect the answering speed, each different stimulus was presented randomly. The 40 crowds were presented in two different orders. Half of the subjects were shown the first order and the other half worked with the second one.

Each participant was individually evaluated, and after the instructions, 12 training stimuli were presented. In these training crowds, 32 drawings appeared. In six of them all the drawings were the same, and in the other six one drawing was different from the others.

Table 1
Types of matrices

Type of matrix	Description	Expression	
Type A (ten crowds)	32 photographs corresponded to the same model with the same expression	two crowds of Happiness two crowds of Anger two crowds of Fear two crowds of Sadness two crowds of Neutral faces	
Type B (twenty crowds)	32 photographs corresponded to the same model: the same expression in 31 photograph and a different facial expression in the other one	<i>Background model with predominant expression</i> four crowds of Happiness four crowds of Anger four crowds of Fear four crowds of Sadness four crowds of Neutral faces	<i>Target expression the four remaining expressions (one in each crowd)</i> Happiness Anger Fear Sadness Neutral
Type C (Ten crowds)	32 photographs: 31 of the photographs were the same model and one photograph corresponded to other model	two crowds of Happiness two crowds of Anger two crowds of Fear two crowds of Sadness two crowds of Neutral faces	The other model expressed the same emotion as the model in the background on one crowd and a different emotion on another crowd

Results

The results have been divided into two sections. In the first one, the number of correct responses was studied and the average response latency in relation to differences in the type of crowd and group effect. In the second, response latencies were estimated for each of the crowds in which the one different photograph varied in relation to the facial expression, since this type of crowd was the one most relevant to the study objectives.

Type of crowd

Three ANOVAs were performed with the factor group and the dependent variable was the number of correct responses. Each analysis corresponded to each type of matrix (all photographs the same, one with a different expression, one photograph of a different model). These analyses indicated that there were no differences in the number of correct responses when all the photographs were the same ($F(2,77) = 0.26, p = 0.77$) or when one of the photographs showed the same model with a different expression ($F(2,77) = 1.87, p = 0.16$). However, a significant effect of the factor group was obtained when one of the photographs showed a different model to the rest ($F(2,76) = 5.74, p < 0.01$). In this case, the RTL group obtained worse results than the HC group (tukey $\alpha < 0.01$). The means and standard deviations corresponding to the number of correct responses in each type of crowd are shown in Table 2.

Next, three ANOVAs were applied in which the factor was group once again, but in this case the dependent variable was the mean response latency in each type of crowd. In this analysis, a significant effect was obtained for the factor group in the crowds in which one of the photographs corresponded to the same model,

displaying a different facial expression ($F(2,77) = 7.05, p < 0.01$); in which the LTL group presented a longer response latency than the HC group (tukey $\alpha < 0.01$). No significant differences were found in either the case in which all the photographs were the same ($F(2,77) = 2.3, p = .10$), or when one of the photographs corresponded to a different model ($F(2,77) = 1.34, p = 0.26$). Descriptive data of the mean response latencies in each type of crowd are recorded in Table 3.

Crowd in which one of the facial expressions differed from the rest

Firstly, five MANOVAs were applied in which the dependent variable was always the response latency and the factor group. Each of the MANOVAs corresponded to matrices in which the crowd (background) had the same expression: one MANOVA for a background of happiness, another for a background of anger, another for a background of fear, another for a background of sadness, and, finally, an analysis with a neutral background. In each crowd, the four possible targets were compared (for example, anger versus fear, sadness and neutral expression in the happiness crowd). The means and standard deviations corresponding to the response latency in seconds for each of the stimuli in which one of the photographs corresponded to the same model with a different facial expression are shown in Table 4.

With the exception of the MANOVA in which the intra-crowd variable was neutral expression, in the other four the intragroup variable had a significant effect; subsequent comparisons (tukey $\alpha < 0.05$) showed that:

- (1) In a happiness crowd, participants could identify more quickly a fear expression and an anger expression than a neutral or sad expression ($F(1,30) = 6.2, p < 0.05$).

Table 2
Number of correct responses in relation to the stimulus

Type of matrix *	HC group		LTL group		RTL group	
	M	Sx	M	Sx	M	Sx
All photographs the same	9.7	0.4	9.7	0.5	9.8	0.4
One photograph of a different expression	16.4	2.7	14.7	3.5	15.8	3.9
One photograph of a different model	9.6	0.4	9.2	1	8.6	1.3

* The matrices in which all the photographs are the same and those in which a model for one photograph is different have a maximum of 10. In matrices with the same model, but with a different expression in one photograph the maximum is 20

Table 3
Mean response latency in seconds in the different types of matrices

Type of matrix *	HC group		LTL group		RTL group	
	M	Sx	M	Sx	M	Sx
All photographs the same	4.5	1.6	6.6	5.1	5.6	2.7
One photograph of a different expression	3.2	1.9	4.9	2.1	4.1	1.3
One photograph of a different model	2.4	0.8	2.8	1.1	2.6	1

* The matrices in which all the photographs are the same and those in which a model for one photograph is different have a maximum of 10. In matrices with the same model, but with a different expression in one photograph the maximum is 20

Table 4
Mean response latency in seconds in the different types of matrices

Same expressions	Different expression	HC group		LTL group		RTL group	
		M	Sx	M	Sx	M	Sx
Happiness	Anger	3.5	1.9	4.2	2.3	4.3	3
	Fear	3.1	1.9	4.5	3.3	4	2.5
	Sadness	3.8	1.3	5.3	2.6	5	2.6
	Neutral	4.7	2.1	6.5	3.5	5.9	3.3
Anger	Happiness	3.8	2.5	5.7	3.3	4.2	1.9
	Fear	2.3	1.1	3.9	3	3	1.7
	Sadness	3.1	1.4	4.4	3.5	3.6	1.9
	Neutral	3.7	1.8	6.2	4.3	5	3.8
Fear	Happiness	1.9	1.5	2.1	1.1	2.2	1.5
	Anger	3.8	2	4.3	2.6	3.7	2.1
	Sadness	3	1.2	3.9	2.4	3.3	1.7
	Neutral	2.5	1.7	3.5	2.8	3.3	2.6
Sadness	Happiness	4	3.5	6.8	7.9	5.3	4.2
	Anger	2.7	1	4.7	5.4	4.5	4.9
	Fear	1.9	1.3	3.3	2	3	1.2
	Neutral	1.9	1	2.9	2.2	2.9	2.2
Neutral	Happiness	3.3	2.4	4.3	4.3	3.8	2
	Anger	4.7	2.9	6.9	9.7	5.2	1.8
	Fear	3	1.4	7.9	8.6	3.8	1.7
	Sadness	3.9	2.4	4.5	3.3	4.6	2.1

- (2) In an anger crowd, the expression distinguished most quickly was that of fear ($F(1,29)= 18,97, p<0.001$).
- (3) In a fear crowd, the expression identified most quickly was happiness, followed by the neutral expression, sadness expression and, finally, anger expression ($F(1,50)= 15.26, p<0.001$).
- (4) In a sadness crowd, the first expressions identified were fear and neutral expressions, followed by anger and, finally, happiness ($F(1,36)= 7,8, p<0.01$).

Finally, ten MANOVAs were performed in which the response latencies to facial expressions of pairs of emotions were compared (for example, a MANOVA in which the response latency in a happiness crowd with an anger target was compared to that with an anger crowd with a happiness target). In each of the analyses, the effect of the factor group was considered. The objective of these analyses was to establish whether an expression was identified more quickly than another if it belonged to the crowd (background) or the target (different photograph). Since the perceptive difficulty was the same in both cases, the two expressions were the same, the difference in response latency in the two cases could indicate neural response characteristics. Of the ten comparisons carried out, only the four involving the fear expression were significant. More specifically, one happy face in a crowd of fear was identified more quickly than an expression of fear among a crowd of happy faces ($F(1,47)= 31.1, p<0.0001$). In contrast, when making comparisons for pairs of facial expressions, the fear expression was identified more quickly among a crowd of sad faces than one sad face among a crowd of fear expressions ($F(1,49)= 7.4, p<0.01$). Similar results were also obtained for the case of anger ($F(1,51)= 165.2, p<0.0001$) and neutral expression ($F(1,51)= 4.4, p<0.05$), where, once again, the expression of fear was identified among a crowd of angry or neutral expressions more quickly than these expressions were identified among a crowd of fear.

Moreover, the group effect was also significant when comparisons were made between expressions of fear and sadness ($F(2,49)= 3,8, p<0.05$). Subsequent comparisons revealed that, in this case, the LTL group took longer than the HC group to pick out the different face (tukey *a*, $p<0.05$).

Discussion

As mentioned in the introduction, the information conveyed by the face is essential for social communication, in that it enables one to identify individuals, to know their mood and, therefore, to predict their probable behaviour. From the information provided by the face, cognitive models (Bruce & Young, 1986) postulate the existence of a dissociation of the processing of facial identity and of facial expression. This dissociation has also been confirmed, at least partially, by neuropsychological studies (Braun, Denault, Cohen, & Rouleau, 1994; Esslem Pascual-Marqui, Hell, Kochi, & Lehmann, 2004).

In the specific case of facial expression, the main focus of this work, the brain regions involved in its processing are known. However, there is still not sufficient information about the way in which these regions are linked and whether emotion is a process that operates at a nervous level or whether a different network exists for each emotion (for a review of these two possibilities see the meta-analyses carried out by Murphy, Nimmo-Smith, & Lawrence, 2003; and by Phan, Wager, Taylor, & Liberzon, 2003).

In order to study how processing of facial expressions occurs, we propose a study in which subjects with unilateral temporal lobectomy and control subjects must distinguish the different photograph from among a crowd of photographs that are all the same. To do this, two situations were studied: in one of these the photograph differed in relation to the identity of the model used, and in the other, the difference was in the model's facial expression. The results suggested, firstly, that the neural response to facial identity is different from the response to facial expression and, secondly, that processing of the emotional expression is closely related to the amygdaline complex. This complex presents a degree of functional specialization; in relation to the type of emotion processed and the involvement of each brain hemisphere.

Regarding the first result, the number of correct responses obtained in the crowd in which the different model had to be detected was high for all participants. However, patients with a right lobectomy made more mistakes than control subjects. If we take into consideration the patients' characteristics, the common feature of all of them was that they had undergone unilateral resection of the hippocampus and amygdala. Nonetheless, according to the specific clinical characteristics of each patient, the intervention covered, to a greater or lesser extent, restricted regions of the periamygdaline cortex. Numerous studies have revealed that the brain regions responsible for processing facial identity are mainly located in the right temporal lobe, around the fusiform gyrus or adjacent regions (Adolphs, Damasio, Tranel, Cooper, & Damasio 2000; Borod et al., 1998; Dolan et al., 1996; Gorno-Tempini et al., 2001; Haxby, Hoffman, & Gobbins, 2000). Therefore, it is not surprising that the differences obtained in crowds in which discrimination was based on the model, affect patients with right temporal lobectomy, since these patients are the ones who have been surgically deprived of some of the regions associated with processing facial identity.

Secondly, the results obtained suggest that the amygdaline complex is involved in processing facial emotions. Hence, regardless of whether patients or control subjects were used, in crowds in which one photograph showed the same model with a different facial expression, it was observed that, both in the happiness crowd and in the fear crowd, the emotion fear was identified in the shortest time. Taking into consideration studies of patients with selective damage to the amygdala and functional neuroimaging studies in subjects in the general population, there is agreement about the role played by the amygdala in processing negative emotions, especially fear (Adolphs, 2002; Adolphs et al., 1994, 1995; Aggleton et al., 2000; Dolan, 2002; Hyman, 1998). In fact, it has been speculated that the increased neuronal activity described in the temporo-occipital neocortex during the processing of negative emotions was in fact a reflection of the feedback exerted by the amygdala (Vuilleumier et al., 2004). It seems, therefore, that the data of this study are indirectly in accordance with the relationship established in previous studies between the fear emotion and the amygdala.

In accordance with this, both in patients and in control participants, when pairs of emotions were compared in relation to which emotion belonged to the crowd and which to the target, significant differences were only obtained in the comparisons involving the emotion fear. In spite of the fact that the tasks to discriminate the background or target have the same complexity, when the same expressions were used in both cases, we found that the fear expression was identified more quickly in a background of

anger, sadness and neutral expressions compared to the opposite situation, in which fear was used as the background expression and the target expression was anger, sadness or neutral. In contrast, for the happy expression the opposite occurred. In other words, the happiness expression was identified more quickly among a crowd with an expression of fear than the expression of fear in a crowd (background) of happiness; in spite of the perceptive complexity being once again the same in both cases. The special characteristics presented by the happiness emotion could explain, although indirectly, why this expression was processed more quickly among a background of fear than the fear expression among a background of happiness. Although some studies with neuroimaging techniques have revealed a relationship between the amygdala and a happy emotion (Breiter et al., 1996; Hamann, Ely, Graftan, & Kitts, 1999; Yang, Menon, Eliez, Blasey, & White, 2002; Yang, Menon, Reid, Gotlib, & Reis, 2003), it is clear that happiness is mainly processed in regions of the left hemisphere or bilateral regions of the orbitofrontal cortex (Gorno-Tempini et al., 2001; Habel Kelin, Kellerman, Shan, & Scheneider, 2005). This lesser dependence on subcortical processing could respond to the preferential role that happiness plays in social interaction, and would give its processing an advantage over that of other emotions (Carvajal et al., 2004; Dolan 1996; Habel et al., 2005; Kirouac & Dore, 1983).

Another result which emphasizes the role of the amygdala in emotional processing has more direct implications. This concerns the higher mean response latency of patients with left temporal lobectomy compared with control participants when trying to identify the facial expression that is different from the rest. With the exception of one study (Peper, Karcher, Wohlfarth, Reinshagen, & Deluoux, 2001), which concluded that both amygdala make a similar contribution to emotional processes, there is general agreement that this is not the case. In cases which explicitly concern an emotional task (when a subject is instructed to make a judgement based on the emotional characteristics of the stimulus), the left amygdala is more important than the right. The latter could, however, play a more important role in implicit and subliminal tasks (see, among others, Markowitsch, 1999; Morris, Ohman, & Dolan, 1998; Phillips et al., 2001; Sato, Yoshikawa, Kochiyama, & Matsumura, 2004).

One final result we wish to discuss, concerns the finding that the greatest difference between patients with left temporal lobectomy and participants from the general population, was produced when discriminating between expressions of fear and sadness. Both are negative expressions triggered by the same type of events, although they differ in relation to when they manifest, since fear is often the first expression after a negative stimulus, while sadness would be the reaction after the event has taken place (Barr-Zisowitz, 2000). The fact that these emotions share certain aspects in relation to their function could suggest that discrimination between these emotions would require increased involvement of the left amygdala. However, there are no data to support this in the literature and with the information available we can only suggest that, in addition to a hemispherical specialization, the amygdala could also have some degree of functional specialization in the processing of negative emotions.

Taken collectively, our findings indicate that there is a dissociation between processing facial identity and facial expression, and a degree of functional and hemispherical specialization. In patients with temporal lobectomy, the impairments described lead to worse results than those obtained in control subjects, both for processing identity in patients with right temporal lobectomy and processing facial expression in patients with left temporal lobectomy. Nonetheless, we must point out that the impairment did not prevent the individuals from successfully performing the tasks proposed, suggesting that unilateral damage can be partially compensated for by the other hemisphere. These results, consistent with previous studies (Ishai et al., 2005), show that although processing of facial information may require participation of specific centres in one or the other hemisphere, it may involve a neural network that connects the cortical and subcortical regions of both hemispheres.

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References

- Adolphs, R. (2002). Neural systems for recognizing emotion. *Current Opinion in Neurobiology*, *12*, 169-179.
- Adolphs, R., Damasio, H., Tranel, D., Cooper, G., & Damasio, A.R. (2000). A role of somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *Journal of Neurosciences*, *20*, 2683-2690.
- Adolphs, R., Tranel, D., Damasio, H., & Damasio, A.R. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, *372*, 669-672.
- Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1995). Fear and the human amygdala. *Journal of Neurosciences*, *15*, 5879-91.
- Aggleton, J.P. & Young, A.W. (2000). The enigma of the amygdala: on its contribution to human emotion. In Lane, R.D. & Nadel L. (eds.): *Cognitive Neuroscience of Emotion*. (pp. 106-128). New York: Oxford University Press.
- Ballesteros, S., Reales, J.M., García, E., & Carrasco, M. (2006). Selective attention affects implicit and explicit memory for familiar pictures at different delay conditions. *Psicothema*, *18*, 88-89.
- Barr-Zisowitz, C. (2000) «Sadness»-Is there such a thing? In Lewis, M. & Haviland-Jones, J.M. (eds.): *Handbook of Emotions* (2nd ed) (pp. 607-622). New York: The Guilford Press.
- Borod, J.C., Cicero, B., Obler, L.K, Welkowitz, J., Erham, H.M., Santschi, C., Grunwald, I.S. Agosti, R.M., & Whalen, J.R. (1998). Right hemisphere emotional perception: Evidence across multiple channels. *Neuropsychology*, *12*, 446-458.
- Bowers, D., Blonder, L.X., & Heilman (1991). *Florida Affect Battery*. FL: University of Florida.
- Braun, C.M., Denault, C., Cohen, H., & Rouleau, I. (1994). Discrimination of facial identity and facial affect by temporal and frontal lobectomy patients. *Brain and Cognition*, *24*, 198-212.
- Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Guckner, R.L., Strauss, M.M., Hyman, S.E., & Rosen, B.R. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron*, *17*, 1223-1226.

- Bruce, V. & Young, A.W. (1986). Understanding face recognition. *British Journal of Psychology*, *77*, 305-327.
- Carvajal, F. & Iglesias, J. (2002). Face-to-face emotion interaction studies in Down syndrome infants. *International Journal of Behavioral Development*, *26*, 104-112.
- Carvajal, F., Vidriales, R., Rubio, S., & Martín, P. (2004). Effect of the changes in facial expression and/or identity of the modelo in a face discrimination task. *Psicothema*, *16*, 587-591.
- Dolan, R.J., Fletcher, P., Morris, J., Kapur, N., Deakin, F.W., & Fritch (1996). Neural activation during covert processing of positive emotional facial expressions. *Neuroimage*, *4*, 194-200.
- Dolan, R.J. (2002). Emotion, cognition and behaviour. *Science*, *298*, 1191-1194.
- Dolcos, F., LaBar, K.S., & Cabeza R. (2004). Interaccion between the amygdala and the medial temporal lobe memory system predicts better memory for emotional events. *Neuron* *42*, 855-863.
- Dolcos, F., LaBar, K.S., & Cabeza, R. (2005). Remembering one year later: role of the amygdala and the medial temporal lobe memory system in retrieving emotional memories. *Proc. Natl. Acad. Sci. USA* *102*, 2626-2631.
- Esslen, M., Pascual-Marqui, R.D., Hell, D., Kochi, K., & Lehmann, D. (2004). Brain areas and time course of emotional processing. *NeuroImage*, *21*, 1189-1203.
- Gorno-Tempini, M.L., Pradelli, S., Serafini, M., Pagnoni, G., Baraldi, P., Porro, C., Nicoletti, R., Umità, C., & Nichelli, P. (2001). Explicit and incidental facial expression processing: An fMRI study. *NeuroImage*, *14*, 465-473.
- Habel, U., Klein, M., Kellermann, T., Shan, N.J., & Schneider, F. (2005). Same or different? Neural correlates of happy and sad mood in healthy males. *NeuroImage*, *26*, 206-214.
- Hamann, S.B., Ely, T.D., Grafton, S.T., & Kilts, C.D. (1999). Amygdala activity related to enhanced memory for pleasant and aversive stimuli. *Nature Neuroscience*, *2*, 289-293.
- Hansen, C.H. & Hansen, R.D. (1988). Finding the face in the crowd: An anger superiority effect. *Journal of Personality and Social Psychology*, *54*(6), 917-924
- Haxby, J.V., Hoffman, E.A., & Gobbini, M.I. (2000). The distributed human neural system for face perception. *Trends Cognitive Science*, *4*, 223-233.
- Hyman, S.E. (1998). A new image for fear and emotion (news; comment). *Nature*, *393*, 467-470.
- Ishai, A., Schmidt, C.F., & Boesiger, P. (2005). Face perception is mediated by a distributed cortical network. *Brain Research Bulletin*, *67*, 87-93.
- Kirouac, G. & Dore, F.Y. (1983). Accuracy and latency of judgment of facial expression of emotions. *Perceptives, Motor Skills*, *57*, 683-686.
- Labar, K.S., LeDoux, J.E., Spencer, D.D., & Phelps, E.A. (1995). Impaired fear conditioning following unilateral temporal lobectomy in humans. *Journal of Neurosciences*, *15*, 6846-55.
- Labar, K.S. & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Review*, *7*, 54-64.
- Markowitsch, H.J. (1999). Differential contribution of right and left amygdala to affective information processing. *Behavioral Neurology*, *11*: 233-244.
- Martín, P., Maestú, F., Sola, R. (2002). Effects of surgical treatment on intellectual performance and memory in a spanish sample of drug-resistant partial onset-temporal lobe epilepsy patients. *Seizures*, *11*, 151-156.
- McDonald, A.J. (1988). Cortical pathways to the mammalian amygdala. *Progress in Neurobiology*, *55*, 257-332.
- Morris, J.S., Öhman, A., & Dolan, R.J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, *393*, 467-470.
- Murphy, F.C., Nimmo-Smith, I., & Lawrence, A.D. (2003). Functional neuroanatomy of emotions: a meta-analysis. *Cogn. Affect. Behav. Neurosci*, *3*, 207-233.
- Pacheco, V., Flores, C., González, F., Canales, C., & Carpio, C. (2005). Efectos de la consistencia e inconsistencia de las relaciones intrasitio-reforzador y muestra-reforzador en igualación a la muestra. *Psicothema*, *17*, 118-122.
- Peper, M., Karcher, S., Wohlfarth, R., Reinshagen, G., & LeDoux, J.E. (2001). Aversive learning in patients with unilateral lesions of the amygdala and hippocampus. *Biological Psychology*, *58*, 1-23.
- Phan, K.L., Wager, T., Taylor, S.F., & Liberzon, I. (2003). Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage*, *16*, 331-348.
- Phillips, R.G. & LeDoux, J.E. (1992). Differential contribution of amygdala and hippocampus to cued and contextual fear conditioning. *Behavioral Neurosciences*, *106*, 274-285.
- Phillips, M.L., Medford, N., Young, A.W., Williams, L., Williams, S.C., Bullmore, E.T., Gray, J.A., & Brammer, M.J. (2001). Time courses of left and right amygdalar responses to fearful facial expressions. *Human Brain Mapping*, *12*, 193-202.
- Purcell, D.G. & Stewart, A.L. (1981). A face superiority effect. *Bulletin of the Psychonomic Society*, *24*, 118-120.
- Richardson, M.P., Strange B.A., & Dolan R.J. (2004). Encoding of emotional memories depends on amygdala and hippocampus and their interactions. *Nature Neuroscience* *7*, 278-285.
- Sarter, M. & Markowitsch, H.J. (1985). The involvement of the amygdala in learning and memory: A critical review with emphasis on anatomical relations. *Behavioral Neuroscience*, *99*, 342-380.
- Sato, W., Yoshikawa, S., Kochiyama, T., & Matsumura, M. (2004). The amygdala processes the emotional significance of facial expressions: an fMRI investigation using the interaction between expression and face direction. *NeuroImage*, *22*, 1006-1013.
- Schwartz, G.M., Izard, C.E., & Ansel, S.E. (1985). The five-month-old's ability to discriminate facial expressions of emotion. *Infant Behavior and Development*, *8*, 65-77.
- Vuilleumier, P., Richardson, M.P., Armony, J.L., Driver, J., & Dolan, R.J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience*, *7*, n° 11, 1271-1278.
- Yang, T.T., Menon, V., Eliez, S., Blasey, C., White, C.D., & Reid, V. (2002). Amygdalar activation associated with positive and negative facial expressions. *NeuroReport*, *13*, 1737-1741.
- Yang, T.T., Menon, V., Reid, A.J., Gotlib, I.H., & Reiss, A.L. (2003). Amygdalar activation associated with happy facial expressions in adolescents: A 3-T functional MRI study. *Journal of the American Academy of Child & Adolescent Psychiatry*, *42*, 979-985.
- Zald, D.H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research Review*, *41*, 88-123.