A Temporal Dissociation of Subliminal versus Supraliminal Fear Perception: An Event-related Potential Study

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Abstract

■ Current theories of emotion suggest that threat-related stimuli are first processed via an automatically engaged neural mechanism, which occurs outside conscious awareness. This mechanism operates in conjunction with a slower and more comprehensive process that allows a detailed evaluation of the potentially harmful stimulus (LeDoux, 1998). We drew on the Halgren and Marinkovic (1995) model to examine these processes using event-related potentials (ERPs) within a backward masking paradigm. Stimuli used were faces with fear and neutral (as baseline control) expressions, presented above (supraliminal) and below (subliminal) the threshold for conscious detection. ERP data revealed a *double dissociation* for the supraliminal versus subliminal perception of fear. In the subliminal condition, responses to the perception of fear stimuli were enhanced relative to neutral for the N2 "excitatory" component, which is thought to represent orienting and automatic aspects of face processing. By contrast, supraliminal perception of fear was associated with relatively enhanced responses for the late P3 "inhibitory" component, implicated in the integration of emotional processes. These findings provide evidence in support of Halgren and Marinkovic's temporal model of emotion processing, and indicate that the neural mechanisms for appraising signals of threat may be initiated, not only automatically, but also without the need for conscious detection of these signals. ■

INTRODUCTION

Within the field of cognitive neuroscience, there is a growing body of evidence from both human and animal studies that emotion processing is initiated and can proceed without conscious awareness (e.g., Bernat, Bunce, & Shevrin, 2001; Bunce, Bernat, Wong, and Shevrin, 1999; Morris, Öhman, & Dolan, 1998, 1999; Öhman & Soares, 1998; Whalen et al., 1998; Wong, Shevrin, & Williams, 1994; Wong, Bernat, Bunce, & Shevrin, 1997). Animal studies, which focus on fear conditioning paradigms, suggest that fear-related responses are subserved by a direct subcortical and short-latency "low road" pathway from the thalamus direct to the amygdala, allowing threat stimuli to be processed automatically and outside awareness (Davis, 1992; LeDoux 1986, 1995, 1997). This fast subcortical pathway has adaptive survival value because it allows an immediate and reflexive response to a potential threatening stimulus. In this way, the fear detection system can begin to operate prior to the conscious appraisal of the stimulus. By contrast, the "high road," involving cortical as well as subcortical thalamic–hippocampal–amygdala networks, enables a slower conscious processing of stimulus details and context, and allows the engagement of appropriate behavioral responses. It is thought that such systems have evolved to facilitate the optimal detection and response to dangerous stimuli (LeDoux, 1998). This study aims to investigate these distinctions between "nonconscious" (below awareness) and conscious processes from a temporal perspective using human subjects.

On the basis of their depth and scalp recording ERP research, Halgren and Marinkovic (1995) proposed a temporal stage model of the appraisal and response to emotional stimuli that is compatible with LeDoux's animal model. It provides a suitable framework for making predictions concerning the transition from nonconscious to conscious processing in terms of ERPs (Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994, Halgren, Baudena, Heit, Clarke, Marinkovic, et al., 1994). The first two stages of the model, "orienting" and "event integration," are of particular interest in distinguishing nonconscious from conscious emotion perception. Orienting refers to the automatic disruption of ongoing processing in order to focus attention towards a novel and significantly threatening event so to mobilize cognitive and behavioral resources for action or defense (Halgren & Marinkovic, 1995). The orienting response is thought to be independent of conscious deliberation (Kenemans, 1992). In terms of ERP components, this orienting response is characterized by the N2/P3a/slow wave complex, with peaks around 200, 280, and

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350 msec post stimulus onset, respectively (Halgren & Marinkovic, 1995). More specifically, convergent evidence suggests that the N2 is modulated specifically by face stimuli and facial expressions of emotion (Sokolov & Bouscein, 2000; Bentin, Allison, Puce, Perez, & McCarthy, 1996; Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, et al., 1994). The P3a (or early P3) has been associated with the automatic aspects of the orienting response that are involved in detecting novel and/or threatening stimuli (Freidman, Cycowicz, & Gaeta, 2001; Lagopoulos et al., 1998; Johnston, Miller, & Burleson, 1986).

The subsequent ''event integration'' stage in Halgren and Marinkovic's (1995) model is defined by the N4/P3b sequence with peaks around 430 and 600 msec post stimulus, respectively (Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994). It is proposed that during this phase, cognitive integration of the stimulus into the current context via controlled processing, as influenced by the initial automatic stages, acts to create conscious emotional experience. The N4 is thought to be involved specifically in the integration of the current attended event with the associated cognitive context in order to bring about neural encoding (Halgren & Marinkovic, 1995), and provides an index of semantic processing (Kiefer & Spitzer, 2000). The P3b (as the second component of ''event integration'') occurs in response to the controlled registration of the stimulus that generated the initial orienting response, and the subsequent updating of stimulus context. It has been suggested that the combined N4/P3b (or late P3) complex is associated with the ''global integration of an event considered to be the essence of controlled or conscious processing'' (Halgren & Marinkovic, 1995, p. 1145).

A principal paradigm used to investigate below-awareness responses to threat perception in humans is the backward masking protocol in which threat-related facial expressions (fear, anger) are followed immediately by a neutral face mask. Evidence for the unconscious perception of masked faces has been revealed in terms of subjective report (Esteves & Öhman, 1993; Esteves, Dimberg, & Öhman, 1994), autonomic activity (Morris, Buchel, & Dolan, 2001; Öhman & Soares, 1998), and functional brain imaging measures (PET; Morris et al., 1998, 1999: fMRI; Whalen et al., 1998; Breiter et al., 1996). In terms of ERPs, backward masking has been used to examine the time course of neural responses to word stimuli (Kiefer & Spitzer, 2000). Consistent with Halgren and Marinkovic's (1995) temporal model, conscious conditions were distinguished by enhanced N4 and subconscious conditions showed a decay in evoked responses after 200 msec post stimulus onset, consistent with the N2 being involved in automatic processing.

Halgren and Marinkovic (1995) provide a structure on which to base specific predictions regarding the time course of ERP activity in response to subliminal (low road) versus supraliminal (high road) processing of emotion stimuli in the current study. It was expected that fear stimuli would generally be processed more quickly and to a greater extent than neutral stimuli, reflected in decreased ERP latency but enhanced amplitude. It was also expected that, if subliminal stimuli are processed by a low road, which is characterized by quick responses, this would be indicated by more rapid processing and thus reduced latency of the ERP components in this condition compared to the supraliminal condition. We predicted the subliminal fear condition to show a more prominent N2/P3a complex associated with automatic ''orienting'' and commencement of early stages of emotional integration (Halgren & Marinkovic, 1995). By contrast, it was predicted that the supraliminal fear stimuli would reveal a more prominent N4/late P3 complex, associated with the controlled integration and cognitive elaboration of emotional information.

In order to test the above predictions, ERPs were recorded during the presentation of face stimuli depicting fear versus neutral expressions, within a passive viewing backward masking paradigm. Target faces (fear or neutral) were presented either *subliminally*, below the objective detection threshold for awareness (10 msec stimulus onset asynchrony [SOA], with immediate onset, and spatially offset mask) or *supraliminally* (170 msec SOA, with equivalent mask). Following ERP recording, behavioral ratings of emotion recognition accuracy and emotion intensity for each stimulus were completed.

RESULTS

Behavioral Data Analyses

The posttest emotion identification task showed that subjects were able to correctly recognize the emotion in fear faces (mean = 86% correct) and neutral faces (mean = 80%, with chance level for both expressions being 14.29%). This indicates that subjects perceived the correct emotion within the passive viewing recording period (consciously perceived only in the supraliminal condition).

Event-Related Potential Data Analysis

Figure 1 depicts the analogue ERP data for responses to fear and neutral stimuli in subliminal and supraliminal conditions at midline sites Fz, Cz, and Pz.

Amplitude Results

Increased amplitude of all ERP components for fear stimuli. The significant main effect for emotion at Fz indicated that N2 amplitude was generally enhanced for fear versus neutral stimuli in the frontal region, $F(1,19) = 6.14$, $p < .023$, but did not differ according to threshold condition. There was also a significant main effect for emotion at Cz, reflecting enhanced early P3

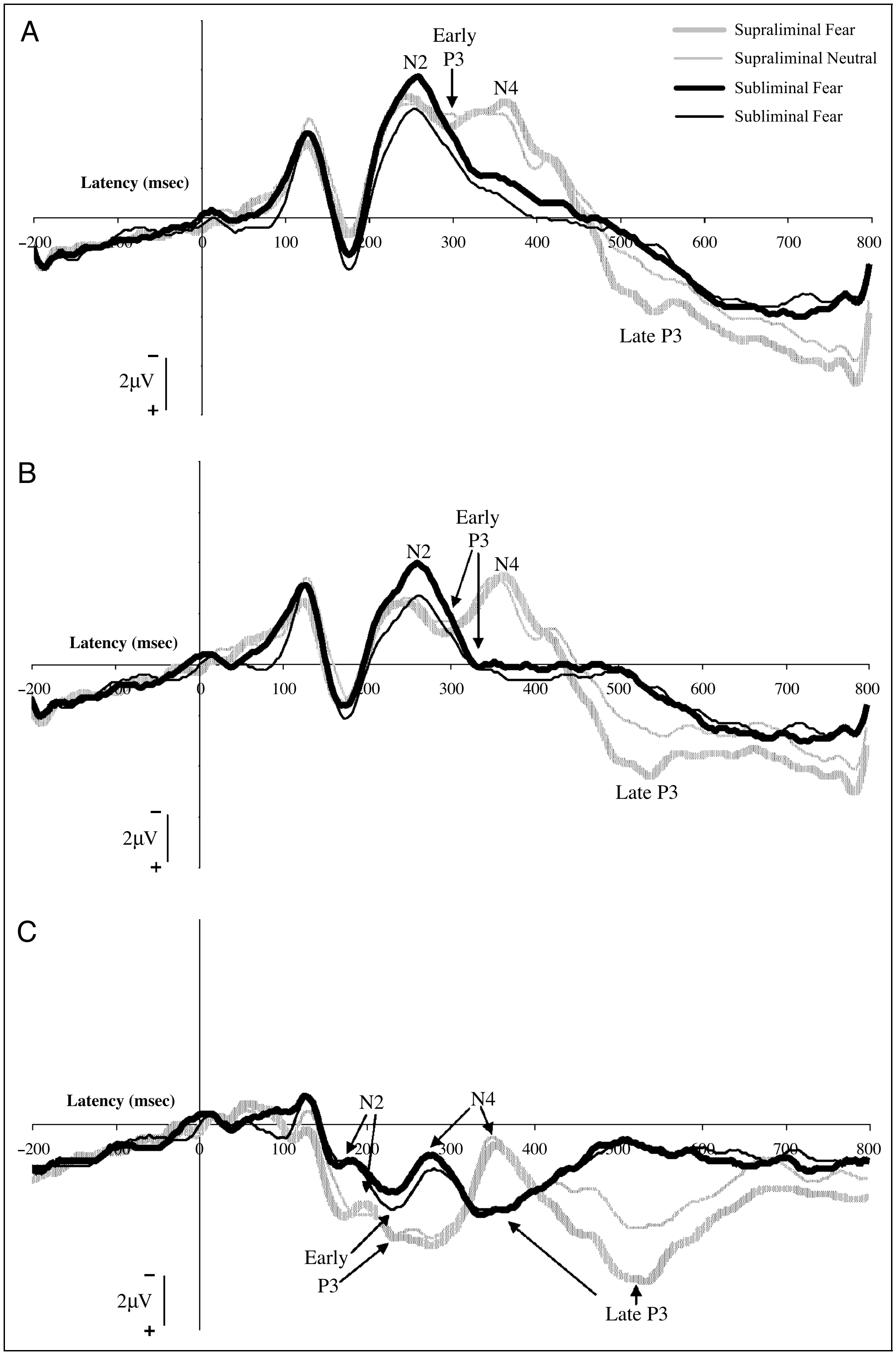

Figure 1. ERP grand average waveforms recorded from (A) midline site Fz (frontal); (B) midline site Cz (central); (C) midline site Pz (parietal). ERPs are superimposed for the *fear* masked by neutral condition (for both the supraliminal [170 msec] and the subliminal [10 msec] conditions) and for the *neutral* masked by neutral condition (again for both the supraliminal [170 msec] and the subliminal [10 msec] conditions).

amplitude for the fear faces, $F(1,19) = 5.18$, $p < .035$. Continuing this trend, N4 amplitude was somewhat enhanced for fear stimuli at the frontal (Fz) site, $F(1,19) = 3.79$, $p < .07$. There were significant main effects for emotion found for the late P3 component, due to enhanced amplitude for fear (vs. neutral) at both Cz, $F(1,19) = 15.28$, $p < .001$, and Pz, $F(1,19) = 6.83$, $p < .017$.

Increased amplitude of N2 and early P3 in the subliminal condition. There was a significant main effect for threshold condition due to relatively larger N2 responses under the subliminal condition, $F(1,19) = 6.42$, $p < .02$, compared to the supraliminal condition in the posterior region (Pz). The amplitude of the early P3 was also significantly larger at Fz, $F(1,19) = 10.35$, $p < .005$, for the subliminal condition.

Increased amplitude of N2 specific to fear in the subliminal condition. For N2 amplitude, there was a significant interaction for *threshold condition* by *emotion* at Cz, $F(1,19) = 6.24$, $p < .022$. Post hoc protected t tests revealed that this interaction was due to significantly enhanced N2 responses to fear relative to neutral stimuli in the subliminal condition, $t(19) = -3.022$, $p < .007$. This finding did not translate to the second component of the ''orienting'' complex, the early P3.

Increased amplitude of N4 and late P3 in the supraliminal condition. Supraliminal N4 responses were significantly larger than those in the subliminal condition both frontally (Fz), $F(1,19) = 28.32$, $p < .0001$, and centrally (Cz), $F(1,19) = 27.52$, $p < .0001$. An additional trend towards a main effect for threshold condition at the late P3 component showed that the supraliminal responses were also relatively enhanced at the central (Cz), $F(1,19) = 3.86$, $p = .064$, and parietal (Pz), $F(1,19) = 3.41$, $p = .081$, regions.

Increased amplitude of the late P3 specific to fear in the supraliminal condition. For the late P3 amplitude, there was a strong trend towards a *threshold condition* by *emotion* interaction at Pz, $F(1,19) = 3.90$, $p = .06$, due to enhanced responses to supraliminal fear stimuli over and above (a) neutral faces in the supraliminal condition, $t(19) = 3.52$, $p < .002$, (b) fear faces in the subliminal condition, $t(19) = 2.52$, $p < .021$, and (c) neutral faces in the subliminal condition, $t(19) = 2.682$, $p < .015$.

Latency Results

Faster latency of N4 and late P3 to fear stimuli presentations. There was a main effect of borderline significance for emotion at Pz, reflecting relatively faster N4 responses to fear stimuli over neutral stimuli, $F(1,19) = 4.23$, $p = .05$. A similar effect of borderline significance was also found for the late P3 component at Cz, $F(1,19) = 4.34$, $p = .05$.

Faster latency of all ERP components in the supraliminal condition, most apparent frontocentrally. A main effect for threshold condition at Pz, $F(1,19) = 8.70$, $p < .008$, indicated that N2 responses were relatively faster under the supraliminal condition compared to the subliminal. This trend was also found to occur frontocentrally for the components early P3, Fz: $F(1,19) = 30.93$, $p < .000$; Cz: $F(1,19) = 21.68$, $p < .000$, N4, Fz: $F(1,19) = 8.56$, $p < .009$; Cz: $F(1,19) = 11.68$, $p < .003$, and late P3, Fz: ($F(1,19) = 22.79$, $p < .000$; Cz: $F(1,19) = 9.26$, $p < .007$.

Faster latency of N4 and late P3 in the subliminal condition, in the posterior region. By contrast to the above latency findings, at the posterior recording site, N4 responses were significantly faster for the *subliminal*, compared to the *supraliminal*, condition, $F(1,19) = 48.45$, $p < .000$. This result was also found for the late P3 component at Pz, $F(1,19) = 106.03$, $p < .0001$.

Faster latency of the early P3 specific to fear in the subliminal condition. There was an interaction of borderline significance at Pz, $F(1,19) = 4.16$, $p = .05$, for early P3. Post hoc t tests (significant at the uncorrected alpha level) showed that this interaction was explained primarily by the faster early P3 responses to fear stimuli in the subliminal, compared to supraliminal, condition, $t(19) = -2.104$, $p < .05$. By contrast, early P3 responses to neutral were significantly faster (also at the uncorrected level) in the supraliminal condition, $t(19) = -2.147$, $p < .045$.

DISCUSSION

In this study, ERPs provided a temporal correlate of conscious (supraliminal) versus nonconscious (subliminal) perception of facial expressions of emotion. We investigated whether the N2/early P3 ''orienting'' and N4/late P3 ''event integration'' ERP complexes would respectively dissociate the subliminal and supraliminal perception of fear (vs. neutral control) face stimuli. Crucially, results indicated that there was a double dissociation for subliminal versus supraliminal perception of fear (vs. neutral) stimuli in which subliminal fear perception was associated with enhanced N2 and faster early P3 responses at centroparietal sites. By contrast, late P3 amplitude was enhanced in response to supraliminal fear perception at the parietal midline site. These results suggest that the time course of fear perception may be differentiated with regard to an early, automatic, and relatively unconscious stage of processing (subliminal) versus a later, more controlled, and conscious stage of processing (supraliminal), consistent with Halgren and Marinkovic's (1995) orienting (N2/P3a) versus event integration (N4/P3b) temporal model of emotion perception.

The results indicated that ERP responses to fear stimuli were generally larger and faster across all ERP components compared to neutral baseline responses. This pattern was in accordance with previous ERP findings for threat-related signals (e.g., Sokolov & Boucsein, 2000; Lang, Nelson, & Collins, 1990) and provides some confirmation that the fear stimuli used in this study were emotionally salient. Complex stimuli such as fear faces may be critical to communicating signals of threat (Sokolov & Boucsein, 2001) and may therefore be given processing priority over unexpressive, but similarly complex, faces. The observation that ''nonconscious'' fear perception was enhanced over nonconscious neutral perception in the subliminal fear condition, indexed by the earlier automatic ERP components, reflects the view that humans have the ability to discriminate emotionally significant stimuli, perhaps threat in particular, at levels below conscious awareness (Mayer & Merckelbach, 1999).

The supraliminal condition was associated with greater responses (increased amplitude) for the later ERP complex, which suggests a greater magnitude of processing in the post 350-msec time window. This pattern is consistent with the view that the frontal brain networks are involved in more controlled processes of working memory, context updating and semantic elaboration (Damasio, 1996; Posner, 1994). The supraliminal condition was also consistently associated with faster responses (reduced latency) across all ERP components investigated, especially at frontocentral sites. This indicates a greater efficiency of processing when faces are consciously detected across ERP complexes that represent both automatic and controlled stages of processing. Notably, the latency pattern of supraliminal versus subliminal responses at frontocentral sites was largely reversed at the parietal (Pz) site. The N4 and late P3 responses were relatively faster, whereas the N2 was slower, for subliminal perception at Pz. This observation suggests that a topographical dissociation also contributes to the differing time courses of responses to sub- versus supraliminal perception of face stimuli, consistent with evidence for parallel neural systems (LeDoux, 1998).

The interaction between emotion and threshold condition observed in this study is consistent with Halgren and Marinkovic's (1995) stage model, and build upon the implications of this model for LeDoux's (1997, 1998) "high versus low road" hypothesis, derived from animal fear conditioning studies. The predicted observation that responses to subliminal fear faces were enhanced relative to neutral control faces for the earlier N2 component (and the early P3 in terms of latency), but not for the later components, is consistent with the view that a low road may be engaged automatically when a rapid response to signals of threat is required. The N2/early P3 automatic stage of processing may provide a temporal correlate of the operation of the low road. This profile of subliminal activity is consistent with recent fMRI evidence, which suggests that subcortical neural structures vital to the processing of threat-related stimuli such as the amygdala, are activated in response to such stimuli being presented outside of awareness (Critchley et al., 2000; Morris et al., 1998, 1999, 2001; Whalen et al., 1998). By contrast, the finding that responses to supraliminal fear stimuli were enhanced for the later P3 component is consistent with the activation of a slower high road circuit for detailed conscious evaluation of threat stimuli. In this regard, the N4/late P3 complex may signify the function of the high road.

The current findings support an integrative model for the perception of emotional stimuli at different levels of awareness, defined by both quantitative and qualitative dimensions of response (Shevrin, 2001), and which builds upon both Halgren and Marinkovic's (1995) stage model and LeDoux's (1998) fear conditioning model of emotional processing. A dissociation of subliminal versus supraliminal perception of threat with regard to the temporal correlates of information processing is consistent with an evolutionary view in which survival requires rapid and automatic responses to threat-related stimuli in particular (Panksepp, 1998). Even complex signals of fear, such as facial expressions, may be detected via a subcortical low road when consciousness is precluded (as indexed by enhanced N2 and faster early P3 responses), although we might expect some degree of cortical engagement given the complexity of the stimuli. Such a quick-acting system may facilitate our detection and reaction to fear stimuli prior to the onset of subjective realization and experience of fear. When stimulus presentation is sustained, as in the supraliminal condition, the brain is able to engage in further elaborative and excitatory processes, which are highly efficient and build upon the preliminary automatic mechanisms already initiated. Potential malfunctions of this system may underlie the development of disorders such as PTSD and phobias (Öhman, 1999), which are thought to encompass difficulties in appropriately appraising threatening environments.

METHODS

Subjects

Twenty healthy participants were recruited from the general Western and Central Sydney community (mean age = 24.85 years, *SD* = 7.34). The sample comprised 10 men and 10 age-matched women. Inclusion criteria were predominant right-handedness and normal or corrected-to-normal vision. Exclusion criteria were history of psychopathology for self or immediate family, epilepsy, head injury, and drug or alcohol use (especially use in the 24 hr prior to testing), assessed using the Westmead Hospital Clinical Information Base (WHCIB; Horley et al., 2001). Participation was entirely voluntary and in accordance with the National Health and Medical Research Council ethical guidelines.

Design and Procedure

Behavioral Data

Behavioral data were acquired following ERP testing. Participants were asked to identify the facial expression of emotion depicted on each of the 32 faces presented in this study (8 fear, 8 disgust, 8 anger, and corresponding baseline neutral faces from the Ekman and Friesman, 1976, series). They were asked to circle the emotion label that best described the facial expression from a choice of seven options (neutral, fear, happy, sad, anger, disgust, and surprise). Subjects were also asked to rate the intensity of the emotion on a forced-choice rating scale of 1 (*weak intensity*) to 5 (*very intense*).

Experimental Task

Participants sat within a quiet, dimly lit room. Visual images were presented on an SVGA monitor (refresh rate, 100 Hz), which was situated 60 cm from the participants' eyes. The face stimuli consisted of gray-scale photographs of eight different individuals depicting both fearful (100% fearful facial expressions) and neutral (mildly [25%] happy)[1] expressions selected from *The Pictures of Facial Affect* series (Ekman & Friesman, 1976). All images were equiluminant and subtended a horizontal visual angle of 11° and a vertical visual angle of 15°.

An initial psychophysiological study was conducted in which the duration of target face stimuli were systematically varied in order to establish specific threshold conditions (Williams et al., 2004). The thresholds established and thus employed in the current study were (1) an *objective detection threshold* that represents the subliminal condition (defined as the stimulus duration where there is an inability to significantly discriminate between the presence or absence of the stimulus [Merikle, Smilek, & Eastwood, 2001]) and (2) a *subjective identification threshold* that represents the supraliminal condition (defined as the overt discrimination of the face and its emotional expression).

The paradigm followed a backward masking procedure. Each threshold condition consisted of an alternating AB block design, with each block presented five times. Block A consisted of neutral face target stimuli presented for either 10 msec (subliminal threshold condition) or 170 msec (supraliminal condition), followed by a neutral face mask presented for 100 msec. Block B consisted of a fear face target stimuli, presented for 10 or 170 msec, followed by a neutral mask, again presented for 100 msec. In both Blocks A and B, no target and mask pair depicted the same individual. The mask was also spatially offset by 1° visual angle in order to control against any apparent ''morphing'' effects that may be perceived when superimposing a neutral face mask directly on top of a target fear face (e.g., apparent movement of the eyebrows between neutral and fear facial expressions), and may thereby increase the subjects' awareness of the emotional expression. Each block consisted of 30 target–mask pairings, with an interstimulus interval of 1 sec. In total there were 300 target–mask pairs consisting of 150 neutral–neutral pairs and 150 fear–neutral pairs in each threshold condition. The subliminal (10 msec) condition was presented prior to the supraliminal (170 msec) condition. The conditions were not counterbalanced across subjects in order to avoid the confounding effects of supraliminal perception on subliminal perception (Bernat et al., 2001; Wong et al., 1994). The initial threshold-setting study, as well as post hoc briefings, confirmed that subjects were unable to detect target emotion stimuli in the subliminal condition (Williams et al., 2004).

Participants were given explicit instructions that pairs of target–mask faces would be presented. It was emphasized that sometimes the first face would be difficult to see, but to concentrate as best they could on this first face, and that they would be asked questions about these faces after the ERP recording. The participants were required to passively observe the stimuli during ERP recording. A previous neuroimaging study has shown that this task and an implicit sex classification task produce similar brain responses (Lange et al., 2003). The emotional content of the target faces was not revealed in these instructions to avoid expectancy effects.

ERP Acquisition

ERPs were recorded from 19 scalp electrode sites according to the International 10-20 system, using an electrocap (Blom & Anneveldt, 1982). The sites of primary interest in this study were the midline sites (Fz, Cz, Pz). Linked earlobes served as a reference point. Horizontal eye movement potentials were recorded using two electrodes placed laterally 1 cm from the outer canthus of each eye, and vertical eye movement potentials were recorded by placing electrodes 1 cm above and below the left eye. A DC system (SYNAMPS, equipped with a 16-bit A/D converter) was used with a sampling rate of 250 Hz. All electrode impedances were less than or equal to 5 kΩ. For the EEG/EOG channels, the amplification was 200, resulting in an input range of ± 13.75 mV, with a resolution of 0.42 μV.

ERP Scoring

Prior to scoring, EEG data were corrected for artefact due to eye movements using a technique based on Gratton, Coles, and Donchin (1983). Amplitude and latency for the ERP components of focal interest (N2, early P3, N4, and late P3) were measured according to a 200-msec prestimulus baseline. All scoring was conducted baseline to peak using an automated system (Haig, Gordon, Rogers, & Anderson, 1995) and peaks thus identified were confirmed through visual inspection. The latency window criteria for each component peak were 200–300 msec (N2), 240–350 msec (Early P3), 300–500 msec (N4) and 400–700 msec (Late P3). The latency and amplitude of each ERP component were quantified by the highest peak within each respective latency window.

Outliers were defined as greater than three standard deviations above or below the latency or amplitude mean. These outliers were replaced with the next most extreme value in the data set (within three standard deviations of the mean). This procedure was used instead of mean replacement in order to best reflect the spread of individual data (Tabachnick & Fidell, 1989).

Data Analysis

ERP amplitude and latency for each midline-recording site were analyzed using MANOVA, in which threshold condition (sub- vs. supraliminal) and emotion (fear vs. neutral) were within-group factors. Significant effects were explored using protected (corrected α level = .025) t tests.

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Note

1. Mildly happy stimuli were used given the propensity for 100% neutral stimuli to be perceived as slightly negative (Phillips et al., 1997).

REFERENCES

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8,* 551–565.

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

Blom, J. L., & Anneveldt, M. (1982). An electrode cap tested. *Electroencephalograpy and Clinical Neurophysiology, 54,* 591–594.

Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., Strauss, M. M., Hyman, S. E., & Rosen, B. R. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron, 17,* 875–887.

Bunce, S. C., 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 Psychiatric Research, 33,* 341–347.

Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., Van Amelsvoort, T., Robertson, D., David, A., & Murphy, D. (2000). Explicit and implicit neural mechanisms for processing of social information from facial expressions: A functional magnetic resonance imaging study. *Human Brain Mapping, 9,* 93–105.

Damasio, A. R. (1996). The somatic marker hypothesis and the possible functions of the prefrontal cortex. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 351,* 1413–1420.

Davis, M. (1992). The role of the amygdala in fear and anxiety [Review]. *Annual Review of Neuroscience, 15,* 353–375.

Ekman, P., & Friesen, W. (1976). *Pictures of facial affect.* Palo Alto: Consulting Psychologists Press.

Esteves, F., Dimberg, U., & Öhman, A. (1994). Automatically elicited fear: Conditioned skin conductance responses to masked facial expressions. *Cognition and Emotion, 8,* 393–413.

Esteves, F., & Öhman, A. (1993). Masking the face: Recognition of emotional facial expressions as a function of the parameters of backward masking. *Scandinavian Journal of Psychology, 34,* 1–18.

Freidman, D., Cycowicz, Y. M., & Gaeta, H. (2001). The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience and Biobehavioral Reviews, 25,* 355–373.

Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography Clinical and Neurophysiology, 55,* 468–484.

Haig, A. R., Gordon, E., Rogers, G., & Anderson, J. (1995). Classification of single-trial ERP sub-types: Application of globally optimal vector quantization using simulated annealing. *Electroencephalography and Clinical Neurophysiology, 94,* 288–297.

Halgren, E., Baudena, P., Heit, G., Clarke, M., & Marinkovic, K. (1994). Spatio-temporal stages in face and word processing. 1. Depth recorded potentials in the human occipital and parietal lobes. *Journal of Physiology (Paris), 88,* 1–50.

Halgren, E., Baudena, P., Heit, G., Clarke, M., Marinkovic, K., & Chauvel, P. (1994). Spatio-temporal stages in face and word processing. 2. Depth recorded potentials in the human frontal and Rolandic cortices. *Journal of Physiology (Paris), 88,* 51–80.

Halgren, E., & Marinkovic, K. (1995). Neurophysiological networks integrating human emotions. In M. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1137–1151). Cambridge: MIT Press.

Horley, K., Gonsalvez, C., Williams, L., Lazzaro, I., Bahramali, H., & Gordon, E. (2001). Event-related potentials to faces in schizophrenia. *International Journal of Neuroscience, 107,* 113–130.

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

Kenemans, J. L. (1992). Visual stimulus change and the orienting reaction: Event-related potential evidence for a two-stage process. *Biological Psychology, 33,* 97–114.

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

Lagopoulos, J., Gordon, E., Barhamali, H., Lim, C. L., Li, W. M., Clouston, P., & Morris, J. G. L. (1998). Dysfunctions of automatic (P300a) and controlled (P300b) processing in Parkinson's disease. *Neurological Research, 20,* 5–10.

Lang, S. F., Nelson, C. A., & Collins, P. F. (1990). Event-related potentials to emotional and neutral stimuli. *Journal of Clinical and Experimental Neuropsychology, 12,* 946–958.

Lange, K., Williams, L. M., Young, A. W., Bullmore, E. T., Brammer, M. J., Williams, S. C. R., Gray, J. A., & Phillips, M. L. (2003). Task instructions modulate neural responses to fearful facial expressions. *Biological Psychiatry, 53,* 226–232.

LeDoux, J. E. (1986). The neurobiology of emotion. In J. E. LeDoux & W. Hirst (Eds.), *Mind and brain: Dialogues for cognitive neuroscience.* Cambridge: Cambridge University Press.

LeDoux, J. E. (1995). Emotion: Clues from the brain. *Annual Review of Psychology, 46,* 209–235.

LeDoux, J. E. (1997). Emotion, memory and the brain: Mysteries of the mind [Special issue]. *Scientific American,* 68–75.

LeDoux, J. E. (1998). *The emotional brain: The mysterious underpinnings of emotional life.* New York: Touchstone.

Mayer, B., & Mercekelbach, H. (1999). Unconscious processes, subliminal stimulation and anxiety. *Clinical Psychology Review, 19,* 571–590.

Merikle, P. M., Smilek, D., & Eastwood, J. D. (2001). Perception without awareness: Perspectives from cognitive psychology. *Cognition, 79,* 115–134.

Morris, J. S., Buchel, C., & Dolan, R. J. (2001). Parallel neural responses in amygdala subregions and sensory cortex during implicit fear conditioning. *Neuroimage, 13,* 1044–1052.

Morris, J. S., Öhman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature, 393,* 467–470.

Morris, J. S., Öhman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating ''unseen'' fear. *Proceedings of the National Academy of Sciences, U.S.A., 96,* 1680–1685.

Öhman, A. (1999). Distinguishing unconscious from conscious emotional processes: Methodological considerations and theoretical implications. In T. Dalgleish & M. Power (Eds.), *Handbook of cognition and emotion* (pp. 321–352). Chichester: Wiley.

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: General, 127,* 69–82.

Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions.* New York: Oxford University Press.

Phillips, M. L., Young, A. W., Senior, C., Brammer, M., Andrews, C., Calder, A. J., Bullmore, E. T., Perrett, D. I., Rowland, D., Williams, S. C. R., Gray, J. A., & David, A. S. (1997). A specific neural substrate for perceiving facial expressions of disgust. *Nature, 389,* 495–498.

Posner, M. I. (1994). Attention: The mechanisms of consciousness. *Proceedings of the National Academy of Sciences, U.S.A., 91,* 7398–7403.

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

Sokolov, E. N., & Boucsein, W. (2000). A psychophysiological model of emotional space. *Integrative Physiological and Behavioral Science, 35,* 81–119.

Tabachnick, B. G., & Fiddell, L. S. (1989). *Using multivariate statistics.* New York: Harper & Row.

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. *The Journal of Neuroscience, 18,* 411–418.

Williams, L. M., Liddell, B. J., Rathjen, J., Brown, K. J., Gray, J., Phillips, M., Young, A., & Gordon, E. (2004). Mapping the time course of nonconscious and conscious perception of fear: An integration of central and peripheral measures. *Human Brain Mapping, 21,* 64–74.

Wong, P. S., Bernat, E.; Bunce, S., & Shevrin, H. (1997). Brain indices of nonconscious associative learning. *Consciousness & Cognition: An International Journal, 6,* 519–544.

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 visually masked stimuli. *Psychophysiology, 31,* 87–101.