Neuropsychology of facial expressions. The role of consciousness in processing emotional faces

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Abstract

Neuropsychological studies have underlined the significant presence of distinct brain correlates deputed to analyze facial expression of emotion. It was observed that some cerebral circuits were considered as specific for emotional face comprehension as a function of conscious vs. unconscious processing of emotional information. Moreover, the emotional content of faces (i.e. positive vs. negative; more or less arousing) may have an effect in activating specific cortical networks. Between the others, recent studies have explained the contribution of hemispheres in comprehending face, as a function of type of emotions (mainly related to the distinction positive vs. negative) and of specific tasks (comprehending vs. producing facial expressions). Specifically, ERPs (event-related potentials) analysis overview is proposed in order to comprehend how face may be processed by an observer and how he can make face a meaningful construct even in absence of awareness. Finally, brain oscillations is considered in order to explain the synchronization of neural populations in response to emotional faces when a conscious vs. unconscious processing is activated.

Keywords: Face; Consciousness; Brain; Brain oscillations; ERPs

1. Face and consciousness

Rapid detection of emotional information is highly adaptive, since it provides critical elements on environment and on the attitude of the other people (Darwin, 1872; Eimer & Holmes, 2007). Indeed faces are a critically important source of social information and it appears we are biologically prepared to perceive and respond to faces in an unique manner (Balconi, 2008; Ekman, 1993). Recent investigations of emotional processing have uncovered components of a complex network for the detection and analysis of emotionally significant information from faces. Brain areas generally involved in evaluation of the emotional and motivational significance of facial expressions appear to be mediated by the amygdala and orbitofrontal cortex, while structures such as the anterior cingulate, prefrontal cortex and somatosensory areas are linked to the conscious representation of emotional facial expression for the strategic control of thought and action (Adolphs, 2003).

Between the cortical and subcortical structures, in neurophysiological studies in monkey, some neurons in the amygdala have been found to selectively respond to facial stimuli (Balconi, Brambilla & Falbo, 2009a; Nakamura, Mikami & Kubota, 1992; Leonard, Rolls, Wilson & Baylis, 1985). A particularly notable finding is that the left amygdala was more greatly activated during the processing of fearful expressions than during the processing of happy expressions (Morris, Frith, Perret, Rowland, Young, Calder & Dolan 1996; Morris, Friston, Buchel, Frith, Young, Calder & Dolan 1998). Further, an increasing intensity of sad facial expressions was associated with enhanced activity in the left amygdala (Blair, Morris & Frith, 1999).

2. What type of unconscious processing of facial expression?

Nevertheless, there is an increasing evidence supporting the idea that significant affective processes happen outside consciousness (Calvo & Esteves, 2005; Dimberg, Elmehed & Thunberg, 2000; LeDoux, 1996). About facial expressions, it has been shown that the affective information contained in facial expression is perceived involuntarily (Eastwood & Smilek, 2005) and is able to constrict the focus of attention. Considering the critical social relevance of facial expressions of emotion, it is not surprising that the emotions displayed in facial expression can be perceived even when subjects have no conscious experience of perceiving these expressions (Balconi & Lucchiari, 2005a).

Thus, attentive and pre-attentive facial stimulus processing is an important topic to explain how people comprehend affective disposition in others. Research on consciousness introduced a distinction between automatic and conscious (Posner, 1978) or automatic and controlled (Shiffrin & Schneider,

1977) information processing. This concept was developed to account for the fact that the selectivity of attention is better described in terms of a flexible and strategic distribution of limited processing resources across stimuli and tasks. The effect of perceived but not consciously elaborated emotional stimulus is critique for a great amount of neuropsychological research, on both normal and pathological subjects (Balconi et al., 2009b; Bunce, Bernat, Wong & Shevrin, 1999; Dimberg & Öhman, 1996; Wong, Shevrin & Williams, 1994). Specifically, facial expressions of emotion are considered unique in their ability to orient the subjective cognitive resources, even if people are unable to process information consciously. Secondly, it was hypothesized that subjects are able to assign a semantic value to the emotional content of faces even in an unaware condition (Balconi & Pozzoli, 2005a; Dimberg et al., 2000; Wong & Root, 2003).

In humans, evidence for the unconscious perception of emotional face has been revealed in terms of subjective reports (Esteves, Parra, Dimberg & Ohman, 1994), autonomic reactions (Morris & Dolan, 2001), brain imaging measures (Whalen, Rauch, Etcoff, McInerney, Lee & Jenike, 1998), as well as ERPs (Kiefer & Spitzer, 2000) and brain oscillations (Balconi & Pozzoli, 2007; 2008). The EEG approach (for both ERP and brain oscillations) will be explored in the next paragraphs. An obvious and well-known example of unconscious perception of emotion is subliminal stimulation effect. This phenomenon was studied in a limited number of cases (Wong et al., 1994; Stone & Valentine, 2007). Animal studies suggest that fear-related responses are elicited by a direct subcortical pathway from the thalamus direct to the amygdala, allowing emotional (and specifically threat) to be processed automatically and outside awareness. In addition, unconscious stimulation showed to be sensitive to the emotional content of the stimuli, as revealed by different behavioural and physiological measures (Lang, Bradley & Cuthbert, 1997).

Unconsciously processing for facial stimuli can also be demonstrated in clinical context, such as in case of prosopagnosia. In most cases prosopagnosics appear to recognize familiar faces even though they fail to identify the persons verbally. Therefore, the patients showed an unconscious recognition that cannot be accessed consciously (Tranel & Damasio, 1985). However, although the existence of unconscious affect elaboration was accepted, the question concerning its importance for emotional decoding is still open. Only a limited number of studies has explored the significance of conscious vs. unconscious face comprehension, based on priming effect or subliminal stimulation (Balconi & Lucchiari, 2007; Batty & Taylor, 2003; Holmes, Vuilleumier & Eimer, 2003).

3. How to explore consciousness correlates of facial expression comprehension: the ERP contribution

Although the existence of unconscious elaboration was accepted, the question concerning its importance for emotional decoding is still open. Only little studies have explored the significance of conscious vs. unconscious face comprehension based on priming effect or subliminal stimulation (Balconi & Lucchiari, 2007; Batty & Taylor, 2003; Holmes et al., 2003). Moreover, an another useful measure to analyze conscious and unconscious perception of faces is the masking procedure. By low intensity and brief exposure, a target stimulus can be made unrecognized when another stimulus is presented simultaneously, shortly before (forward masking), or shortly after (backward masking) (Balconi & Mazza, 2010; Rolls, 2006). This paradigm is used to investigate below awareness response to emotional perception in which facial expressions are followed immediately by a masking face. Nevertheless, the effect of this masking technique was not largely used for the emotional face detection. So, we have no precise knowledge of the actual effect of masked emotional stimulus on the elaboration of the target one.

A second main point is that most of the recent research on the detection and analysis of emotionally significant information from face have used fMRI measures, which are based on relatively slow hemodynamic brain responses, and the studies on the time course of emotional processing have been relatively scarce (Simons, Hannula, Warren & Day, 2007). Thus these methods need to be completed with measures that provide insights into temporal parameters of emotional comprehension, such as event-related potential (ERP). Specifically, ERP measures are very useful tools to examine the time course of the conscious vs. unconscious stimulus elaboration at a very high temporal resolution (Balconi & Pozzoli, 2005b; Shevrin, 2001; Snodgrass, 2000). Secondly, by comparing wave profiles between conditions, they may furnish a valid measure of the qualitative nature of the emotional mechanisms, checking the resemblance of the underlying processes for attentive and not attentive emotional elaboration (Balconi & Lucchiari, 2005b; 2007; Brázdil, Rektor, Daniel, Dufek & Jurak, 2001).

For this reason it is interesting to compare ERP profiles in conscious vs. unconscious condition, in order to verify the similarity of the comprehension processes, firstly in terms of the resemblance of the two processes, attentive and pre-attentive, from a qualitative point of view (morphological analysis); secondly about the existence of some differences related to the type and the amount of cognitive resources required to process the two types of stimuli (ERP modulation in terms of peak amplitude); finally about the temporal course of this processes, with a delayed or anticipated effect for unconscious elaboration (ERP modulation in terms of peak latency).

Previous research have found a general qualitative similarity between conscious/unconscious conditions (Balconi & Lucchiari, 2005a; Balconi & Mazza, 2009a; Shevrin, 2001). Nevertheless actually it is not clear at what extent the two processes can be analogous, specifically with respect of the semantic value of unconscious face detection. A specific ERP measure for emotional face comprehension was found, that is an early negative deflection at about 240 ms post-stimulus, related to emotional faces more than neutral faces for an explicit (Streit, Wolwer, Brinkmeyer, Ihl & Gaebel, 2000) or an implicit task (Sato, Kochiyama, Yoshikawa & Matsumura, 2001). It was discussed as a cognitive marker of the complexity and the relevance of the stimulus (Carretié & Iglesias, 1995; Eimer & Holmes, 2007). On the other hand, it was interpreted such as an emotional-face index (Balconi & Pozzoli, 2009; Herrman, Aranda, Ellgrin, Mueller, Strik, Heidrich & Fallagatter, 2002), able to evidence the conscious comprehension of emotional significance of faces. Based on this evidence, it is expected a modulation of N200 as a function of attentive (conscious) vs. pre-attentive (unconscious) elaboration. The former condition could be marked by an ampler deflection that signals the attentional resources allocation by the subjects.

The effect of unconscious elaboration for emotional relevant stimuli was previously tested even through a second ERP effect, the P300 modulation. In general, it was found not to be exclusive for faces, since it was observed for other objects with an emotional content (Bernat, Bunce & Shevrin, 2001). P300 was shown to be related even to unconsciously processed stimuli, that result to be relevant for the subject (Kotchoubey, 2005; Lang et al., 1997). This deflection, generally more posteriorly localized (parietal sites), was found to be related to decisional process, and it is activated even in absence of attentive resource allocation (Balconi & Mazza, 2009a; Polich, 2007). Specifically, a subcomponent of P300, P3a (in contrast to the P3b), is relatively attention-independent and may serve as a component of the response. Moreover, the P3a was previously associated with the automatic aspects of the orienting response that are involved in detecting a relevant (in some cases threatening) stimulus (Liddell, Williams, Rathjen, Shevrin & Gordon, 2004). For previous reasons we expected that responses to emotional face should be marked by P3a component in a greater measures for pre-attentive processing than for attentive one. This should put in evidence the rapid detection of emotional relevant stimuli, that will be processed in more details in a successive cognitive conscious phase.

The comparison between attentive and pre-attentive processes was conducted even by considering the temporal effect they produced. As shown by some studies, delayed unaware information processing represents a distinctive feature of unconscious visual perception (Balconi, 2006; Bernat et al., 2001; Junghöfer, Bradley, Elbert & Lang, 2001), and it was explained as a consequence of a more complex process underlying unconscious elaboration. Contrarily, some other studies have found an anticipated peak modulation for unconscious compared to conscious perception (Brádzil et al., 2001). Thus the time of emergence of peak variation as a function of consciousness is a main topic to be considered, in order to have more information on the nature of the cognitive processes implicated.

4. Emotional valence of faces and cortical response: some experimental evidences

A main issue to be considered is related to the semantic significance of unconsciously processed stimulus (Stenberg, Lindgren, Johansson, Olsson & Rosen, 2000). Thus, as it was shown by previous results, a main factor to be effective in orienting subject's response to the emotional cues in case of unconscious stimulation is the content of the stimulus. A second main factor is related to the cortical contribution by two different hemispheres in responding to different emotional types. The intervention of different cortical modules for conscious and unconscious information elaboration (lateralization effect) or with respect of specific facial pattern (emotion-effect) is an important point that requires to be elucidated. On this level, divergent results were obtained, even if previous research used a reduced range of emotions, fact that prevents them to answer exhaustively to this matter.

Firstly, responses to unconscious stimulation showed to be sensitive to the emotional content of the facial stimuli, as revealed by different behavioural and physiological measures (Lang et al., 1997; Balconi & Lucchiari, 2007; Kiss & Eimer, 2008). Facial expressions are an important key to explain the emotional situation and they can consequently produce different reactions in a viewer. As suggested by Russell's circumflex model (Russell, 2003; Russell & Bullock, 1985), each emotion and its facial expression represents a specific response to a particular kind of significant event, that is it is evaluated by the subject in line with its motivational significance. This appraisal process is regulated by two main criteria: the arousing power of the stimulus (high or low); the valence of the emotional stimulus (positive or negative) (Balconi & Mazza, 2010). Thus, the entire emotional universe is represented by the two axes, and the "significance" attributed to the emotional expressions may have a direct effect on the cognitive level and the degree of attention allocated.

Previous ERP studies in conscious condition have pointed out the effect of arousing power and valence of expressions on subjective responses to emotional faces. In particular, a larger negative peak was shown at about 230 ms post-stimulus (N230) in response to some emotional types (Streit et al., 2000; Sato et al., 2001; Balconi & Pozzoli, 2003; Balconi & Lucchiari, 2007), that are high arousing, threatening and negative faces. So, it was assumable that emotional expressions are distributed along a continuum, as function of arousing and threatening power (from higher to lower) and hedonic value (from negative to positive). Thus, the motivational significance of emotions has an effect on subjects' responses, since it was found that emotionally salient stimuli (unpleasant compared to neutral) generate greater magnitude of ERP response, for both N200 (Balconi & Lucchiari, 2005a; Junghöfer et al., 2001) and P300 (Morita, Morita, Yamamoto, Waseda & Maeda, 2001; Schupp, Cuthbert, Bradley, Cacioppo, Ito & Lang, 2000) measures. Thus we hypothesized that significance of emotional expressions in terms of the importance and of the experiential meaning they have for the subjects could influence the degree of attentional resources allocated, with an effect on ERP amplitude modulation (Frijda, 1996; Schorr, 2001).

The impact of different emotional patterns should be tested for both attentive and pre-attentive mechanisms, and the attended effect has been theoretically related to motivated attention, in which motivationally relevant stimuli naturally arouse and direct attentional resources (Hamm, Schupp & Weike, 2003; Keil, Bradley, Hauk, Rockstroh, Elbert & Lang, 2002). In fact, also unconscious condition seems to produce similar responses. Information presented under the conscious threshold may be processed on a high level even if the subject is unaware of this information, since pre-attentive response to emotional faces is effective in eliciting psychophysiological autonomic modulations (Regan & Howard, 1995; Öhman & Soares, 1998). In addition, ERPs have been shown to be sensitive to unconscious perception of affective words (Chapman, McCrary & Martin, 1980; Cacioppo, Crites & Gardner, 1996; Skrandies & Weber, 1996), pictures (Johnston, Miller & Burleson, 1986; Yee & Miller, 1987), and faces (Kayser, Tenke, Nordby, Hammerborg, Kennet & Gisela, 1997; Kiss & Eimer, 2008). For example, some investigations were applied to the classical oddball paradigm (Bernat et al., 2001; Brázdil et al., 2001), and they found a P3 ERP effect for unconscious stimuli similar to supraliminal condition. Also the emotional faces can be positively or negatively evaluated without conscious recognition and they are able to induce a specific psychophysiological response into the observer (Balconi & Lucchiari, 2005a; 2007).

5. Brain oscillation and facial patterns

In parallel, brain oscillations of the EEG were found a powerful tool to analyze the cognitive processes related to emotion comprehension in general (Krause, 2003; Balconi & Lucchiari, 2006), and, even if less studied, to unconscious perception (Summerfield, Jack & Burgess, 2002). Some studies have examined the alpha frequency band modulation and they have revealed that this band can uncover the cortical correlates of relatively small differences in emotion processing (Aftanas, Koshkarov, Pokrovskaja, Lotova & Mordvintsev, 1996). Nevertheless, it was found an anterior asymmetry in alpha reduction, that was explained as correlate of changes on individual affective state (Davidson, 1998; Dimberg & Petterson, 2000). Moreover, Klimesch, Russegger, Doppelmayr and Pachinger (1998) reported that lower-1 alpha frequency (7-12 Hz) desynchronizes as a response to a presented warning stimulus. These authors suggested that the responses of this lowest alpha band probably reflect brain processes associated to phasic alertness.

Recently Güntekin and Başar (2007) observed that angry faces evoke higher amplitude alpha (9-13 Hz) responses in the posterior cortical areas, whereas increased beta (15-24 Hz) responses were observed in anterior areas in comparison to happy face stimulation. The authors stated that subject experienced negative valence while processing faces with angry expressions: this valence effect influenced the brain responses such that significantly increased amplitudes were found over left frontal and central electrodes in the 15-24 Hz frequency range, as well as over parietal, temporal and occipital areas in the 9-13 Hz frequency range.

Moreover, alpha activity in response to emotional cues was related to the lateralization effect (Balconi et al., 2009; Balconi & Mazza, 2010). EEG research has confirmed what stated by the valence hypothesis: relative increase of left hemisphere activity was found with positive emotional stimuli (Davidson & Henriques, 2000; Waldstein, Kop, Schmidt, Haufler, Krantz & Fox, 2000). More recently, the approach-withdrawal model of emotion regulation posits that emotional behaviours are associated with a balance of activity in left and right frontal brain areas that can be explained in an asymmetry measurement (Davidson, 1995). Resting frontal EEG asymmetry has been hypothesized to relate to appetitive (approach-related) and aversive (withdrawal-related) emotions, with heightened approach tendencies reflected in left-frontal activity and heightened withdrawal tendencies reflected in relative right-frontal activity (Balconi et al., 2009; Davidson, 1992). Subjects with relatively less left- than right-frontal activity exhibit larger negative affective responses to negative emotions and smaller positive affective responses to positive emotions (Wheeler, Davidson & Tomarken, 1993). Some interesting results were collected in relationship with specific facial emotional patterns, such as anger and fear. In particular, anger correlated positively in a significant measure with right alpha power and negatively with left alpha power. The lateralization effect was revealed even by Harmon-Jones (2004), who indicated the importance of the prefrontal cortex in emotional processing. The author argued that the emotions with motivational tendencies are related to greater left frontal EEG activity.

6. Brain oscillations in unconscious processing of faces

Only more recently brain oscillations were considered as useful measure to analyze the cortical distribution of brain activation in response to emotional face not consciously elaborated, taking into account the subjective predisposition for different types of emotional stimuli (positively and negatively valenced; more/less threatening). It was shown that brain oscillations respond to different types of emotional faces presented in unconscious condition (Balconi & Mazza, 2009b). Brain response to emotional stimuli has been investigated in several studies, since frequency band variations were found a powerful tool to analyze the cognitive processes related to emotion comprehension (Balconi & Lucchiari, 2007; Balconi & Pozzoli, 2009; Başar et al., 1999; Knyazev, 2007; Krause, 2003). Few previous studies on brain responses to emotion-related stimuli have examined the narrow frequency bands (Aftanas, Varlamov, Pavlov, Makhnev & Reva, 2002). Recent researches showed that the event-related theta band power responds specifically to prolonged visual emotional stimulation (Balconi et al., 2009a; Krause, Viemero, Rosenqvist, Sillanmaki & Astrom, 2000), and a synchronization was revealed in case of coordinated response indicating readiness to process information (Başar, 1999). Thus, theta EEG power typically increases with increasing attentional demands and/or task difficulty. Also the effect of valence in affective picture processing was studied, showing that valence discrimination is associated with the early time-locked synchronized theta activity (Aftanas et al., 2001; Balconi & Pozzoli, 2009). Accordingly, it was concluded that the delta response is related to signal detection and decision making. About motivational processing, Karakaş, Erzengin and Basar (2000) found a significant increased of delta as a function of task-relevant responding that necessitates conscious stimulus evaluation and stimulus updating. More recently Knyazev (2007) shown that delta oscillations depend on activity of motivational systems and participate in salience detection. Moreover, as regard of alpha frequency (7-12 Hz), Klimesch et al. (1998) reported that alpha frequency (in particular lower-1 alpha) desynchronizes as a response to a presented warning stimulus (Balconi & Pozzoli, 2008). These authors suggested that the responses of this lowest alpha band most probably reflect brain processes associated to phasic alertness. Some other studies have examined the alpha frequency band of the EEG and have revealed that this band can uncover the cortical correlates of relatively small differences in emotion processing (Aftanas et al., 1996). Nevertheless, it was found an anterior asymmetry in alpha reduction, that was explained as correlates of changes on individual affective state (Balconi & Mazza, 2010; Davidson, 1998; Dimberg & Petterson, 2000). The contrasting results obtained by previous research may have been inducted by different frequency ranges selected to differentiate upper- and lower- alpha band, that could have introduced some methodological limits (Doppelmayer, Klimesch, Pachinger & Ripper, 1998).

Moreover, beta oscillations were scarcely explored in response to emotional stimuli. In most cases it was found a beta modulation as a function of visual patterns of facial stimuli (Okazaki, Kaneki, Yumoto & Arima, 2008): in other cases its correlation with the emotional stimuli was mediated by psychological constructs such as anxiety (Knyazev, Bocharov, Levin, Savostyanov & Slobodskoj-Plusnin, 2008). A specific study that has explored beta modulation by facial expressions of emotion revealed a significant effect only for anger face (increased beta), whereas no other effect was significant (Güntekin & Basar, 2007). On the contrary, other studies did not reveal any effect of this band for the emotional processing (Balconi & Pozzoli, 2007; Knyazev, 2007).

Finally, recent research has demonstrated that the modulation of gamma band activity (20-50 Hz) in time windows between 200 and 400 ms following the onset of a stimulus is associated with perception of coherent visual objects (Balconi & Lucchiari, 2008; Müller, Keil, Gruber & Elbert, 1999), and may be a signature of active memory. In parallel, gamma was found sensitive to emotional vsnonemotional stimuli and more specifically it was related to the arousal effect: early gamma was enhanced in response to aversive or highly arousing stimuli compared to neutral pictures (Keil, Muller, Gruber, Wienbruch, Stolarova & Elbert, 2001). This result was revealed in accordance with previous research that employed ERP measures for arousing pictures or emotional face (Balconi & Lucchiari, 2005a; Balconi et al., 2009b; Sato et al., 2001), since these studies found a modulation of the increased arousal on ERPs.

Finally, gamma band activity (GBA) was more studied for consciousness/unconsciousness comparison (Balconi et al., 2009b; Summerfield et al., 2002). In general it was found that GBA was enhanced by supraliminal more than subliminal stimuli, as well as more by high arousal (anger and fear) than low arousal (happiness and sadness) faces in both conscious and unconscious condition (Balconi & Lucchiari, 2008).

Nevertheless, unconscious modulation of frequency bands as a function of emotional facial expressions was not widely investigated. Thus, although the existence of unconscious elaboration of emotional faces was accepted, the question concerning its importance for emotional comprehension is still open. Secondly, these results were mainly acquired by using subliminal stimulation procedure, while other unconscious induction techniques were scarcely explored.

7. Cortical lateralization effect and the role of emotional type in frontal brain area modulation

Although frequency bands have recently been investigated in various perceptive and cognitive domains, their specific role for emotion processing is unclear (Balconi & Pozzoli, 2008; Başar, 1999), and contrasting results were obtained (Balconi et al., 2009a; Knyazev, 2007; Güntekin & Basar, 2007). Some interesting results were collected in response to specific emotional patterns, showing a localized frontal area response to each emotional cues. In particular, sadness was correlated positively with right alpha power and negatively with left alpha power, whereas happiness was mainly related to left-side activation (Davidson & Fox, 1982). For other emotions, such as anger, results were more heterogeneous. More generally, lateralized electrophysiological parameters (decreased alpha power EEG), measured during the recollection of events associated with anger, increased within the right hemisphere (Waldstein et al., 2000). However, contrasting results have been collected in some studies (Coan, Allen & Harmon-Jones, 2001). Increased left frontal cortical activity was associated with anger (Harmon-Jones & Sigelman, 2001). In addition, increased left frontal activity and decreased right frontal activity were associated with trait anger (Harmon-Jones & Allen, 1998) and state anger (Harmon-Jones & Sigelman, 2001).

Different explicative models were proposed, in order to justify this lateralization effect. The right hemisphere model supposes that the right side is specialized for the perception, expression, and experience of emotion, regardless the valence (positive or negative) of the emotional content (Davidson & Schwartz, 1976; Heilman & Bowers, 1990). Specifically, regarding the perception of emotion, recent studies on faces have demonstrated left visual field superiority (right hemisphere) for discriminating emotional faces (Adolphs, Damasio, Tranel & Damasio, 1996; Borod, Cicero, Obler, Welkowitz, Erhan & Santschi, 1998). About the expression of emotions, a facial asymmetry was found, with a more expressive left side (right-controlled) during emotion expression (Balconi, 2008; Borod, Haywood & Koff, 1997; Gainotti, 1972). Also it was identified a reduced ability forfacial emotional expression in case of right-hemisphere damage. Brain damage studies have confirmed this effect, showing that patients with right-hemisphere lesions performed worse than patients with left-hemisphere lesions in recognizing facial expressions (Adolphs et al., 1996; Ahern, Schomer, Kleefield & Blume, 1991). Moreover, ERP and fMRI studies supported the hypothesis of right hemisphere specialization for the processing of facial emotions (Balconi & Pozzoli, 2007; Narumoto, Okada, Sadato, Fukui & Yonekura, 2001).

Nevertheless, alternative hypotheses were recently formulated on the lateralization effect, which offered different explanations of hemispheric differences. The valence model supposes that, as opposed to the right-hemisphere hypothesis, cortical differences between the two hemispheres are attributable to positive vs. negative valence of emotions (Everhart, Carpenter, Carmona, Ethridge & Demaree, 2003; Silberman & Weingartner, 1986). In general, this model was tested for expression and perception of emotions, as well as for emotional experience. Based on this model, the right hemisphere is specialized for negative emotions and the left hemisphere for positive emotions. Generally, right hemisphere injury prevents the patient to process more negative vs. positive expressions (Borod et al., 1998). Some EEG research has supported the valence hypothesis: relative increase of left hemisphere activity was found with positive emotional states (Davidson & Henriques, 2000; Waldstein et al., 2000), though other EEG studies have also found some opposite results (Schellberg, Besthorn, Pfleger & Gasser, 1993).

More recently, the approach-withdrawal model of emotion regulation posits that emotional behaviours are associated with a balance of activity in left and right frontal brain areas that can be explained in an asymmetry measurement (Balconi et al., 2009b; Davidson, 1995; Harmon-Jones & Allen, 1997; Sutton & Davidson, 1997). Resting frontal EEG asymmetry has been hypothesized to relate to appetitive (approach-related) and aversive (withdrawal-related) motivation and emotion, with heightened approach tendencies reflected in left-frontal activity and heightened withdrawal tendencies reflected in relative right-frontal activity (Davidson, 1992). Subjects with relatively less left- than right-frontal activity exhibit larger negative affective responses to negative aversive emotions and smaller positive affective responses to positive approach emotions (Wheeler et al., 1993).

However, some contrasting results remain to be explained, mainly about the real significance of each emotion with respect to its functional value. In fact, facial expressions are an important key to explain the emotional situation and, consequently, they can produce different reactions in a viewer. As a whole, the significance of emotional expressions for the subject (in terms of their high/low averseness, valence and coping potential related to the corresponding emotion) should influence both the physiological and cognitive level, with interesting correspondence on EEG modulation. It was assumed that emotional expressions are distributed along a continuum as a function of the motivational significance of the emotional cue in terms of averseness (from higher to lower) and hedonic value (from negative to positive) and coping potential (Balconi & Lucchiari, 2005a; 2007; Sato et al., 2001; Streit et al., 2000).

According to this assumption, the "functional model" of emotional expression supposes that people adopt a behaviour that is functional to their coping activity (Frijda, 1994; Frijda, Kuipers & Terschure, 1989). Coping activity determines the significance of emotional situation, since it is able to orient the subject's behaviour as a function of the individual expectancies about successfully acting to alter the situation/external context. In fact, whereas some negative emotional expressions, such as anger and sadness, are generated by negative, aversive situations, the coping potential may introduce some differences in subjective response as a function of how people appraise their ability to cope with the aversive situation (Frijda, 1993; Lazarus, 1991; Hewig, Hagemann, Seifert, Naumann & Bartussek, 2004). From this perspective, anger may be appraised as a negative but also an active emotion, that arouses approach motivation.

References

Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. *Nature Reviews Neuroscience*, 4, 165-178.

Adolphs, R., Damasio, H., Tranel, D., & Damasio, A.R. (1996). Cortical systems for the recognition of emotion in facial expressions. *Journal of Neuroscience*, 16 (23), 7678-7687.

Aftanas, L.I., Koshkarov, V.I., Pokrovskaja, V.L., Lotova, N.V., & Mordvintsev, Y. (1996). Event-related desynchronization (ERD) patterns to emotion-related feedback stimuli. *International Journal of Neuroscience*, 87, 151-173.

Aftanas, L.I., Varlamon, A.A., Pavlov, S.V., Makhnev, V.P., & Reva, N.V. (2001). Affective picture processing: event-related synchronization within individually defined human theta band is modulated by valence dimension. *Neuroscience Letters*, 303, 115-118.

Aftanas, L.I., Varlamov, A.A., Pavlov, S.V., Makhnev, V.P., & Reva, N.V. (2002). Time-dependent cortical asymmetries induced by emotional arousal: EEG analysis of event-related synchronization and desynchronization in individually defined frequency bands. *International Journal of Psychophysiology*, 44, 67-82.

Ahern, G.L., Schomer, D.L., Kleefield, J., & Blume, H. (1991). Right hemisphere advantage for evaluating emotional facial expressions. *Cortex*, 27 (2), 193-202.

Balconi, M. (2006). Exploring consciousness in emotional face decoding: an event-related potential analysis. *Genetic, Social, and General Psychology Monographs*, 132, 129-150.

Balconi, M. (2008). *Neuropsicologia della comunicazione*. Milano: Springer-Verlag.

Balconi, M., Brambilla, E., & Falbo, L. (2009a). BIS/BAS, Cortical oscillations and coherence in response to emotional cues. *Brain Research Bulletin*, 80, 151-157.

Balconi, M., Brambilla, E., & Falbo, L. (2009b). Appetitive vs defensive responses to emotional cues. Autonomic measures and brain oscillation modulation. *Brain Research*, 1296, 72-84.

Balconi, M., Falbo, L., & Brambilla, E. (2009). BIS/BAS responses to emotional cues: self-report, autonomic measure and alpha band modulation. *Personality and Individual Differences*, 47, 858-863.

Balconi, M., & Lucchiari, C. (2005a). In the face of emotions: event-related potentials in supraliminal and subliminal facial expression recognition. *Genetic, Social, and General Psychology Monographs*, 131 (1), 41-69.

Balconi, M., & Lucchiari, C. (2005b). Event-related potentials related to normal and morphed emotional faces. *Journal of Psychology*, 139, 176-192.

Balconi, M., & Lucchiari, C. (2007). Consciousness and emotional facial expression recognition: subliminal/supraliminal stimulation effect on N200 and P300 ERPs. *Journal of Psychophysiology*, 21, 100-108.

Balconi, M., & Lucchiari, C. (2008). Consciousness and arousal effects on emotional face processing as revealed by brain oscillations. A gamma band analysis. *International Journal of Psychophysiology*, 67, 41-46.

Balconi, M., & Mazza, G. (2009a). Consciousness and emotion. ERP modulation and attentive vs pre-attentive elaboration of emotional facial expressions by backward masking. *Motivation and Emotion*, 33, 113-124.

Balconi, M., & Mazza, G. (2009b). Brain oscillations and BIS/BAS (behavioral inhibition/activation system) effects on processing masked emotional cues. ERS/ERD and coherence measures of alpha band. *International Journal of Psychophysiology*, 74, 158-165.

Balconi, M., & Mazza, G. (2010). Lateralisation effect in comprehension of emotional facial expression: a comparison between EEG alpha band power and behavioural inhibition (BIS) and activation (BAS) systems. *Laterality*, 3, 1257-1268.

Balconi, M., & Pozzoli, U. (2003). ERPs (event-related potentials), semantic attribution, and facial expression of emotions. *Consciousness and Emotion*, 4, 63-80.

Balconi, M., & Pozzoli, U. (2005a). Morphed facial expressions elicited a N400 ERP effect. A cerebral domain-specific semantic module. *Scandinavian Journal of Psychology*, 46, 467-474.

Balconi, M., & Pozzoli, U. (2005b) Comprehending semantic and grammatical violations in Italian. N400 and P600 comparison with visual and auditory stimuli. *Journal of Psycholinguistic Research*, 34, 71-98.

Balconi, M., & Pozzoli, U. (2007). Event-related oscillations (EROs) and event-related potentials (ERPs) comparison in facial expression recognition. *Journal of Neuropsychology*, 1, 283-294.

Balconi, M., & Pozzoli, U. (2008). Event-related oscillations and event-related potentials in emotional face recognition. A regression analysis. *International Journal of Neuroscience*, 2, 4-24.

Balconi, M., & Pozzoli, U. (2009). Arousal effect on emotional face comprehension. Frequency band changes in different time intervals. *Physiology and Behavior*, 97, 455-462.

Başar, E. (1999). *Brain Function and Oscillations. II. Integrative Brain Function. Neurophysiology and Cognitive Processes*. Heidelberg: Springer.

Başar, E., Demiralp, T., Schürmann, M., Basar-Eroglu, C., & Ademoglu, A. (1999). Oscillatory brain dynamics, wavelet analysis, and cognition. *Brain and Language*, 66, 146-183.

Batty, M., & Taylor, M.J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research*, 17, 613-620.

Bernat, E., Bunce, S., & Shevrin, H. (2001). Event-related brain potentials differentiate positive and negative mood adjectives during both supraliminal and subliminal visual processing. *International Journal of Psychophysiology*, 42, 11-34.

Blair, R.J.R., Morris, J.S., Frith, C.D., Perret, D.I., & Dolan, R.J. (1999). Dissociable neural responses to facial expressions of sadness and anger. *Brain*, 122, 883-893.

Borod, J.C., Cicero, B.A., Obler, L.K., Welkowitz, J., Erhan, H.M., Santschi, C., Grunwald, L.S., Agosti, R.M., & Whalen, J.R. (1998). Right hemisphere emotional perception: evidence across multiple channels. *Neuropsychology*, 12, 446-458.

Borod, J.C., Haywood, C.S., & Koff, E. (1997). Neuropsychological aspects of facial asymmetry during emotional expression: a review of the normal adult literature. *Neuropsychology Review*, 7 (1), 41-60.

Brázdil, M., Rektor, I., Daniel, P., Dufek, M., & Jurak, P. (2001). Intracerebral event-related potentials to subthreshold target stimuli. *Clinical Neurophysiology*, 112, 650-661.

Bunce, V., Bernat, E., Wong, P.S., & Shevrin, H. (1999). Further evidence for unconscious learning: preliminary support for the conditioning of facial EMG to subliminal stimuli. *Journal of Psychiatry Research*, 33, 341-347.

Cacioppo, J.T., Crites, S.L., & Gardner, W.L. (1996). Attitudes to the right: evaluative processing is associated with lateralized late positive event-related brain potentials. *Personality and Social Psychology Bulletin*, 22, 1205-1219.

Calvo, M.G., & Esteves, F. (2005). Detection of emotional faces: low perceptual threshold and wide attentional span. *Visual Cognition*, 12, 13-27.

Carretié, L., & Iglesias, J. (1995). An ERP study on the specificity of facial expression processing. *International Journal of Psychophysiology*, 19, 183-192.

Chapman, R.M., McCrary, J.W., Chapman, J.A., & Martin, J.K. (1980). Behavioral and neural analyses of connotative meaning: word classes and rating scales. *Brain and Language*, 11, 319-339.

Coan, J.A., Allen, J.J.B., & Harmon-Jones, E. (2001). Voluntary facial expression and hemispheric asymmetry over the frontal cortex. *Psychophysiology*, 38 (6), 912-925.

Darwin, C. (1872). *The Expression of the Emotions in Man and Animals*. London: John Murray.

Davidson, R.J. (1992). Anterior cerebral asymmetry and the nature of emotion. *Brain and Cognition*, 20 (1), 125-151.

Davidson, R.J. (1995). *Cerebral Asymmetry, Emotion, and Affective Style*. Cambridge, MA: MIT Press.

Davidson, R.J. (1998). Anterior electrophysiological asymmetries, emotion, and depression: conceptual and methodological conundrums. *Psychophysiology*, 35, 607-614.

Davidson, R.J., & Fox, N.A. (1982). Asymmetrical brain activity discriminates between positive and negative affective stimuli in human infants. *Science*, 218 (4578), 1235-1237.

Davidson, R.J., & Henriques, J. (2000). *Regional Brain Function in Sadness and Depression*. New York: Oxford University Press.

Davidson, R.J., & Schwartz, G.E. (1976). Patterns of cerebral lateralization during cardiac biofeedback versus the self-regulation of emotion: sex differences. *Psychophysiology*, 13 (1), 62-68.

Dimberg, U., Elmehed, K., & Thunberg, M. (2000). Unconscious facial reactions to emotional facial expressions. *Psychological Sciences*, 11, 86-89.

Dimberg, U., & Öhman, A. (1996). Behold the wrath: psychophysiological responses to facial stimuli. *Motivation and Emotion*, 20, 49-182.

Dimberg, U., & Petterson, M. (2000). Facial reactions to happy and angry facial expressions: evidence for right hemisphere dominance. *Psychophysiology*, 37, 693-696.

Doppelmayer, M., Klimesch, W., Pachinger, T., & Ripper, B. (1998). Individual differences in brain dynamics. Important implications for the calculation of event-related band power. *Biological Cybernetics*, 79, 49-57.

Eastwood, J.D., & Smilek, D. (2005). Functional consequences of perceiving facial expressions of emotion without awareness. *Consciousness and Cognition*, 14, 565-584.

Eimer, M., & Holmes, A. (2007). Event-related brain potential correlates of emotional face processing. *Neuropsychologia*, 45, 15-31.

Ekman, P. (1993). Facial expression and emotions. *American Psychologist*, 48, 384-392.

Esteves, F., Parra, C., Dimberg, U., & Öhman, A. (1994). Nonconscious associative learning: Pavlovian conditioning of skin conductance responses to masked fear relevant facial stimuli. *Psychophysiology*, 31, 375-385.

Everhart, D.E., Carpenter, M.D., Carmona, J.E., Ethridge, A.J., & Demaree, H.A. (2003). Adult sex-related P300 differences during the perception of emotional prosody and facial affect. *Psychophysiology*, 40 (S1), S39.

Frijda, N.H. (1993). The place of appraisal in emotion. *Cognition and Emotion*, 7 (3-4), 357-387.

Frijda, N.H. (1994). Emotions are functional, most of the time. In: Ekman, P., & Davidson, R.J. (eds.), *The Nature of Emotion: Fundamental Questions*. New York: Oxford University Press, pp. 112-122.

Frijda, N.H. (1996). The laws of emotions. *Zeitschrift fur Psychosomatische Medizin und Psychotherapie*, 42, 205-221.

Frijda, N.H., Kuipers, P., & Terschure, E. (1989). Relations among emotion, appraisal and emotional action readiness. *Journal of Personality and Social Psychology*, 57 (2), 212-228.

Gainotti, G. (1972). Emotional behavior and hemispheric side of the lesion. *Cortex*, 8 (1), 41-55.

Güntekin, B., & Başar, E. (2007). Emotional face expressions are differentiated with brain oscillations. *International Journal of Psychophysiology*, 64, 91-100.

Hamm, A.O., Schupp, H.T., & Weike, A.I. (2003). Motivational organization of emotions: autonomic change, cortical response and reflex modulation. In: Davidson, R.J., Scherer, K.R., & Goldsmith, H.H., *Handbook of Affective Science*. New York: Oxford University Press, pp. 187-212.

Harmon-Jones, E. (2004). Contributions from research on anger and cognitive dissonance to understanding the motivational functions of asymmetrical frontal brain activity. *Biological Psychology*, 67, 51-76.

Harmon-Jones, E., & Allen, J.J.B. (1997). Behavioral activation sensitivity and resting frontal EEG asymmetry: covariation of putative indicators related to risk for mood disorders. *Journal of Abnormal Psychology*, 106, 159-163.

Harmon-Jones, E., & Allen, J.J.B. (1998). Anger and frontal brain activity: EEG asymmetry consistent with approach motivation despite negative affective valence. *Journal of Personality and Social Psychology*, 74 (5), 1310-1316.

Harmon-Jones, E., & Sigelman, J. (2001). State anger and prefrontal brain activity: evidence that insult-related relative left-prefrontal activation is associated with experienced anger and aggression. *Journal of Personality and Social Psychology*, 80 (5), 797-803.

Heilman, K.M., & Bowers, D. (1990). *Neuropsychological Studies of Emotional Changes Induced by Right and Left Hemispheric Lesions*. Hillsdale: Lawrence Erlbaum Associates.

Herrmann, M.J., Aranda, D., Ellgring, H., Mueller, T.J., Strik, W.K., Heidrich, A., & Fallagatter, A.J. (2002). Face-specific event-related potential in humans is independent from facial expression. *International Journal of Psychophysiology*, 45, 241-244.

Hewig, J., Hagemann, D., Seifert, J., Naumann, E., & Bartussek, D. (2004). On the selective relation of frontal cortical asymmetry and anger-out versus anger-control. *Journal of Personality and Social Psychology*, 87 (6), 926-939.

Holmes, A., Vuilleumier, P., & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials. *Cognitive Brain Research*, 16, 174-184.

Johnston, V.S., Miller, D.R., & Burleson, M.H. (1986). Multiple P3s to emotional stimuli and their theoretical significance. *Psychophysiology*, 23, 684-694.

Junghöfer, M., Bradley, M.M., Elbert, T.R., & Lang, P.J. (2001). Fleeting images: a new look at early emotion discrimination. *Psychophysiology*, 38, 175-178.

Karakaş, S., Erzengin, Ö.U., & Başar, E. (2000). The genesis of human event-related responses explained through the theory of oscillatory neural assemblies. *Neuroscience Letters*, 285, 45-48.

Kayser, J., Tenke, C., Nordby, H., Hammerborg, D., Kenneth, H., & Gisela, E. (1997). Event-related potential (ERP) asymmetries to emotional stimuli in a visual half-field paradigm. *Psychophysiology*, 34, 414-426.

Keil, A., Bradley, M.M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P.J. (2002). Large-scale neural correlates of affective picture-processing. *Psychophysiology*, 39, 641-649.

Keil, A., Müller, M.M., Gruber, T., Wienbruch, C., Stolarova, M., & Elbert, T. (2001). Effects of emotional arousal in the cerebral hemispheres: a study of oscillatory brain activity and event-related potentials. *Clinical Neuropsychology*, 112, 2057-2068.

Kiefer, M., & Spitzer, M. (2000). Time course of conscious and unconscious semantic brain activation. *Neuroreport*, 11, 2401-2407.

Kiss, M., & Eimer, M. (2008). ERPs reveal subliminal processing of fearful faces. *Psychophysiology*, 45, 318-326.

Klimesch, W., Russegger, H., Doppelmayr, M., & Pachinger, T. (1998). A method for the calculation of induced band power: implications for the significance of brain oscillations. *Electroencephalography and Clinical Neurophysiology*, 108, 123-130.

Knyazev, G.G. (2007). Motivation, emotion and their inhibitory control mirrored in brain oscillations. *Neuroscience and Biobehavioral Review*, 31, 377-395.

Knyazev, G.G., Bocharov, A.V., Levin, E.A., Savostyanov, A.N., & Slobodskoj-Plusnin, J.Y. (2008). Anxiety and oscillatory responses to emotional facial expressions. *Brain Research*, 1227, 174-188.

Kotchoubey, B. (2005). Event-related potential measures of consciousness: two equations with three unknowns. *Progress in Brain Research*, 150, 427-444.

Krause, C.M. (2003). Brain electric oscillations and cognitive processes. In: Hugdahl, K. (ed.), *Experimental Methods in Neuropsychology*. New York: Kluwer, pp. 11-130.

Krause, C.M., Viemerö, V., Rosenqvist, A., Sillanmäki, L., & Åström, T. (2000). Relative electroencephalographic desynchronization and synchronization in humans to emotional film content: an analysis of the 4-6, 6-8, 8-10 and 10-12 Hz frequency bands. *Neuroscience Letters*, 286, 9-12.

Lang, P.J., Bradley, M.M., & Cuthbert, B.N. (1997). Motivated attention: affect, activation, and action. In: Lang, P.J., Simons, R.F., & Balaban, M. (eds.), *Attention and Orienting: Sensory and Motivational Processes*. Mahwah: Lawrence Erlbaum Associates, pp. 97-135.

Lazarus, R.S. (1991). *Emotion and Adaptation*. New York: Oxford University Press.

LeDoux, J.E. (1996). *The Emotional Brain: the Mysterious Underpinning of Emotional Life*. New York: Simon and Schuster.

Leonard, C.M., Rolls, E.T., Wilson, F.A.W., & Baylis, G.C. (1985). Neurons in the amygdala of the monkey with responses selective for faces. *Behavioural Brain Research*, 15, 159-176.

Liddell, B.J., Williams, L.M., Rathjen, J., Shevrin, H., & Gordon, E. (2004). A temporal dissociation of subliminal versus supraliminal fear perception: an event-related potential study. *Journal of Cognitive Neuroscience*, 16, 479-486.

Morita, Y., Morita, K., Yamamoto, M., Waseda, Y., & Maeda, H. (2001). Effects of facial affect recognition on the auditory P300 in healthy subjects. *Neuroscience Research*, 41 (1), 89-95.

Morris, J., & Dolan, R. (2001). The amygdala and unconscious fear processing. In: De Gelder, B., De Haan, E.H.F., & Heywood, C.A. (eds.), *Out of Mind: Varieties of Unconscious Processes*. New York: Oxford University Press, pp. 185-204.

Morris, J., Frith, C., Perret, D., Rowland, D., Young, A., Calder, A., & Dolan, R.J. (1996). Differential neural response in the human amygdala to fearful and happy facial expressions. *Nature*, 383, 812-881.

Morris, J.S., Friston, K.J., Buchel, C., Frith, C.D., Young, A.W., Calder, A.J., & Dolan, R.J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, 121, 47-57.

Muller, M.M., Keil, A., Gruber, T., & Elbert, T. (1999). Processing of affective pictures modulates right-hemispheric gamma band EEG activity. *Clinical Neurophysiology*, 110, 1913-1920.

Nakamura, K., Mikami, A., & Kubota, K. (1992). The activity of single neurons in the monkey amygdala during performance of a visual memory task. *Journal of. Neurophysiology*, 67, 1447-1463.

Narumoto, J., Okada, T., Sadato, N., Fukui, K., & Yonekura, Y. (2001). Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cognitive Brain Research*, 12 (2), 225-231.

Öhman, A., & Soares, J.J.F. (1998). Emotional conditioning to masked stimuli: expectancies for aversive outcomes following nonrecognized fear-relevant stimuli. *Journal of Experimental Psychology*, 127, 69-82.

Okazaki, M., Kaneko, Y., Yumoto, M., & Arima, K. (2008). Perceptual change in response to a bistable picture increases neuromagnetic beta-band activities. *Neuroscience Research*, 61, 319-328.

Polich, J. (2007). Updating P300: an integrative theory of P3a and P3b. *Clinical Neurophysiology*, 118, 2128-2148.

Posner, M.I. (1978). *Chronometric Explorations of Mind*. Oxford: Lawrence Erlbaum.

Regan, M., & Howard, R. (1995). Fear conditioning, preparedness, and the contingent negative variation. *Psychophysiology*, 32, 208-214.

Rolls, E.T. (2006). Consciousness absent and present: a neurophysiological exploration of masking. In: Ögmen, H., & Breitmeyer, B.G. (eds.), *The First Half Second: the Microgenesis and Temporal Dynamics of Unconscious and Conscious Visual Processes*. Cambridge: MIT Press, pp. 89-108.

Russell, J.A. (2003). Core affect and the psychological construction of emotion. *Psychological Review*, 110, 145-172.

Russell, J.A., & Bullock, M. (1985). Multidimensional scaling of emotional facial expressions: similarity from preschoolers to adults. *Journal of Personality and Social Psychology*, 48, 1290-1298.

Sato, W., Kochiyama, T., Yoshikawa, S., & Matsumura, M. (2001). Emotional expression boosts early visual processing of the face: ERP recording and its decomposition by independent component analysis. *Neuroreport*, 12 (4), 709-714.

Schellberg, D., Besthorn, C., Pfleger, W., & Gasser, T. (1993). Emotional activation and topographic EEG band power. *Journal of Psychophysiology*, 7, 24-33.

Schorr, A. (2001). Appraisal: the evolution of an idea. In: Scherer, K.R., Schorr, A., & Johnstone, T. (eds.), *Appraisal Processes in Emotion: Theory, Methods, Research*. New York: Oxford University Press, pp. 20-34.

Schupp, H.T., Cuthbert, B.N., Bradley, M.M., Cacioppo, J.T., Ito, T., & Lang, P.J. (2000). Affective picture processing: the late positive potential is modulated by motivational relevance. *Psychophysiology*, 37, 257-261.

Shevrin, H. (2001). Event-related markers of unconscious processes. *International Journal of Psychophysiology*, 42, 209-218.

Shiffrin, R.M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychology Review*, 84, 127-190.

Silberman, E.K., & Weingartner, H. (1986). Hemispheric lateralization of functions related to emotion. *Brain and Cognition*, 5 (3), 322-353.

Simons, D.J., Hannula, D.E., Warren, D.E., & Day, S.W. (2007). Behavioral, neuroimaging, and neuropsychological approaches to implicit perception. In: Zelazo, P.D., Moscovitch, M., & Thompson, E. (eds.), *The Cambridge Handbook of Consciousness*. New York: Cambridge University Press, pp. 207-250.

Skrandies, W., & Weber, P. (1996). Dimensinality of semantic meaning and segments of evoked potential field. In: Ogura, C., Koga, Y., & Shimokochi, M. (eds.), *Recent Advances in Event-related Brain Potential Research: Proceedings of the 11th Internatinal Conference on Event-relate Potentials (EPIC)*. New York: Elsevier, pp. 125-162.

Snodgrass, J.M. (2000). *Unconscious Perception: Theory, Method, and Evidence*. Amsterdam: John Benjamins.

Stenberg, G., Lindgren, M., Johansson, M., Olsson, A., & Rosen, I. (2000). Semantic processing without conscious identification: evidence from event-related potentials. *Journal of Experimental Psychology: Learning Memory, and Cognition*, 26, 973-1004.

Stone, A., & Valentine, T. (2007). The categorical structure of knowledge for famous people (and a novel application of Centre-Surround theory). *Cognition*, 104 (3), 535-564.

Streit, M., Wolwer, W., Brinkmeyer, J., Ihl, R., & Gaebel, W. (2000). Electrophysiological correlates of emotional and structural face processing in humans. *Neuroscience Letters*, 278, 13-16.

Summerfield, C., Jack, A.I., & Burgess, A.P. (2002). Induced gamma activity is associated with conscious awareness of pattern masked nouns. *International Journal of Psychophysiology*, 44, 93-100.

Sutton, S.K., & Davidson, R.J. (1997). Prefrontal brain asymmetry: a biological substrate of the behavioral approach and inhibition systems. *Psychological Science*, 8, 204-210.

Tranel, D., & Damasio, A.R. (1985). Knowledge without awareness: an automatic index of facial recognition by prosopoagnosics. *Science*, 228, 1453-1454.

Waldstein, S.R., Kop, W.J., Schmidt, L.A., Haufler, A.J., Krantz, D.S., & Fox, N.A. (2000). Frontal electrocortical and cardiovascular reactivity during happiness and anger. *Biological Psychology*, 55 (1), 3-23.

Whalen, P.J., Rauch, S.L., Etcoff, N.L., McInerney, S.C., Lee, M.B., & Jenike, M.A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, 18, 411-418.

Wheeler, R.E., Davidson, R.J., & Tomarken, A.J. (1993). Frontal brain asymmetry and emotional reactivity: a biological substrate of affective style. *Psychophysiology*, 30 (1), 82-89.

Wong, P.S., & Root, J.C. (2003). Dynamic variations in affective priming. *Consciousness and Cognition*, 12, 147-168.

Wong, P.S., Shevrin, H., & Williams, W.J. (1994). Conscious and nonconscious processes: an ERP index of an anticipatory response in a conditioning paradigm using visual masked stimuli. *Psychophysiology*, 31, 87-101.

Yee, C.M., & Miller, C.M. (1987). Affective valence and information processing. In: Johnson, R., Rohrbaugh, J.W., & Parasuraman, R. (eds.), *Current Trends in Event-relatedpotential Research (EEG Supplement 40)*. Amsterdam: Elsevier, pp. 300-307.