Unconscious processing of emotions and the right hemisphere
Neuropsychologia (January 2012)

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Unconscious emotional processing | Right hemisphere dominance for emotions | Subcortical route to the right amygdala | Emotional action schemata | Non-removed unconscious memories

Highlights
► The right hemisphere is dominant for different forms of unconscious emotions. ► Unconscious and conscious emotions oppositely activate the right and left amygdala. ► Unconscious emotional stimuli reach the right amygdala through a subcortical route. ► ‘Non-removed unconscious memories’ are mainly stored in the right hemisphere.

Abstract
This survey takes into account the unconscious aspects of emotions and the critical role played in them by the right hemisphere, considering different acceptations of the term ‘unconscious’. In a preliminary step, the nature of emotions, their componential and hierarchical organization and the relationships between emotions and hemispheric specialization are shortly discussed, then different aspects of emotions are surveyed: first are reviewed studies dealing with the unconscious processing of emotional information, taking separately into account various lines of research. All these studies suggest that unconscious processing of emotional information is mainly subsumed by a right hemisphere subcortical route, through which emotional stimuli quickly reach the amygdala. We afterwards inquire if a right hemisphere dominance can also be observed in automatic emotional action schemata and if ‘non-removed preverbal implicit memories’ also have a preferential link with the right hemisphere. Finally, we try to evaluate if the right hemisphere may also play a critical role in dynamic unconscious phenomena, such as anosognosia/denial of hemiplegia in patients with unilateral brain lesions. In the last part of the review, the reasons that could subsume the right hemisphere dominance for unconscious emotions are shortly discussed.

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1 Introduction
For more than one century, in spite of Freud's discoveries and in part conditioned by the influence of the behaviorist model of mind, academic psychology has ignored or even denied the possibility that 'consciousness' may be a respectable object of scientific inquiry. It is only after Kandel's paper (1999), stressing the need of intimate relationships between psychoanalysis and cognitive neuroscience, that a new interest for the possible links between cognitive and affective research and the psychoanalytic model of mind has been developed. This new approach aimed to take into account the implications that some results, obtained in the field of cognitive and affective neuroscience, could have for some aspects of the psychoanalytical model of mind. In particular, Carhart-Harris and Friston (2010) have tried to re-cast in neuroscientific terms the Freudian notion of primary process (i.e. a non-removed unconscious process), discussing the hierarchical organization of the neural system and the possible contribution of the default-mode network in the primary process. Other authors (e.g. O'Brien, 2011) have discussed the correspondence between the psychoanalytic and neuroscientific concepts of emotional unconscious and still other authors have argued that the construct of 'unconscious', which lies at the core of psychoanalysis, far from being a unitary and homogeneous entity, concerns aspects both of information processing and of behavioral guidance (Bargh & Morsella, 2008). On the other hand, Vuilleumier, Armony, Driver, and Dolan (2001), and Tamietto and de Gelder (2010) have distinguished, within the non-conscious perceptual phenomena an 'attentional unawareness', due to the attenuated or abolished perception of items that lie outside the focus of attention, from a 'sensory unawareness', due to the weakness or the very short duration of the stimulus to be perceived. Finally, some authors (e.g. Mancia, 2003, 2006) have noticed that even within Freud's theory it is possible to distinguish a 'dynamic' unconscious (resulting from an active mechanism of motivated suppression of conscious information) from a 'non-removed' unconscious (Freud, 1922) referring to events, experienced in the earliest periods of life, for which an active process of removal cannot be hypothesized. An attempt to disentangle these different acceptations of the term 'unconscious', focusing attention on the unconscious aspects of emotions, will, therefore, constitute one of the aims of the present review.

A second aim, complementary to the first one, will be to show that, in spite of the distinction among different 'unconscious' emotional activities, the right hemisphere plays a major role in each of them. Not all these areas of research will, however, receive the same attention in our survey. We will review in greater detail the problem of the unconscious processing of emotional information (and of its relationship with the right hemisphere), than the issue of the unconscious guidance of behavior, because it is in the first area that the greatest amount of experimental research has been conducted in recent years. Furthermore, we will pay more attention to the problem of the 'non-removed' than to that of the 'dynamic' unconscious, because the former is more easily related to neuroscience, whereas the latter remains more clinical and speculative. In order to propose a theoretically consistent interpretation of these different unconscious emotional activities, we have deemed necessary a preliminary presentation of a general model of the emotional system and of its functional architecture.

We will, therefore, start our survey by shortly discussing the nature of emotions and their componential and hierarchical organization, summarizing the main hypotheses that have been advanced about the relationships between emotions and hemispheric specialization, and, in particular between emotions and the right hemisphere. After these introductory sections, we will go on to analyse the unconscious processing of emotional information in some detail and (more shortly) the unconscious emotional guidance of behavior, considering the critical role that the right hemisphere seems to play in each of them. In the final part of our survey we will consider the problem of the 'non-removed' and of the 'dynamic' forms of unconscious, also discussing the question of their possible relations with the right hemisphere.

2 The nature of emotions, their main components and the hierarchical organization of the emotional system
From the biological viewpoint, namely restricting attention to basic emotions, such as joy, sadness, anger and fear, that are generally considered as innate products of evolution (Ekman, 1984; Izard, 1990; LeDoux, 1996; Panksepp, 1989, 2010; Plutchik, 1980) emotion can be considered as a multi-component adaptive system, whose functional architecture has developed across phylogeny, spanning from very primitive, hard-wired survival related behavioral schemata to much more complex and learned...
social patterns, highly integrated with the cognitive system. According to Oatley and Johnson-Laird (1987), the organism has two operative systems at its disposal to face a partially unpredictable environment: (1) the emotional system, considered as an emergency system, able to interrupt the ongoing activity to rapidly select a new operative scheme; (2) the cognitive system, considered as a more complex and evolved system, but requiring much more time to carry out its work. Both structural similarities and functional differences exist between the emotional and cognitive system. The structural similarity consists in the fact that both systems base their activity on the integrated work of components that must: (a) analyse the sensory data to compute their significance; (b) select the most appropriate response patterns; (c) put all this information into appropriate memory systems. The functional differences (which concern the manner in which each system deals with sensory information and selects specific action schemata) derive, on the other hand, from the different logic of the two systems.

2.1 Main components of the emotional system
A different level of analysis of sensory data is performed by the emotional and the cognitive system, because an exhaustive analysis of highly processed information is carried out by the cognitive system, whereas a quick computation of poorly processed sensory data is sufficient to decide if an external situation has an emotional (pleasant or dangerous) meaning for an individual. The action schemata activated by the process of emotional and cognitive evaluation of the external data are equally different. The former are automatically selected from a small number of innate operative patterns, corresponding to the basic emotions (Ekman, 1984) and include expressive–communicative components, postural changes, locomotion, bodily movements and a sizeable recruitment of the autonomic nervous system. On the other hand, actions selected by the cognitive system consist of controlled strategic plans, which usually do not include a communicative–expressive component and do not require a concomitant strong activation of the autonomic nervous system. Very different are also the learning mechanisms used by the basic emotional and the cognitive system, since the construction of the first emotional schemata (see the next section) is typically based on mechanisms of conditioned, unconscious learning, whereas the cognitive system uses conscious and controlled mechanisms to store new information in declarative memory.

2.2 Hierarchical organization of the emotional system
The description of emotions that has just been given refers above all to the simplest forms of emotional behavior and to the earliest stages of the emotional development, because emotional and cognitive systems become more and more interconnected during the development and the complexity of emotions evolves accordingly. All these reasons have prompted the construction of hierarchically organized developmental models of emotions, that aim to explain how complex emotions can be formed starting from the simplest ones and how the highest components of this structure keep the lowest parts of the emotional system under control. In particular, Leventhal (1974, 1987) has put forward a developmental model which proposes that human emotions may be based on three functional levels: (a) the sensori-motor, (b) the schematic and (c) the conceptual level.

The sensori-motor level consists of a set of innate, universal expressive-motor programs, which are triggered automatically by a certain number of stimuli and include components of motor and autonomic activation, as well as the corresponding subjective emotional feelings. During individual development, these basic programs are linked, through mechanisms of conditioned learning, to situations of individual experience, building the ‘emotional schemata’, which are the units of the second schematic level of emotional processing. These emotional schemata are automatically elicited, correspond to spontaneous emotions and are accompanied by subjective feelings, which are the hallmarks of a true emotion. The last stage of this model is the conceptual level, which is based on mechanisms of conscious declarative memory and does not store instances of concrete emotional experiences, but abstract notions about emotions and about the social rules dealing with their expression.

Within the context of the present survey, our attention will be focused on the schematic level, because it concerns spontaneous emotions, elicited at the individual level by external stimuli that automatically trigger the appropriate action schemata.

3 Main models about the relations between emotions and the right hemisphere
Three main models have been advanced concerning the relationships between emotions and brain laterality. The first model (‘valence hypothesis’) assumes an opposite dominance of the left hemisphere for positive emotions and of the right hemisphere for negative emotions; the second model (‘right hemisphere hypothesis’) supposes a general dominance of the right hemisphere for every kind of emotional response, regardless of affective valence and the third model (‘emotional type hypothesis’) assumes a different modulation of the right hemisphere for basic emotions and of the left hemisphere for more evolved social emotions.

3.1 The ‘valence hypothesis’
The ‘valence hypothesis’ was first proposed by authors (Alemà & Donini, 1960; Perria, Rosadini, & Rossi, 1961; Terzian & Cecotto, 1959) who had noticed that the emotional reactions of patients submitted to intracarotid Amytal injection were different according to the side of the injection. A ‘depressive-catastrophic’ reaction was observed following pharmacological inactivation of the left hemisphere, whereas an opposite ‘euphoric-manic’ reaction was produced by injecting sodium amytal into the right carotid artery. These authors interpreted their data as pointing to a disruption of a ‘center for positive emotions’ located in the left hemisphere and, respectively, of a ‘center for negative emotions’ located in the right hemisphere.

A revised version of the ‘valence’ hypothesis was later proposed by Davidson (1998, 2001), who assumed that the ‘right hemisphere hypothesis’ might be valid for the comprehension of emotional information (in which the right hemisphere should be dominant, irrespectively of valence) whereas the ‘valence hypothesis’ might account for the emotional response (and the corresponding subjective experience).

3.2 The ‘right hemisphere hypothesis’
The ‘right hemisphere hypothesis’ was proposed by Gainotti (1969, 1972) on the basis of observations made in patients with unilateral brain damage (BD), because this author noted that patients with left BD often showed a ‘catastrophic reaction’ in front of their difficulties in verbal communication, whereas patients with right BD showed a strange ‘indifference reaction’ toward failures
and disabilities. However, in contrast with the interpretation advanced by the previously mentioned authors, Gainotti considered the ‘catastrophic reaction’ of left BD patients as a dramatic, but psychologically appropriate form of emotional reaction and only the ‘indifference reaction’ of right BD patients as an inappropriate form of emotional response. This led him to suggest that the abnormal emotional reactions of right BD patients could be due to disruption of a right hemisphere network playing a critical role in emotional functions. Clinical and experimental data gathered in following years, have shown that the right hemisphere plays a crucial role in emotional communication (e.g. Blond, Burns, Bowers, Moore, & Heilman 1993; Borod, Haywood, & Koff 1997; Ross, 1981.), in autonomic functions (e.g. Meadows & Kaplan, 1994.) and in the subjective experience of emotions (e.g. Marmurcani et al., 1988; Wittling & Roschmann, 1993.), and have supported the ‘right hemisphere’ much more than the ‘valence hypothesis’ (see Borod, Zgaljardic, Tabert, & Koff, 2001; Gainotti, 2001, 2005 for reviews).

3.3 The ‘emotional type hypothesis’
The ‘emotional type hypothesis’ has been proposed by Ross, Homan, and Buck (1994) on the basis of observations made during the Wada test and drawing on Buck and Duffy’s (1980) distinction between basic emotions, associated with innate displays and complex emotions, developed later during childhood and modulating facial emotional displays for social purposes. Results obtained by Ross et al. (1994) in their original study and in subsequent investigations (e.g. Ross & Monnot, 2008, 2011) led these authors to suggest that the right hemisphere modulates schematic/primary emotions, whereas the left hemisphere modulates social emotions and associated display rules.

3.4 Recent studies about the relations between emotions and right hemisphere
Contrasting results concerning the relationships between emotions and brain laterality have been obtained in recent clinical investigations and in functional magnetic resonance imaging (fMRI) studies. Clinical investigations, performed in patients with a right or left variant of fronto-temporal dementia, have confirmed the results of previous clinical studies conducted in right and left stroke patients, showing that emotional and social disturbances usually prevail in patients with right fronto-temporal atrophy (Li et al., 2004; Mendez et al., 2006; Perry et al., 2001; Rankin, Kramer, Mychack, & Miller, 2003.). The results of fMRI experiments are more controversial, since a recent voxel-based meta-analysis of studies employing emotional faces paradigms in healthy subjects (Fusar-Poli et al., 2009), has failed to support both the ‘right hemisphere’ and the ‘valence’ hypothesis, whereas some evidence of a right hemisphere specialization for the unconscious processing of emotions has been found by Costafreda, Brammer, David, and Fu (2008). These authors conducted a meta-analysis of fMRI studies of emotional processing, examining the effects of experimental characteristics on the probability of detecting amygdala activity. They found a relative left-lateralization for stimuli containing language and a relative right-lateralization for emotional masked stimuli. In our opinion, the negative results obtained by Fusar-Poli et al. (2009) can be explained on methodological grounds, because, in most of the studies surveyed by these authors subjects had been requested to identify a face portraying a specific emotion (anger, fear, happiness, sadness, surprise or disgust) using the Ekman and Friesen (1976) series of pictures. Now, this task can be considered as a cognitive (categorization) task accomplished with emotional material, that probably involves the ‘conceptual level’ of Leventhal’s (1974, 1987) model, whereas the right hemisphere dominance for emotions probably concerns the ‘schematic level’ on which we have focused our attention.

4 Unconscious processing of emotional information and the prevalence of the right hemisphere
Due to the tendency of academic psychology to deny the possibility that ‘consciousness’ may be a suitable object of scientific research, experimental data showing that psychological processes can be unconsciously mediated met considerable resistance. Even data gathered by the ‘New Look on Perception’, which claimed to have demonstrated unconscious influences on perception (e.g. McGinnies, 1949) were submitted to a severe critical scrutiny. To overcome some of the methodological objections raised against these studies, Lazarus and McCleary (1951) proposed a conditioning paradigm, which has been subsequently extensively developed and which consisted in demonstrating a skin conductance response (SCR) to consciously non recognized conditioned words. In more recent years this method has been developed by Ohman and Wiens (2001), who used backward masking (namely shortly presented conditioned target pictures, followed by long-lasting masking stimuli) to covertly activate human emotions, revealing possible hemispheric asymmetries in unconscious emotional processing. Marcel (1983) has, indeed, shown that, even though the target is blocked from conscious access, it is still processed to a considerable depth and this process may automatically activate a given response, before the mask disrupts more elaborate processing. With this methodology, Tamietto et al. (2009) have shown that nonrecognizable facial emotional stimuli can elicit a tendency to synchronize our facial expressions with those of others (“emotional contagion”), whereas Dimberg, Thunberg, and Elmehed (2000) have recorded both autonomic and electromyographic appropriate facial emotional responses. Other authors (e.g. de Gelder & Hadjikhani, 2006; Morris, Ohman, & Dolan, 1998, 1999; Noesselt, Driver, Heine, & Dolan, 2005), have conducted neuroimaging experiments, aiming to clarify the brain mechanisms underlying this unconscious form of emotional responses. Three main lines of research suggest a right hemisphere dominance in the unconscious processing of emotional information. The first consists of behavioral studies, conducted in normal subjects, contrasting conscious and unconscious perception of emotions, expressed through facial and bodily movements. The second is based on results of functional neuroimaging and neurophysiological experiments, conducted in normal subjects using the backward masking, ‘attentional unawareness’ or subliminar stimuli to hamper conscious perception of emotional faces. The third consists of investigations, assessing unconscious processing of emotional stimuli in various kinds of brain pathology. Results obtained following these three lines of research are reported in Tables 1–3.

4.1 Behavioral studies, conducted in normal subjects, contrasting conscious with unconscious perception of emotions
Data reported in Table 1 start from the observation of Spence, Shapiro, and Zaidel (1996) that when normal subjects are shown slides depicting negative emotional and neutral scenes, briefly lateralized to the right or left cerebral hemispheres, the largest physiological responses are obtained for emotional slides projected to the right hemisphere, whereas a left hemisphere superiority is observed on a cognitive task consisting in categorizing each slide as emotional or neutral. The right hemisphere dominance in
the processing of unconscious negative emotions is confirmed by results obtained by Sato and Aoki (2006), using a subliminal affective priming paradigm combined with unilateral visual presentation and by Tamietto and de Gelder (2008) evaluating the influence of emotional facial expressions presented unilaterally or bilaterally (with unilateral backward masking) over conscious recognition of emotions. Furthermore, results consistent with the same hypothesis were obtained by Roether, Omlor, and Giese (2008), investigating motor asymmetries in emotionally expressive walking. Taken together, results reported in Table 1 strongly suggest that only the right hemisphere is able to produce an appropriate and selective autonomic response to the unconscious presentation of emotional material and that the generation of the appropriate autonomic response can be dissociated from the conscious, cognitive evaluation of the eliciting stimulus.

4.2 Functional neuroimaging and neurophysiological experiments, conducted in normal subjects, using backward masking or subliminal stimuli to hamper conscious perception of emotional faces. Consistent with results obtained in the previous section are data reported in Table 2, which start with the influential results obtained by Morris et al. (1998), who studied the mechanism of an unconscious form of emotional learning in which an aversively conditioned masked emotional face elicited an unconscious emotional response, using positron emission tomography (PET). The masked presentation of the conditioned emotional face provoked a significant neural response in the right, but not the left amygdala, whereas the unmasked presentation of the same stimulus enhanced neural activity in the left but not the right amygdala. The authors concluded that the right amygdala plays a major role in unconscious and the left in conscious forms of emotional learning. In a further paper, the same authors (Morris et al., 1999) tried to clarify the mechanisms through which this unconscious emotional learning can be mediated. To do this, they took into account, on the one hand, the crucial role of the amygdala in classical emotional conditioning (LeDoux, 1996) and on the other hand the existence of a cortical and a subcortical route (LeDoux, Sakauchi, Iwata, & Reis, 1986; Papez, 1937) through which perceptual stimuli might reach the amygdala. The covariance of right and left amygdala response with activity in important cortical substructures during presentation of masked and non-masked conditioned emotional faces was taken separately into account. An increased correlation was observed between right amygdala, pulvinar and superior colliculus during the unconscious (masked) presentation of conditioned emotional stimuli, but no masking-dependent changes in correlation were observed among the same subcortical structures and the left amygdala. Morris et al. (1999) concluded that emotionally laden stimuli can be detected, processed and learned without conscious awareness by a right hemisphere subcortical pathway, mediating unconscious emotional learning. These results have been confirmed with different neuroimaging and electrophysiological techniques by Vuilleumier et al. (2001), Noesselt et al. (2005), Williams et al. (2006), Balconi and Lucchiani (2008), Pegna, Landis, and Khateb (2008), and Luo et al. (2009). Vuilleumier et al. (2001) showed, with an event-related fMRI study, that in normal subjects, the amygdala responses to threat-related expressions are unaffected by a manipulation of attention that strongly modulates the response to faces of the fusiform gyri. Noesselt et al. (2005) showed, using event-related fMRI, that projection of unattended fearful faces in the left-hemifield produces a right-lateralized brain activation, whereas no analogous fMRI effects are observed projecting fearful faces in the right visual field. Williams et al. (2006) found that the functional connectivity between amygdala, pulvinar, superior colliculus and extrastriate visual cortex is different during conscious and unconscious perception of fearful faces. A negative connectivity between amygdala and related cortical and subcortical structures was found during conscious perception, whereas a positive connectivity between pulvinar, superior colliculus and right amygdala was found during non-conscious perception of fearful faces. These functional neuroimaging data are in agreement with results of the previously reported meta-analysis of amygdala responsivity to emotional stimuli conducted by Costafreda et al. (2008), which had shown a left-lateralization for stimuli containing language and a greater activation of the right amygdala to masked presentations of affective facial expressions. Passing from results of functional neuroimaging studies to those of electroencephalographic (EEG) or magnetoencephalographic (MEG) investigations, Balconi and Lucchiani (2008) used Gamma band activity (GBA) to study cortical activation patterns during emotional face processing with subliminal vs supraliminal stimuli. They showed that the GBA was distributed more on the right side for emotional (vs non-emotional) stimuli, and more on the left side for conscious (vs unconscious) processing of the same stimuli. Also using GBA, Luo et al. (2009) examined the degree to which an increase in event-related synchronization (ERS) was associated with awareness and/or the emotional content of the stimulus. They found that subliminal emotional stimuli are associated with significant gamma ERS in the right amygdala and medial frontal cortex. Following a complementary line of inquiry, Pegna et al. (2008) tried to assess the time at which the subliminal processing of emotional faces occurs, studying the electrophysiological correlates of conscious and unconscious processing of fearful and neutral faces. They showed that emotional facial expressions are processed at an early stage, giving rise to enhanced activation of extrastriate visual areas, particularly on the right. Both temporal and neuroanatomical data stressed by previous authors have been recently confirmed by Hung et al. (2010). These authors verified the hypothesis that the amygdala processes threat-related information through a fast subcortical route and a slower cortical feedback mechanism, studying with MEG the effect of unattended emotional faces, located in the left or right VF on event-related neural responses. The hypothesis was confirmed, because: (a) the amygdala and anterior cingulate cortex were activated 100ms after presentation of fearful faces and (b) the right amygdala exhibited temporarily dissociated activations to input from different visual fields, suggesting early subcortical vs later cortical processing of fear.

4.3 Results of behavioral and activation studies conducted in patients with various kinds of brain pathology to evaluate unconscious processing of emotional stimuli. The first investigation in this field was conducted by Ládavas, Cimatti, Del Pesce, and Tozzi (1993), who studied the autonomic response and the cognitive evaluation of emotional and non-emotional stimuli, briefly lateralized to the right and left visual fields of a split-brain patient. In full agreement with results obtained in normal subjects by Spencer et al. (1996), they showed that only the right hemisphere is able to produce an appropriate autonomic response to the presentation of emotional material, in the absence of a conscious evaluation of the eliciting stimulus. Results consistent with the above mentioned studies have been obtained by Tamietto, Geminiani, Genero, and de Gelder (2007) using bodily expressions and by Williams and Mattingley (2004) and
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5.1.1 Vocal expression of emotions and emotional gesturing

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5 The right hemisphere unconscious emotional guidance of behavior

The general problem of the relationships between emotions and conscious experience has been the object of several controversies, that have been recently reviewed by Winkielman and Berridge (2004) in their important article on “unconscious emotions”. Bargh and Morsella (2008) challenge, in their influential paper on the ‘unconscious mind’, the tendency of cognitive psychology to equate unconscious processing with subliminal information processing. They prefer to approach this construct from the angle of the mental processes that influence behavior, but of which the individual is at least in part unaware. Starting from this reference point, they stress the fact that behavior is unconsciously guided by preferences and feelings, that unconsciously guide our active tendencies. This description of the unconscious tendencies that orient our behavior is consistent with the general model of emotions that we have proposed in the first part of our review. For this reason, in this section of the present review, we will try to see if the right hemisphere dominance, that we have systematically observed in the unconscious processing of emotional information, can also be observed in those automatic action schemata (such as spontaneous facial and vocal expressions, bodily movements and autonomic activation) that have been considered as action dispositions, preparatory for specific behavioral responses (Frijda, 1986, 2001). We have obviously excluded from this review all the investigations that had required a posed emotional expression, retaining only those that had been based on spontaneous or reactive (i.e. automatic and unconscious) emotional responses.

Our survey of this problem has taken separately into account results obtained in patients with unilateral brain damage and those obtained in normal subjects, assuming that: (a) patients with right brain damage should show a defect of emotional expression across the various output modalities and a flattened vegetative response to emotional stimuli; (b) in normal subjects the left side of the face and of the body should be more emotionally expressive than the right side.

Studies that have shown a greater impairment of facial and vocal emotional expression and a flattened autonomic response in right brain-damaged patients will be considered in the first part of the present section, whereas those that have demonstrated a greater emotional expressiveness of the left side of the face or the body in normal subjects will be taken into account in its second part.

5.1 Defects of facial and vocal emotional expression and reduced vegetative response of right brain-damaged patients

5.1.1 Vocal expression of emotions and emotional gesturing

The first authors who followed this line of research were Tucker, Watson, and Heilman (1977), who demonstrated a defective
evocation of affectively toned speech in patients with right parietal disease. This line of investigation was then pursued by Ross and Mesulam (1979) who showed a loss of affective prosody (aprosodia) and of emotional gesturing in two right brain-damaged patients and by Ross (1981, 1984), Gorelick and Ross (1987) and Ross and Monnot (2008, 2011), who showed that the affective components of language are a dominant function of the right hemisphere and that the organization of affective language in the right hemisphere mirrors that of propositional language in the left hemisphere.

6.1 The distinction between ‘removed’ and ‘non-removed’ forms of unconscious

Within the psychoanalytic theory of mind, Freud (1915) considered the construct of unconscious as tightly linked to that of memory and viewed the unconscious as expression of an active process of removal that begins in the first infancy (original removal) and continues lifelong (removal properly). At a later time, Freud (1922) understood that not all the unconscious processes are dynamic and discussing of the Ego, considered as the representative of consciousness, he wrote: ‘There is not a total overlap between repression and unconscious. Each removed event is unconscious, but not every unconscious is removed. Even a part of the Ego is

5.1.2 Facial expression of emotions

Buck and Duffy (1980) administered a slide viewing technique (designed to assess spontaneous emotional responses) to various groups of brain-damaged patients while their facial/gestural responses were videotaped. Judges watching the video tapes guessed the types of slide being viewed. Aphasic patients were equal to or more expressive than controls, while right hemisphere damaged patients were less expressive. Borod, Koff, Perlman Lorch, and Nicholas (1986) studying the channels of spontaneous emotional expression in right and left brain-damaged patients found that overall RBDs used facial expression less frequently than NC or LBD patients. In a subsequent study, Borod, Koff, Perlman Lorch, and Nicholas (1986) showed that RBDs are significantly impaired, relative to LBDS and NCs, in expressing and perceiving both positive and negative spontaneous facial emotion. More recently, Blonder et al. (1993), compared facial expressivity in RBD patients, LBD patients and NCs during videotaped semistructured interviews. RBD patients showed reduced facial expressivity in comparison to both LDHD and NCs.

5.1.3 Vegetative response to emotional stimuli

Heilman, Schwartz, and Watson (1978), first studied arousal in RBD patients, LBD patients and NCs, by stimulating the forehead ipsilateral to the side of the brain lesion while recording galvanic skin responses (GSRs) from the fingers on the same side. The RBD patients with neglect had lower GSRs than LBD patients and NCs. These results were confirmed by Morrow, Vrtunski, Kim, and Boller (1981), who monitored GSRs and respiration during random presentation of neutral and emotionally loaded visual stimuli and showed that GSRs were significantly smaller in the RBD patients than in LBD patients and NCs. Furthermore, GSRs were significantly larger for the emotional slides than for the neutral ones in the other two groups, but not in the RBD patients. In a similar vein, Meadows and Kaplan (1994), studying autonomic and subjective responses to emotional and neutral slides in BD patients and NCs, found that NCs showed higher GSRs to the emotional than to the neutral slides, while the RHD group showed lower GSRs to both sets of slides. Taken together, all these data show that patients with right brain damage consistently show an impaired ability to express emotions through tone of voice, bodily movements and emotional facial expressions, and do not generate a selective vegetative response to emotional stimuli. Furthermore, results obtained by Heilman et al. (1978), Morrow et al. (1981), and Meadows and Kaplan (1994) mirror the observations made in normal subjects by Spence et al. (1986) and in a split-brain patient by Laderas et al. (1993), showing that the largest physiological responses are provoked by the projection of emotional slides to the right hemisphere.

5.2 Greater emotional expressiveness of the left side of the face or the body in normal subjects

In studies concerned with asymmetries in the emotional expressiveness of the two sides of the face, the standard procedure has usually been that of the composite photograph technique. This technique consists of cutting on the vertical midline the original and the mirror-reversed print of an emotional face and then recombining them to form left–left (L–L) or right–right (R–R) composites. Observers are then asked to rate these composite photographs in terms of intensity of expression. This technique has also been used by Roether et al. (2008) to investigate motor asymmetries in emotionally expressive walking (see Table 1). An alternative, less frequently used technique has consisted in studying facial electromyographic (EMG) activity during emotional events. Using the composite photograph technique, Sackheim, Gur, and Saucy (1978) have shown that composites made from two left (LL) half faces express emotions more intensely than right-side composites. Even if some authors (e.g. Borod & Caron, 1980) have found that L–L composites express more intensely negative, but not positive emotions, most investigators (e.g. Borod, Koff, & White, 1983; Moscovitch & Olds, 1982) agree that L–L composites express more intensely both negative and positive emotions. This viewpoint has been confirmed by Indersmitten and Gur (2003), using three-dimensional photographs to investigate the expression of emotion in L–L and R–R chimeric faces.

Results obtained with the composite photograph technique were confirmed by Dimberg and Petterson (2000) studying the facial EMG activity during the pictorial presentation of happy and angry faces, because the zygomatic activity in response to viewing happy faces and the corrugator activity in response to angry faces were significantly larger on the left side of the face. So, if we try to summarize results concerning the spontaneous, automatic expression of emotions observed in right and left brain-damaged patients through the tone of voice, bodily movements and emotional facial expressions, and the emotional expressiveness of the two sides of face (or of the body), studied in normal subjects with the composite photograph technique or with the study of the facial EMG activity, we can conclude that the right-hemisphere shows a general superiority for all kinds of emotional expression. This finding mirrors the right hemisphere dominance observed in the unconscious processing of emotional stimuli.

6 The right hemisphere lateralization of the ‘non-removed’ forms of unconscious

6.1 The distinction between ‘removed’ and ‘non-removed’ forms of unconscious

Within the psychoanalytic theory of mind, Freud (1915) considered the construct of unconscious as tightly linked to that of memory and viewed the unconscious as expression of an active process of removal that begins in the first infancy (original removal) and continues lifelong (removal properly). At a later time, Freud (1922) understood that not all the unconscious processes are dynamic and discussing of the Ego, considered as the representative of consciousness, he wrote: ‘There is not a total overlap between repression and unconscious. Each removed event is unconscious, but not every unconscious is removed. Even a part of the Ego is
certainly unconscious’. Ensuing authors have tried to further analyse the construct of ‘non-removed unconscious’ showing that it concerns two different aspects of the functioning of the mind. (1) On one hand the possibility, akin to the distinction between automatic/unconscious and controlled/conscious processing of information, proposed by Shiffrin and Schneider (1977) that psychological events may be unconsciously processed. (2) On the other hand, the construct of ‘non-removed unconscious’, which refers to events, experienced in the earliest periods of life (from the end of the pregnancy up to about two years of age), for which an active process of removal could not be hypothesized (Siegel, 1999) because the structures underlying the declarative memory (and in particular the hippocampal formation) should not yet be fully developed. This interpretation has been criticized by authors, such as Rovee-Collier (1997) and Rovee-Collier, Hartshorn, and DiRubbo (1999), who have demonstrated that amnesia for the earliest period of life is not simply due to a neural immaturity of the hippocampus. In any case, since it is difficult to think that this form of amnesia may be based upon a process of active repression, some authors (e.g. Mancia, 2003, 2006) have proposed that this ‘non-removed unconscious’ may be based on preverbal forms of implicit memory.

6.2 The role of the right hemisphere in ‘non-removed’ forms of unconscious
Mancia (2003, 2006) has more specifically assumed that these ‘non-removed unconscious memories’ may have a preferential link with the posterior cortical areas of the right hemisphere, because the emotional information processed by these areas play a critical role in the development of the ‘non-removed, unconscious, primitive nucleus of the Self’. The preverbal system of implicit memories hypothesized by Mancia concerns the impact of the earliest human emotional experiences, extending back to the last periods of the gestation, in which the foetus lives in tight relation with the mother, with her rhythms and her voice memorized and reactivated during breast-feeding. Mehler, Bertoncini, Barriere, and Jassik-Gerschenfeld (1978) and Golinkoff and Hirsh-Pasek (1999) have, indeed, attested variations of the newborn heart and suction rate while listening to the mother’s voice in comparison with other voices. Now, several clinical and experimental data have shown that the right hemisphere plays a critical role not only in the recognition of emotional prosody (e.g. George et al., 1996; Ross, 1981, 1984) but also in the recognition of familiar voices (Gainotti, 2011; Halilstone, Crutch, Vestergaard, Patterson, & Warren, 2010; Neuner & Schweinberger, 2000; Van Lancker & Canter, 1982), and within the latter the recognition of the mother’s voice is particularly relevant. Even more documented is the right hemisphere dominance in the recognition of other non-verbal information that should play a critical role in the development of the infant’s earliest emotional experiences. A right hemisphere superiority has been, indeed, proved for the evaluation of facial emotional expressions, both in patients with unilateral brain damage (e.g. Ahern et al., 1991; Schmitt, Hartje, & Willmes, 1997; see Gainotti, 2001, 2006 for a survey) and in normal subjects (e.g. Burt & Perrett, 1997; Hudghtal, Iversen, Ness, & Flaten, 1989; see Borod et al., 2001, for survey). Furthermore, as in the case of familiar voices, a right hemisphere superiority has also been demonstrated in the recognition of familiar faces (see De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994; Gainotti & Marra, 2011; Sergent & Signoret, 1992, for surveys). The right hemisphere therefore plays a critical role not only in distinguishing pleasant from unpleasant or threatening information, but also in attributing the source of these experiences to a specific, emotionally very relevant, person. Another fundamental source of primitive sensations for which the right hemisphere plays a dominant role is represented by bodily movements and posture (Critchley, Mathias, & Dolan, 2001; Damasio, 1994; de Gelder & Hadjikhani, 2006; Roether et al., 2008), that certainly play a critical role in emotional experience. Finally, some authors have documented both in normal adults (e.g. Antrobus, 1983; Bertini & Violani, 1984; Maquet et al., 1996) and in conditions of brain pathology (e.g. Stavitsky et al., 2008) a right hemisphere prevalence in REM sleep and dreaming, that can be considered as a basic non-verbal form of emotional expression. A further argument in favor of the right hemisphere dominance in the pre-verbal period is represented by developmental data showing that between 1 and 3 years of age, the blood flow shows a right hemispheric predominance, mainly due to the activity in the posterior associative area and that this asymmetry shifts to the left after the age of 3 (Chiron et al., 1997). If we put these specific arguments within the context of a general dominance of the right hemisphere for every kind of emotional comprehension and expression (Gainotti, 2001, 2006) we can acknowledge that Mancia’s (2003, 2006) hypothesis of a preferential link between ‘non-removed unconscious memories’ and right hemisphere posterior cortical areas seems quite reasonable.

7 The ‘removed’ forms of unconscious and the right hemisphere
A final problem that we would shortly take into account here concerns the possibility that the right hemisphere may play a critical role not only in the formation of non-removed unconscious memories, but also in unconscious emotional phenomena, resulting from an active process of repression. Turnbull and Solms (2007) have recently discussed this problem, debating the role that the right hemisphere could have in the unconscious distortion of the cognitive representations of reality. In particular, these authors have mentioned the well established prevalence of anosognosia/denial of hemiplegia in patients with right-sided lesions and explained this prevalence as resulting from the critical role of the right hemisphere in emotion regulation processes. It must be acknowledged, however, that not authors consider anosognosia of left-sided hemiplegia as the consequence of a psychodynamic process of denial. Other authors (e.g. Heilman, Barrett, & Adair, 1998) assume that this disorder may be due to the coexistence of a neglect for the left half space, that leads these patients to ignore the left side of their body and, consequently, their left-sided hemiplegia. So, if the major role played by the right hemisphere in different forms of ‘non-removed’ unconscious activities seems substantially supported, the possibility that the right hemisphere may transform negative emotions into primitive psychodynamic mechanisms still remains open.

8 General discussion
This discussion of results obtained in rather scattered areas, such as the unconscious processing of emotional information, the partly unconscious emotional guidance of behavior, the nature and the prevalent localization of the preverbal implicit memories and the lateralization of unconscious phenomena, resulting from a dynamic process of repression, will be divided in two parts. The first part will deal with the main points that emerge from the review of these different areas, whereas the second part will try to take into account the reasons that could subsume the right hemisphere dominance for unconscious emotions.
8.1 Main points that emerged from the different sections of our review

Four main points emerged from the different sections of our review and will be taken into account in the first part of the present discussion.

The first point is that the right hemisphere seems to play a critical role in each of these sections, even if the strength of evidence is not same in these different areas of inquiry. This evidence is, indeed, very strong in investigations specifically concerning the unconscious processing of emotional information, because in these studies the unconscious nature of the emotional processing was carefully controlled and the right hemisphere prevalence was observed with different experimental paradigms and in different groups of normal and brain-damaged patients.

A right hemisphere (RH) dominance has also been documented in automatic action schemata (such as facial and vocal expressions, bodily movements and vegetative activation) and in the development and storage of the ‘non-removed unconscious memories’. As for the possible lateralization of unconscious phenomena, considered as expression of a dynamic process of repression, the prevalent lateralization to the left side of the body of anosognosia/denial of hemiplegia is supported by most authors, but its mechanism remains controversial.

In the following parts of this discussion we will, therefore, focus attention on the problems of the unconscious processing of emotional information and (to a lesser extent) to that of the automatic production of spontaneous emotional responses, considering as a consequence of them the crucial role that the RH seems to play in the development of the non-removed unconscious preverbal memories.

The second point is that when conscious and unconscious aspects of emotional processing are controlled in the same task, the right hemisphere seems to play a critical role in unconscious and the left hemisphere in conscious forms of emotional processing. This double dissociation is suggested by several sources of evidence. The first is represented by results obtained studying in normal subjects (Spence et al., 1996) and in a split-brain patient (Ládavas et al., 1993) the cognitive evaluation and the autonomic response to subliminal and above threshold presentation of emotional and non-emotional stimuli, briefly lateralized to the right and left visual fields. The second evidence is represented by the observations of Morris et al. (1998) and of de Gelder et al. (2005) that the side of the amygdala activation changes as a function of the conscious or unconscious nature of the eliciting stimuli, and by results of the meta-analysis of amygdala responsivity to emotional stimuli conducted by Costafreda et al. (2008), which showed a greater activation of the right amygdala to masked presentations of affective facial expressions and a relative left-lateralization for (conscious) stimuli containing language. A final line of evidence is represented by studies dealing with the unconscious emotional processing determined by pathological lack of attention resulting from extinction or neglect (Grabowska et al., 2011), because in these patients the attended emotional stimuli activated the left hemisphere (LH), whereas the unconsciously perceived emotional expressions activated cortical and limbic areas of the RH.

The third point is that the subcortical nature of the mechanisms subsuming the right hemisphere unconscious processing of emotional material is quite consistent with the quick and coarse analysis of sensory data that we have described as characteristic of the emotional system. As a matter of fact, our model of emotions maintained that a quick computation of poorly processed sensory data is sufficient to decide if an external situation has an emotional (pleasant or dangerous) meaning for an individual. Now, both the increased connectivity between right amygdala, pulvinar, and superior colliculus documented by Morris et al. (1999) and Williams et al. (2006) with unseen fear-conditioned or fearful faces and the co activation of right superior colliculus and right amygdala reported by de Gelder et al. (2005) when there was a congruence between emotional voice and emotional face presented to the blind field, suggest that the RH subcortical route has just this function of a preliminary quick computation of coarse emotional sensory data. This hypothesis is supported by the electrophysiological data of Pegna et al. (2008) and the MEG data of Hung et al. (2010), who found a very early activation of the amygdala after presentation of subliminal or unattended emotional fearful faces. An objection that could be raised to this model is that the neural circuits forming the ‘subcortical route’ are still controversial. Most authors (e.g. de Gelder et al., 2005; Hung et al., 2010; Morris et al., 1998, 1999) describe, in fact a circuit based on the superior colliculus, the pulvinar and the amygdala. Other authors, however (e.g. Cowey, 2004; Pessoa, 2005), object that an anatomical connection between these various subcortical structures has not yet been demonstrated and still other authors (e.g. Schmid et al., 2010) suggest that the thalamic lateral geniculate nucleus (LGN) might give a critical contribution to this function, through its direct projections to the extrastriate cortex. Nevertheless, a recent diffusion tensor imaging (DTI) study involving patients with cortical blindness and normal subjects (Tamietto, Pullens, Weiskrantz, Goebel, & de Gelder 2010) has shown direct connections between the superior colliculus and amygdala via the pulvinar in all subjects. Furthermore, Day-Brown, Wei, Chomsung, Petrny, and Bickford (2010) have recently shown that in the tree shrew, a prototypical primate for the anatomical organization of its visual system, projections to the lateral amygdala originate from the same portions of the pulvinar receiving visual input from the superior colliculus. Therefore, in this primate a direct connection between the three structures has been demonstrated. Finally, in a recent review of the neural bases of the non-conscious perception of emotional signals, Tamietto and de Gelder (2010) have given a detailed account of their model, explaining why the functional properties of the phylogenetically ancient subcortical network, based on the superior colliculus, the pulvinar and the amygdala, might be consistent with the quick computation of poorly processed sensory data, considered as typical of the perceptual analysis performed by the emotional system.

The fourth point is that the mechanisms subsuming the unconscious analysis of perceptual information seem to apply much more to emotional than to non-emotional material. This claim stems from the fact that when similar emotional and non-emotional visual stimuli are used to assess their unconscious processing, only emotional stimuli are unconsciously recognized and activate the right subcortical pathway centered on the amygdala (de Gelder & Hadjikhani, 2006; de Gelder et al., 1999, 2002; Grabowska et al., 2011; Pegna et al., 2005, 2008). In our opinion, data reported by these authors not only show that the right hemisphere mechanisms subsuming the unconscious analysis of perceptual information apply much more to emotional than to non-emotional stimuli, but also indicate (a) that these mechanisms are elicited by simple patterns (emotional faces and voices, bodily emotional expressions) but not by more complex affective scenes (de Gelder et al., 2002), whose appraisal requires cognitive processes that depend critically on conscious visual analysis; (b) that emotional stimuli give rise to enhanced activation of right extrastriate visual...
cortex at an early stage in the stream of visual processing.

8.2 Reasons that could explain the relationships between unconscious emotional processing and the right hemisphere

A first very general model that could explain the relationships between unconscious emotional processing and right hemisphere taking into account basic aspects of the brain laterality could consist of the fact that a similar form of visual processing (namely a global, holistic style) characterizes both the visual processing of basic emotions through the subcortical pathway (LeDoux, 1996; Tamietto & de Gelder, 2010) and the right hemisphere visual processing functions (Barton, Press, Keenan & O'Connor, 2002; Bradshaw & Nettleton, 1981; Levine & Calvario, 1989; Schiltz & Rossion, 2006; Van Kleek, 1989). Developing a similar line of thought, Serpent (1993) and Shulman, Sullivan, Gish, and Sakoda (1986) have proposed that the holistic right hemisphere processing style could be due to a bias toward processing the low spatial frequency (global) components of a visual stimulus, and an analogous interpretation has been advanced by Tamietto and de Gelder (2010) to explain the coarse visual processing of basic emotions through the subcortical visual network. According to these authors, responses in superior colliculus and pulvinar (that are part of this network) are tuned to coarse information in low spatial frequencies because these structures receive visual information from the magnocellular pathway (Schiller & Malpeli, 1977), whereas cortical areas in the ventral visual stream receive visual information predominantly from the parvocellular pathway, which provides high spatial frequency signals (Livingstone & Hubel, 1988).

A problem with this interpretation of the relationships between unconscious emotional processing and the right hemisphere is that it provides a neural account of the coarse visual processing of basic emotions through the subcortical visual pathway, but does not explain the right hemisphere bias toward processing the low spatial frequency (global) components of visual stimuli. This problem, therefore, requires further considerations, that could concern both the phylogenetic and the ontogenetic development of the brain. Interesting speculations on the phylogenetic determinants of the right hemisphere specialization for emotions have been offered by Vallortigara and Rogers (2005), who suggested that alignment of hemispheric asymmetry originates from social pressures, namely from the need of coordinating the individual's behavior with the behavior of other asymmetrical organisms. This could be especially pertinent in the case of emotions, which can be seen as a prototypical and evolutionary ancient case of social behavior. On the other hand, a clarification of the ontogenetic aspects requires a discussion of the developmental interactions between subcortical and cortical systems, because the critical point is whether right-hemisphere superiority for unconscious emotions is driven exclusively by subcortical asymmetry or by an interaction between the subcortical and cortical systems dealing with emotions. One possibility suggests that specialization of several cortical areas to emotional signals originates from subcortical modulatory effects that occur during early stages of development, because such subcortical sites are more mature at birth and guide cortical specialization. As the subcortical emotion system is lateralized in the right hemisphere, this could explain later lateralization of cortical areas related to emotion processing. A detailed description of this hypothesis relative to face processing can be found in Johnson (2005), and a reformulation in the domain of unconscious emotional signals can be found in Tamietto and de Gelder (2010).

A second interpretation, aiming to explain the results of our review focusing attention only to emotional domain could be related to the general account that we have given of emotions, considered as a phylogenetically older emergency adaptive system, because this definition could orient attention toward a group of danger-related negative emotions, somehow neglecting other less arousing, less negatively connoted and more social types of emotions. This interpretation could have some advantages, since it could reconcile our positions (stressing the 'right hemisphere hypothesis') with the Davidson's (1998, 2001) 'valence hypothesis', with the Ross et al.'s (1994) 'emotional type hypothesis' and with the positions of those authors (e.g. Craig, 2005; Oppenheimer, Gelb, Girvin, & Hachinski, 1992; Wittling, 1995), who have proposed a different hemispheric specialization for sympathetic and parasympathetic components of the vegetative system. The right hemisphere lateralization of the sympathetic section of the autonomic system, typically involved in emergency situations (see Wittling, 1995 for a short review) is, indeed, consistent with our account of emotions considered as an emergency system, able to interrupt the ongoing action to rapidly select a new operative scheme, more appropriate to face a dangerous situation.

Even this last interpretation, that restricts to a limited set of emotions the relationships between unconscious emotional processing and right hemisphere meets, however, some criticisms. The first consists of the fact that, if the right hemisphere dominance for sympathetic activities is accepted by almost all authors (see Gainotti, 2001 for review) not all authors accept the claim of a left hemisphere dominance for the parasympathetic activities. On the contrary, data obtained by Yokoyama, Jennings, Ackles, Hood, and Boller (1987), Caltagirone, Zoccolotti, Originale, Daniele, and Mammucari (1989), Naver, Blomstrand, and Wallin (1996), and Spence et al. (1996) seem to point to a right hemisphere dominance for both sympathetic and for parasympathetic activities.

The second objection stems from the fact that in studies assessing the relationships between unconscious emotional processing and the right hemisphere, effects similar to those obtained with danger-related stimuli have been obtained when the non conscious perception of happiness, sadness or disgust have been tested (e.g. de Gelder & Hadjikhani, 2006; Juruena et al., 2010; Pegna et al, 2005).

9 Concluding remarks

The general picture that emerges from this survey of the relationships between unconscious processing of emotions and right hemisphere suggests that the functional organization of the right hemisphere might be characterized by a higher degree of emotional processing, unawareness and automaticity, whereas the functional organization of the left hemisphere could be characterized by a prevalence of cognitive processing, consciousness and intentionality. This statement is supported by the fact that a dissociation between a prevalence of the right hemisphere in the automatic and of the left hemisphere in the controlled aspects of functional processing can be observed in other important components of behavior, such as the automatic spatial orienting of attention (Bartolomeo & Chockron, 2002; Corbetta & Shulman, 2002; Gainotti, 1996) or the elicitation of face familiarity feelings (Gainotti, 2007). Taken together, all these data support the general hypothesis that automatic and controlled levels of
processing may have a different representation in the right and left hemisphere, the right side being more involved in the earliest automatic and the left side in the more controlled and propositional levels (Gainotti, 2000; Gazzaniga, 1995) of cognitive and emotional functions, probably due to the influence of language (Luria, 1966) in the acquisition of a higher degree of consciousness and intentionality.

Table 1

<table>
<thead>
<tr>
<th>Authors</th>
<th>Methods</th>
<th>Results</th>
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<tbody>
<tr>
<td>Spence et al.</td>
<td>Studied the cognitive evaluation and the autonomic response to subliminal and above threshold presentation of emotional and non-emotional stimuli.</td>
<td>Showed that only the right hemisphere is able to produce an appropriate autonomic response to the presentation of emotional material. This response is dissociated from the conscious evaluation of the stimulus. When the stimuli were presented to the left, but not the right visual fields, the negative primes reduced the subjects’ liking of the targets, suggesting a right hemisphere dominance in the processing of unconscious negative emotions.</td>
</tr>
<tr>
<td>Sato and Aoki (2006)</td>
<td>Combined subliminal affective priming paradigm with unilateral tachistoscopic visual presentation.</td>
<td>They showed that L–L chimeras are rated as more expressive than R–R chimeras.</td>
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<tr>
<td>Roether et al. (2008)</td>
<td>Investigated motor asymmetries in emotionally expressive walking, creating left–left (L–L) and right–right (R–R) chimeric walkers.</td>
<td>The influence of unseen fearful expressions on conscious recognition of emotions was greater when masked expressions were projected to the LVF.</td>
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<tr>
<td>Tamietto and de Gelder (2008)</td>
<td>Evaluated the influence of emotional facial expressions presented unilaterally or bilaterally (with unilateral backward masking) on conscious recognition of emotions.</td>
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Table 2

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<tr>
<th>Authors</th>
<th>Methods</th>
<th>Results</th>
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<tr>
<td>Morris et al.</td>
<td>Studied, using positron emission tomography (PET), the mechanism of an unconscious form of emotional learning, in which an aversively conditioned masked emotional face elicited an unconscious emotional response.</td>
<td>The masked presentation of the conditioned emotional face elicited a significant neural response only in the right amygdala, whereas the unmasked presentation of the same stimulus enhanced neural activity only in the left amygdala. Increased connectivity between right amygdala, pulvinar, and superior colliculus was evident when fear-conditioned faces were unseen. By contrast, the left amygdala showed no masking-dependent changes in connectivity with superior colliculus or pulvinar. Amygdala response to threat-related expressions was unaffected by a manipulation of attention that strongly modulated the fusiform response to faces. They showed lateralized activations in right hemisphere visual areas and amygdala, but no analogous fMRI effects after presentation of fearful faces in the right visual field. Conscious perception was related with negative connectivity, but non-conscious perception was related with positive connectivity between superior colliculus, pulvinar and right amygdala. GBA had a more right-posterior distribution for emotional vs non-emotional stimuli, and a more left-posterior localized during conscious elaboration compared to unconscious. They showed that subliminally presented fearful faces produce a stronger posterior negativity at 170ms (N170) than non-fearful faces. Furthermore, source localization showed that fear produced a greater activation of right extrastriate visual areas.</td>
</tr>
<tr>
<td>Morris et al.</td>
<td>Used measures of right amygdala neural activity, acquired from volunteer subjects viewing masked fear-conditioned faces to evaluate whether a colliculo-pulvinar pathway was engaged during the processing of these unseen target stimuli.</td>
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<td>Vuilleumier et al. (2001)</td>
<td>Used event-related fMRI to assess whether brain responses to fearful vs neutral stimuli are modulated by spatial attention.</td>
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<tr>
<td>Noesselt et al. (2005)</td>
<td>Used event-related fMRI to study brain activation after lateralized presentation of unattended fearful faces.</td>
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<tr>
<td>Williams et al. (2006)</td>
<td>Used fMRI with connectivity analysis between amygdala and related cortical and subcortical structures in healthy human subjects during conscious and unconscious perception of fearful facial expressions.</td>
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<tr>
<td>Balconi and Lucchiar (2006)</td>
<td>Used Gamma band activity (GBA) to study cortical activation patterns during emotional face information processing with subliminal (10ms) vs supraliminal (150ms) stimulation.</td>
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<tr>
<td>Pegna et al. (2008)</td>
<td>Studied the electrophysiological correlates of backward masked fearful and non-fearful faces, to assess the time at which subliminal processing of fearful faces occurs.</td>
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Table 3

Behavioral and activation studies assessing unconscious processing of emotional information in brain-damaged patients.

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<tr>
<th>Authors</th>
<th>Methods</th>
<th>Results</th>
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<tr>
<td>Luo et al. (2009)</td>
<td>Examined, using MEG and a masking paradigm, the degree to which increases in event-related synchronization (ERS) in the Gamma band were associated with awareness and/or the emotional content of the stimulus.</td>
<td>Subliminal emotional stimuli were associated with significant gamma ERS in the right amygdala and medial frontal cortex, whereas this change was not found with neutral stimuli.</td>
</tr>
<tr>
<td>Hung et al. (2010)</td>
<td>Studied, using MEG, the effect of irrelevant emotional expressions located in the left or right VF on event-related neural responses.</td>
<td>They found early activations to fear of the right amygdala and anterior cingulated cortex, suggesting early subcortical processing of fear.</td>
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<tr>
<td>Lådavas et al. (1993)</td>
<td>Studied the autonomic response and the cognitive evaluation of emotional and non-emotional stimuli, briefly lateralized to the right and left visual fields of a split-brain patient.</td>
<td>Only the right hemisphere was able to produce an appropriate autonomic response to the presentation of emotional material, in the absence of a conscious evaluation of the eliciting stimulus.</td>
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<tr>
<td>de Gelder et al. (1999)</td>
<td>Showed to the blind field of a patient (GY) with complete right hemianopia a face pronouncing the same sentence with four different facial expressions.</td>
<td>The patient could discriminate emotional facial expressions, but not facial speech.</td>
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<tr>
<td>de Gelder et al. (2002)</td>
<td>Explored in two patients with complete right (GY) and left (DB) hemianopia the role of conscious and unconscious vision within the blind field of audiovisual pairings, comparing audiovisual integration between congruent vocal and facial emotions.</td>
<td>An audiovisual integration was obtained pairing an emotional voice with an emotional face, but not an emotional voice with a complex picture expressing the same emotion.</td>
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<td>Gläscher and Adolphs (2003)</td>
<td>Showed emotional visual stimuli to patients with left, right and bilateral amygdala damage, with subliminal and supraliminal lateralized presentation to one visual hemifield.</td>
<td>Impaired overall skin conductance responses were observed only after right amygdala damage.</td>
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<tr>
<td>de Gelder et al. (2005)</td>
<td>Measured the effect of emotional congruence between vocal fear expression and presentation of emotional faces to the intact and the blind field in blindsight patient GY.</td>
<td>The (conscious) fear face/voice congruence in the intact field was reflected in left amygdala activation, whereas the (unconscious) face/voice congruence in the blind field was reflected in a co-activation of right superior colliculus and amygdala.</td>
</tr>
<tr>
<td>Pegna et al. (2005)</td>
<td>Assessed the capacity of a patient with bilateral destruction of the visual cortex and cortical blindness to recognize emotional and non emotional visual stimuli and determined the brain structures involved in the spared abilities.</td>
<td>The patient showed a selective ability to guess the type of emotional facial expression being displayed and a concomitant activation of the right amygdala in response to all emotional faces expressing anger, happiness and fear.</td>
</tr>
<tr>
<td>de Gelder and Hadjikhani (2006)</td>
<td>Examined using fMRI whether patients with neglect are more likely to consciously detect in the neglected hemifield, emotionally negative complex scenes rather than visually similar neutral pictures.</td>
<td>Presentation to the blind visual field emotional body images resulted in activation of several cortical and subcortical right hemisphere structures. Fearful bodily expressions presented in the contralesional (unattended) visual field simultaneously with neutral bodies in the ipsilesional field were detected more often than left-side neutral or happy bodies.</td>
</tr>
<tr>
<td>Tamietto et al. (2007)</td>
<td>Tested 3 patients with visual extinction with pictures of fearful, happy, and neutral bodily expressions briefly presented unilaterally or to both fields simultaneously.</td>
<td>Consiously perceived facial emotions presented in the RVF activated cortical areas in the left hemisphere, whereas neglected (unconsciously perceived) facial expressions in the LVF activated cortical and limbic areas in the right hemisphere.</td>
</tr>
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