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What event-related potentials (ERPs) bring to social neuroscience?

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Social cognitive neuroscience is a recent interdisciplinary field that studies the neural basis of the social mind. Event-related potentials (ERPs) provide precise information about the time dynamics of the brain. In this study, we assess the role of ERPs in cognitive neuroscience, particularly in the emerging area of social neuroscience. First, we briefly introduce the technique of ERPs. Subsequently, we describe several ERP components (P1, N1, N170, vertex positive potential, early posterior negativity, N2, P2, P3, N400, N400-like, late positive complex, late positive potential, P600, error-related negativity, feedback error-related negativity, contingent negative variation, readiness potential, lateralized readiness potential, motor potential, re-afferent potential) that assess perceptual, cognitive, and motor processing. Then, we introduce ERP studies in social neuroscience on contextual effects on speech, emotional processing, empathy, and decision making. We provide an outline of ERPs' relevance and applications in the field of social cognitive neuroscience. We also introduce important methodological issues that extend classical ERP research, such as intracranial recordings (iERP) and source location in dense arrays and simultaneous functional magnetic resonance imaging recordings. Further, this review discusses possible caveats of the ERP question assessment on neuroanatomical areas, biophysical origin, and methodological problems, and their relevance to explanatory pluralism and multilevel, contextual, and situated approaches to social neuroscience.

Keywords: ERP; Social neuroscience; Cognitive neuroscience; Contextual effects; Emotion; Empathy; Decision making.

Social neuroscience combines approaches from cognitive neuroscience and social psychology and highlights a multilevel approach to emotional, social, and cognitive phenomena, making it one of the newer, more promising fields of cognitive neuroscience (Cacioppo & Decety, 2011). Event-related potentials (ERPs) are useful for not only obtaining excellent temporal resolution, but also engaging features such as dense arrays, single-trial analysis, source localization algorithms, and connectivity and frequency measures, among others, which provide multiple time sources of brain activity in response to cognitive events.

This review briefly introduces the ERP technique. A basic description of the main components [P1, N1, N170, vertex positive potential (VPP), early posterior negativity (EPN), N2, P2, P3, N400, N400-like, late positive complex (LPC), late positive potential (LPP), P600, error-related negativity (ERN), feedback

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error-related negativity (fERN), contingent negative variation (CNV), readiness potential (RP); lateralized readiness potential (LRP), motor potential (MP), re-afferent potential (RAP)] is provided. We then introduce studies of cognitive and social neuroscience on the contextual effects in language, emotions, emotional body language (EBL), empathy, and decision-making cognition. Intracranial ERP recordings, source location in dense arrays, and co-recordings using functional magnetic resonance imaging (fMRI) are introduced. Finally, methodological limitations and theoretical implications for the understanding of social cognition as contextual, multilevel, and situated phenomena are discussed.

EVENT-RELATED POTENTIALS

ERPs use a precise tool to record time resolution (ms) of electrophysiological activity taken from the scalp resulting from the synchronous activation of several neural subpopulations that occur in response to sensory, motor, or cognitive events (Luck, 2005). ERPs are the summed activation of excitatory postsynaptic potential and inhibitory postsynaptic potential elicited by a new stimulus or subject response. ERPs have an exceptional temporal resolution in milliseconds, but are less precise for the anatomical location of the neural generators.

Electroencephalography (EEG) activity is time-locked to several presentations of similar events (stimuli or participant responses), and these segmented EEGs are averaged. This procedure decreases the presence of noisy activity (i.e., EEG unrelated to experimental events or background noise) while maintaining event-related activity. Filtering (e.g., 0.5–30 Hz), segmentation, artifact detection and correction, bad channel replacements, re-referencing, and baseline correction and averaging are some of the signal-processing steps usually required to obtain a suitable signal-to-noise ratio (SNR) (see Figure 1). After the processing steps are completed, positive or negative voltage changes in ERPs appear at specific latencies.

The simplest ERP parameters are latency (delay of appearance after an event), direction (positive or negative), amplitude (the amount of voltage change), and topological distribution of the component on the surface of the head (frontal, parietal, occipital, etc.). In general, ERP measurements quantify the amplitude and latency (measured in microvolts and milliseconds, respectively) of the waveform associated with a specific stimulus or response. Through this procedure, ERPs can be compared in terms of amplitude or latency. A topographical map (voltage map/topomap) is a continuous reconstruction of electrical activity on the scalp, normally based on spatial interpolation of the electrode sites. Each component usually has a relatively specific topographic distribution. The so-called long-latency components or endogenous components (ERP sensitive to changes in cognitive processing) usually are tracked following an interval of at least 80–100 ms after a stimulus onset (Luck, 2005).

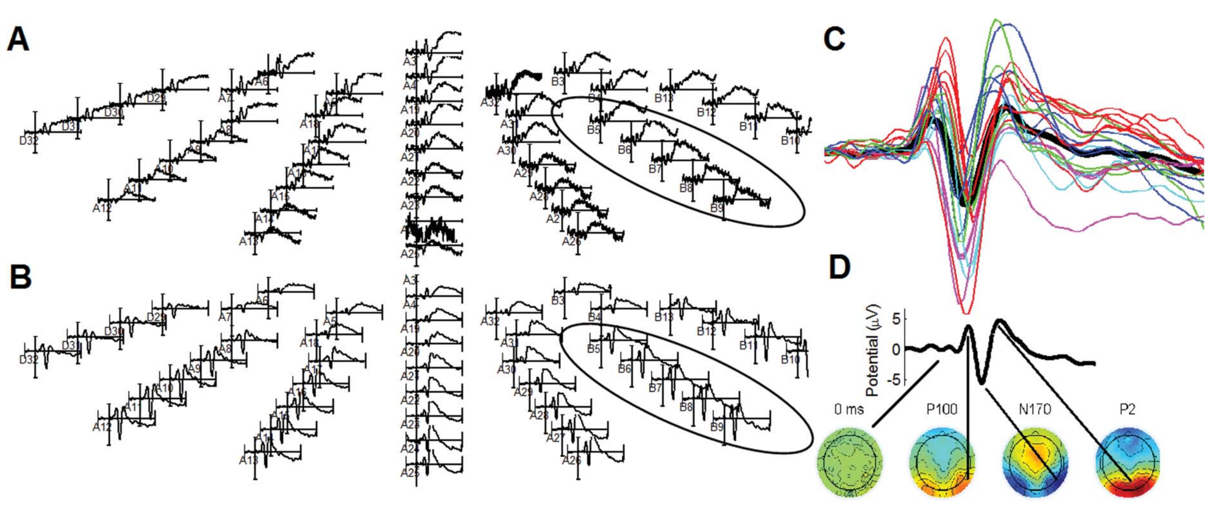

Figure 1. ERP SNR. (a) ERPs at temporo-occipital scalp in response to face stimuli without preprocessing and (b) with preprocessing. The N170 component can be clearly observed after preprocessing over the right occipito-temporal sites (comparing both ellipses). (c) N170 estimation over a representative electrode (T8) demonstrating theSNR reduction in between average waveform (black line). (d) Voltage map reconstruction by interpolation showing the scalp activity at 0 ms, P100, N170, 200, and P2 after the presentation of face stimuli.

A SELECTIVE DESCRIPTION OF MAIN COMPONENTS

P100 and N100 (P1 and N1)

In the 1960s, it was found that visual stimuli situated in visual fields with focused attention elicited components with a larger amplitude (approximately 100 ms after stimulus onset, P1 and N1) (Hillyard, Hink, Schwent, & Picton, 1973) than ignored or unnoticed stimuli (Herrmann & Knight, 2001). This amplitude enhancement reaches its maximum in the temporal–occipital region contralateral to the localization of the stimuli and sensitive to the specific localization of the stimuli in the visual field. Similar results were also obtained in the auditory modality, indicating an increased response in the auditory primary cortex (Herrmann & Knight, 2001). The P1 and N1 components are also modulated by several factors, including emotional saliency (Pourtois & Vuilleumier, 2006) and relevance (Turk et al., 2011).

P200 (or P2)

The P2 component is a positive deflection occurring approximately 200 ms after the onset of a stimulus (Hillyard et al., 1973). P200 is interpreted as indexing selective attention and visual feature detection processes (O'Donnell, Swearer, Smith, Hokama, & McCarley, 1997). Similarly, P2 is shown to be sensitive to orthographic/phonological, semantic categorization, reward–punishment discrimination, and lexical decision tasks (Kotchoubey, 2005; Neely, Verwys, & Kahan, 1998).

N200 (or N2)

The N2 component is a negative deflection resulting from a deviation in the form or context of a prevailing stimulus. Usually, N2 is evoked 180–235 ms following the presentation of a specific visual or auditory stimulus (Folstein & Van Petten, 2008). Although N2 is considered to be a part of a family of different components, its classical component is sensitive to perceptual features, attention and novelty/mismatch, and can be elicited through an experimental oddball paradigm. This component is also associated with conflict detection during the regulation of successful behavior (Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003). The N2 modulation comprises the anterior cingulate cortex (ACC, a brain area susceptible to social monitoring of conflict) and other prefrontal cortex areas (Nieuwenhuis, Holroyd, Mol, & Coles, 2004).

N170/vertex positive potential (N170/VPP)

The N170/VPP complex has a negative peak around 170 ms in the temporal–occipital regions (Bentin, Allison, Puce, Perez, & McCarthy, 1996) and at central–frontal positivity (VPP). The N170 (temporal–occipital) and VPP (frontal positivity) are to some extent functionally equivalent (Joyce & Rossion, 2005). The source of N170 comprises the superior temporal sulcus and the fusiform gyrus (two neural areas associated with specific face processing) (Deffke et al., 2007). Its amplitude is greater for human faces compared to objects or other stimuli (Bentin et al., 1996). During the face-processing task, N170 is sometimes followed by P2 and N250 components modulated by other variables (Zheng, Mondloch, & Segalowitz, 2012). The N170 component has shown amplitude/latency modulation based on racial cues (Balas & Nelson, 2010; Herrmann et al., 2007; Ibanez, Gleichgerrcht, et al., 2010; Ito & Urland, 2003; Ofan, Rubin, & Amodio, 2011; Stahl, Wiese, & Schweinberger, 2008; but see Vizioli, Foreman, Rousselet, & Caldara, 2010), emotional variables (Schyns, Petro, & Smith, 2007), and contextual effects (Fruhholz, Fehr, & Herrmann, 2009; Guillaume & Tiberghien, 2001; Ibanez, Hurtado et al., 2011).

Early posterior negativity

EPN is a mid-latency component associated with valence processing and stimuli arousal (Schupp, Flaisch, Stockburger, & Junghofer, 2006). Many studies have found a modulation for both pleasant and unpleasant emotional categories of pictures (e.g., Dufey, Hurtado, María Fernández, Manes, & Ibáñez, 2010; Wiens, Sand, & Olofsson, 2011). Nevertheless, specific effects (task or stimuli-dependent) on EPN in relation to valence and the influence of arousal should be further assessed.

P300 (or P3)

The P300 component is described as engaging higher-order cognitive operations related to selective attention. The P3 amplitude may serve as a measure of covert attention that arises independently from behavioral responding (Polich, 2007). P300 has also been related to a post-decisional "cognitive closure" mechanism (Lockwood et al., 2008) and to consciousness access (Railo, Koivisto, & Revonsuo, 2011). Its amplitude generally varies as a function of the temporal distance between a target and a preceding outgoing stimulus (e.g., Polich, 2007). There are two subcomponents: P3a and P3b. P3a has a more frontal distribution and appears after an unexpected event, regardless of the type of stimulus. It is usually associated with automatic attentional modulation. P3b is related to attention, working memory, and superior cognitive functions and appears at centro-parietal sites (Koivisto & Revonsuo, 2010). P3b is affected by motivation, sustained attention and novelty, and other psychological processes involved in social cognition tasks (Friedman, Cycowicz, & Gaeta, 2001).

Late positive components (LPP, PPC, P600)

Although initially described by Sutton in 1965 as a unique, frontal bilateral positivity, the LPP is considered a part of a family of components. This late component (300–700 ms) is sensitive to stimuli valence and preceding emotional context (Schupp et al., 2006). Its amplitude, according to several studies, increases in response to motivationally relevant stimuli (Schupp et al., 2006), as well as to the semantic emotional valence of stimuli (Cunningham & Zelazo, 2007) and contextual information (Cornejo et al., 2009; Hurtado, Haye, Gonzalez, Manes, & Ibanez, 2009). The LPC is a component similar to LPP and is related to reanalysis of incongruent stimuli (Ibanez, Manes, et al., 2010; Ibanez, Toro, et al., 2011). Finally, P600 is an index for second-pass parsing processes that are similar to working memory operations (Hahne & Friederici, 1999). P600 is associated with superior frontal, temporal, and parietal regions, which are believed to contribute to information processing during memory recognition.

N400 and N400-like

N400 is a negative component that appears around 400 ms after the presentation of semantically unrelated information between two words or between a context and a word. Although this component is classically studied in the linguistic field (Kutas & Federmeier, 2011), recent studies have included tasks combining action sequences and pictorial stimuli (sometimes called N350 or N400-like), such as congruent–incongruent pictures or videos of gestures, actions, and motor events (Aravena et al., 2010; Ibanez, Cardona, et al., 2012; Sitnikova, Kuperberg, & Holcomb, 2003; Willems & Hagoort, 2007). Although spatial resolution provided by ERP does not allow a precise localization of N400 neural generators, evidence from lesion studies, magnetoencephalogram (MEG), and intracranial recordings (iERP) implicates that the possible sources of N400 are the temporal areas: the left superior/middle temporal gyrus, the anterior–medial temporal lobe, the parahippocampal cortex (PHC), and the anterior fusiform gyrus (Van Petten & Luka, 2006). N400 points to a distributed and multimodal system that responds to both verbal and nonverbal stimuli (Kutas & Federmeier, 2011).

Contingent negative variation

CNV is an extended and prolonged negative potential recorded during warned reaction time paradigms with two sequential stimuli: S1 and S2 (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). Its scalp distribution always begins bilaterally and symmetrically at the midline of the precentral–parietal regions, approximately 1000–1500 ms before response movement. CNV is a correlate of anticipation of the S2 (Zappoli, 2003). CNV is elicited in paradigms designed to assess expectancy, self-regulation, reward/punishment, and decision making (Brunia & van Boxtel, 2001).

Error-related negativity and feedback error-related negativity

ERN is a component observed 50–100 ms after a high-conflict response, in which the typical responses are inconsistent with the correct ones (Nieuwenhuis et al., 2004). ERN is an index for the general sensitivity of the conflict monitoring system, which can be used to predict successful patterns of control. fERN is a negative deflection that distinguishes between wins/losses or correct/incorrect trials in expected and unexpected outcomes (e.g., Ibanez et al., in press; San Martin, Manes, Hurtado, Isla, & Ibanez, 2010). In correct or win trials, the equivalent components are called correct-related negativity and feedback correct-related positivity, respectively. Both ERN and fERN originate in the anterior, medial, and posterior divisions of the cingulate cortex (Nieuwenhuis et al., 2003).

Motor components (RP, LRP, MP, RAP)

Movement-related cortical potentials (MRCPs) are associated with self-paced movements and are a measure of motor cortex excitability. MRCPs index motor preparation and execution (Colebatch, 2007). The RP (or in its original German name, Bereitschaftspotential, described in 1964 by Hans Helmut Kornhuber and Lüder Deecke) precedes voluntary muscle movement and represents the cortical contribution to premotor planning. The LRP is a form of RP that responds to movements on one side (left or right) of the body. Derived from RP, MP, also known as the late motor-related potential, is negativity measured over Cz beginning shortly before the response onset (-90 ms) (Aravena et al., 2010). The MP is likely to represent neuronal activity in the premotor and primary cortex (M1) during motor execution (Ibanez, Cardona, et al., 2012). MP amplitude modulation is associated with measuring movement speed and precision and short-term training effects. In addition, the RAP is a component with a peak over Cz after movement onset (200–300 ms). RAP is an index of movement-related sensory feedback to the primary sensorimotor cortex and is modulated by attention (Colebatch, 2007). Both components (MP and RAP) are modulated by higher level cognitive processes, such as action–language incongruence (Aravena et al., 2010).

REPRESENTATIVE AREAS OF SOCIAL COGNITIVE NEUROSCIENCE

Contextual approaches to language

Context-dependent effects are frequent in everyday cognition, especially in the case of language (Barrett, Lindquist, & Gendron, 2007). We listen to and use words within other streams of words. We perceive facial emotion along with EBL, semantics, prosody, and other situational cues. Language use can be tracked by assessing the influence of context parameters (intonation, lexical choice, prosody, and paralinguistic clues) during communication. ERP studies of early [N170 and early left anterior negativity (ELAN)] and late (N400, LPC, LPP) components have provided important insights into temporal brain dynamics of contextual effects in language.

With regard to early effects, ELAN amplitude modulation appears 100 ms after the onset of a grammatically incorrect stimulus in word-category violation paradigms (as in *the in room* instead of *in the room*) (Friederici, 2004). In addition, left N170 triggered by rapid visual presentations of words together with other stimuli (faces, objects) demonstrates a very early pathway for semantic processing. Thus, reading either words or pseudo-words seems to affect left N170 amplitude modulation (larger N170 for pseudo-words), depending on the contextual information of the sentence (Kim & Lai, 2012). Similarly, late ERP research has demonstrated late multimodal blending of meanings, action–sentence coupling, language and social information coupling, and emotional word processing. For example, ERP research has found N400 amplitude enhancement for different incongruent stimuli (Hagoort, 2008) not only on word matching and picture matching tasks (Guerra et al., 2009), but also on sentence (Ibanez, Lopez, & Cornejo, 2006; Ibanez, Riveros, et al., 2011) and discourse-level semantic manipulations (Nieuwland, Otten, & Van Berkum, 2007).

In addition, contextual ERP studies of language suggest that gestures, body actions, and everyday actions are processed as linguistic meaning. The existence of a distributed and multimodal integrated system affected by both linguistic and nonlinguistic cues (Kutas & Federmeier, 2011) suggests that meaning is constructed as an emergent property of the parallel, coordinated activity of numerous brain areas, including sensory and motor regions.

The N400, LPC, and LPP components have shown a similar modulation (amplitude enhancement of incongruent conditions) as linguistic stimuli in simple co-speech gesture paradigms, action–sentence compatibility tasks, and video presentations of everyday actions. Nonverbal or pragmatic information such as gestures, gaze, body postures, and goal-directed motor behaviors enables us to accurately interact with the conspecifics of daily life. This approach is also consistent with the embodied view of language understanding (Pulvermuller & Fadiga, 2010).

Consequently, it has been suggested that the linguistic and action-related N400 responses are actually reflecting the same component, engaging different brain areas depending on the modality of the information processed (Amoruso, Couto, & Ibanez, 2011; Kutas & Federmeier, 2011). Further research is required to determine whether ERP action understanding indicates a common system indexing facilitatory effect of motor imagery, action/object observation, and speech listening (Fadiga & Craighero, 2004).

Emotion and EBL

Complex social skills depend on basic emotional processing and inference (Grossmann, 2010). Facial emotional expressions act as automatic, rapid shortcuts to mentalizing and intersubjective communication. Some important areas of emotion research include face emotional processing (Eimer & Holmes, 2007), emotion regulation (Hajcak, MacNamara, & Olvet, 2010), and intertwining of attention and emotion (Schupp et al., 2006).

ERP research has demonstrated early, automatic, and unaware processing of emotion in faces, words, and pictures. Early emotional discrimination of semantic processing (Mendez-Bertolo, Pozo, & Hinojosa, 2011) seems to affect left N170 amplitude modulation (larger N170 for pseudo-words and emotional salient words). Emotional and contextual effects indexed with the implicit association test (see Figure 2a) and the dual valence association task evidenced automatic integration of emotional saliency and face familiarity (Hurtado et al., 2009; Ibanez, Gleichgerrcht, et al., 2010; Ibanez, Hurtado, Riveros, et al., 2011; Ibanez, Petroni, et al., 2011; Ibanez, Riveros, et al., 2012; Petroni et al., 2011). Both paradigms evidenced automatic blending of two dimensions: face familiarity and semantic valence. Theoretical models of emotion perception (Vuilleumier & Pourtois, 2007) propose a parallel system that indexes object recognition (e.g., triggered by the fusiform gyrus) and emotional discrimination (e.g., triggered by the amygdala). Emotional signs that can denote confidence or danger may occur before and parallel to object codification. In other words, emotional significance is processed before a stimulus is completely identified.

In addition, LPP and LPC components index complex social stimuli with emotional processing at late stages. For example, emotional awareness (indexed with the international affective picture system) (Wiens et al., 2011) and complex integration of emotional valence and attitudes (Ibanez, Haye, Gonzalez, Hurtado, & Henriquez, 2009; Williams & Themanson, 2011) seem to be indexed at 300–700 ms (see Figure 2b).

EBL is another emergent area in neuroscience research (de Gelder, 2006; de Gelder et al., 2010). Neuroimaging studies have shown that EBL activates areas of emotional face processing, such as the amygdala and the fusiform gyrus. EBL signals are automatically perceived and influence emotional communication and decision making. Meeren, van Heijnsbergen, and de Gelder (2005) created a forced choice task using compound images of fearful and angry faces with bodies of either matched or mismatched emotional expression. A P1 enhancement evidenced a rapid neural mechanism sensitive to the degree of agreement between facial and bodily emotional expressions. Posterior studies with similar face–body paradigms (triggering P1 and N170 components) evidenced a contextual integration of emotional face and body processing (Grezes, Pichon, & de Gelder, 2007; van Heijnsbergen, Meeren, Grezes, & de Gelder, 2007). Thus, ERP research suggests that EMB (a) is automatic and processed early in the brain, (b) influences emotional recognition of face processing, and (c) is integrated with face processing (de Gelder, 2006; de Gelder et al., 2010).

In brief, ERP research provides a background for the dynamics of early and late emotional responses, some of their neurobiological correlates, the effects of context, attention, arousal, and task interaction on emotional processing, and individual and developmental differences (Eimer & Holmes, 2007; Hajcak et al., 2010).

Empathy

A large number of studies using fMRI (review: Decety, 2011), and more recently ERPs, have used the presentation of stimuli depicting people in pain (i.e., people suffering from physical injuries or expressing facial expressions of pain) to detect the neural underpinnings of empathic processing. These studies suggest that pain empathy involves a somatosensory resonance mechanism between the other and the self that draws on the affective and sensory dimensions of pain processing (Jackson, Rainville, & Decety, 2006). This mechanism provides crucial, rapid information for understanding and responding to the affective states of others (Decety, 2011).

The general paradigm of pain empathy assessed with ERPs (Decety, Yang, & Cheng, 2010; Fan & Han, 2008; Han, Fan, & Mao, 2008) contains static visual stimuli of pictures of different body parts (e.g., hand or foot). The pictures depict everyday life events of body parts under nonpainful situations (neutral) or painful situations (mechanical, thermal, and pressure). For each pain situation, a neutral picture involving the same conditions is also presented. Studies (Decety et al., 2010; Fan & Han, 2008; Han et al., 2008) have shown two basic correlates of empathy: an early and automatic response of stimuli type effects (pain vs. nonpain, indexed by a N1 frontal component) and a controlled processing of pain empathy (as indexed by a central–parietal P3 component). In addition, further studies have shown early modulation by the contextual reality of stimuli and late modulation based on cognitive task demands (Decety et al., 2010; Han et al., 2008; Yamada, Lamm, & Decety, 2011), as well as *own* versus *other* information (e.g., another person's angry face vs. the participant's own face) or priming of

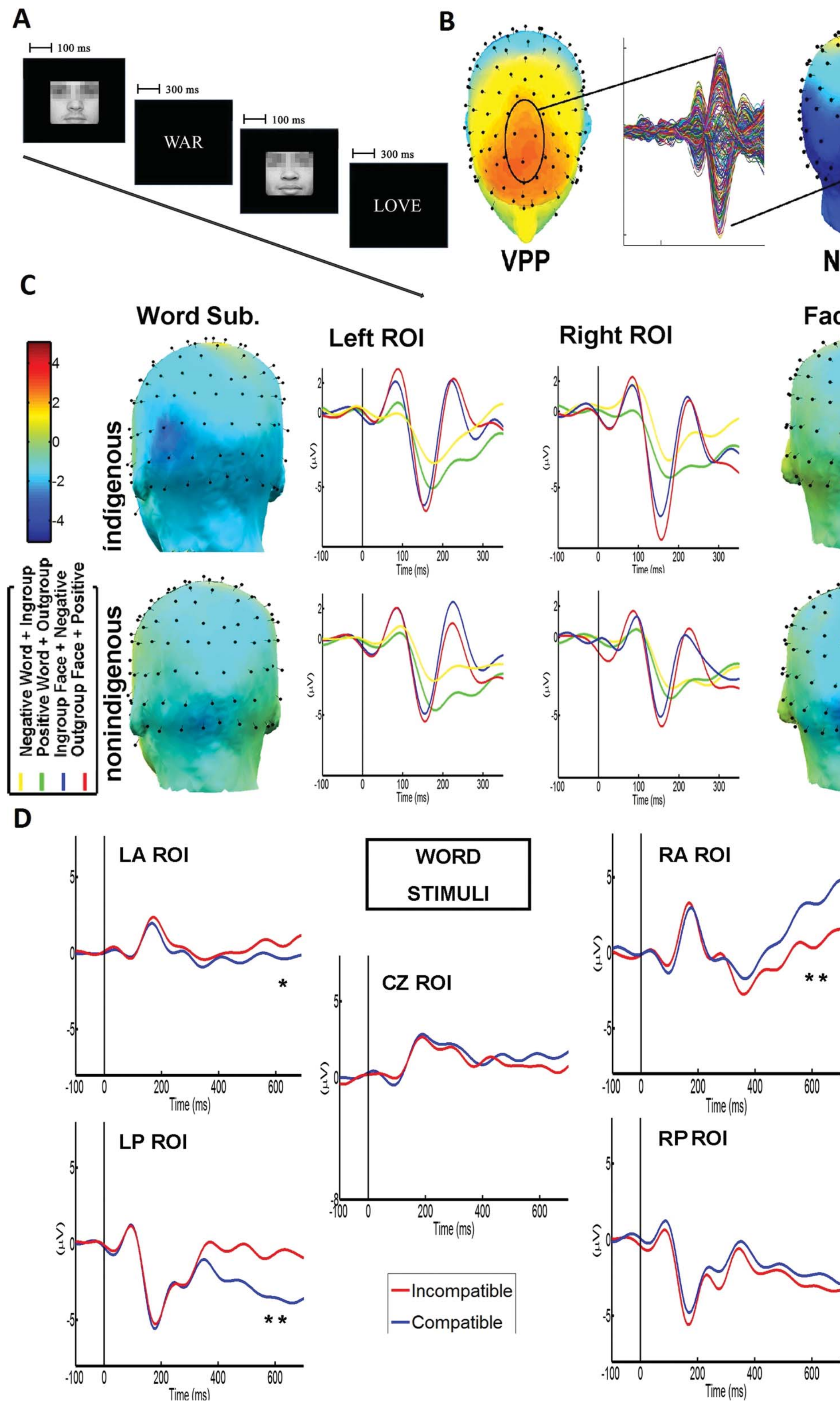

Figure 2. Early and late stages of emotional–cognitive processing. (a) Schematic representation of implicit association test (IAT). The IAT is a simultaneous stimulus categorization task that works by comparing subjects' reaction times with ERP when classifying a word (positive vs. negative) or a face (ingroup or outgroup) shown on a computer screen into one of the two response categories. Both ingroup and outgroup faces, along with words of positive and negative valence, are presented. The subject is required to classify each stimulus to the left or to the right according to labels displayed on top of the screen. (b) Early (N170) effects of IAT. (c) N170 contextual modulation based on valence and membership stimuli. (d) Late processing (LPP) of semantic stimuli compatibility. Modified with permission from BioMed Central Ltd (Hurtado et al., 2009) and from Frontiers in Human Neuroscience (Ibanez et al., 2010).

threat signaling (Ibanez, Hurtado, Lobos, et al., 2011). Therefore, ERP studies have provided key insights regarding context-dependent processing in automatic controlled processing of pain empathy.

Decision making and reward

Evidence from animals, healthy human volunteers, and neuropsychiatric patients (Gleichgerrcht, Ibanez, Roca, Torralva, & Manes, 2010; Rangel, Camerer, & Montague, 2008) highlights the role of the frontostriatal and limbic loops in decision making. Three main systems are thought to be involved in the frontostriatal and limbic loops: a stimulus-encoding system (orbitofrontal cortex), a reward-based action selection and monitoring system (cingulate cortex), and an expected reward system (basal ganglia and amygdala). These systems are crucial in the decision-making process in both healthy volunteers (Gleichgerrcht et al., 2010) and patients with neurodegenerative diseases (Figure 3).

The action selection and monitoring system can be tracked directly with P2, ERN, and fERN (Nieuwenhuis et al., 2004; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). It can be assumed that the anterior P200 is the beginning of fERN (Holroyd & Coles, 2008) and is modulated by feedback like in wins versus losses trials (San Martin et al., 2010). Classical studies of the ERN consist of trial and error elicitation. Miltner and colleagues asked participants to estimate the duration of an interval (Miltner, Braun, & Coles, 1997). Following a cue, participants were asked to press a button when they believed that 1 s had elapsed. After 600 ms, participants were given positive or negative feedback. The study concluded that ERN peaks within 100 ms after an incorrect response, and fERN appears around 240 ms after positive or negative feedback. ERN and fERN amplitudes in error trials were enhanced after implicit learning.

Gambling and decision-making tasks can also be assessed with P2, ERN, and fERN (Ibanez et al., in press; San Martin et al., 2010; Santesso, Dzyundzyak, & Segalowitz, 2011). In these paradigms, enhanced ERP amplitude modulation of wins/losses is similar to amplitude modulation in correct/error trials. Moreover, ERP results on decision making highlight the frontostriatal circuits' temporal dynamics modulated by dopaminergic, serotoninergic, noradrenergic, and cholinergic neurotransmitters (Krebs, Boehler, Roberts, Song, & Woldorff, 2012). For example, methylphenidate-treated attention deficit

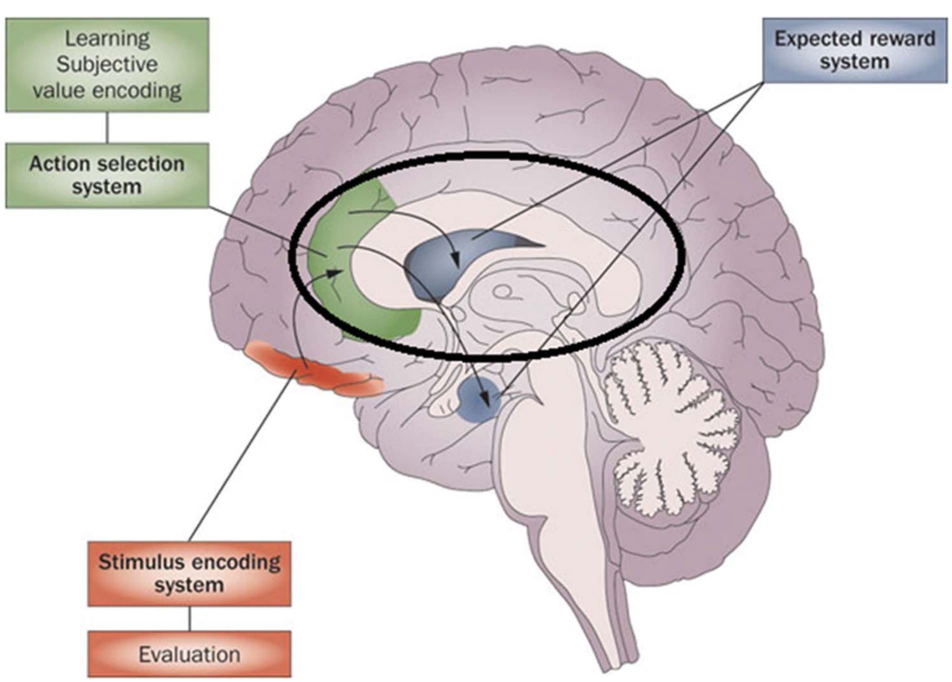

Figure 3. A neuroanatomical model of decision making. Three main systems are thought to be involved in decision making: a stimulus-encoding system (orbitofrontal cortex shown in red); an action selection system (ACC shown in green); and an expected reward system (basal ganglia and amygdala shown in blue). The anterior, medial, and posterior cingulate cortices, together with basal ganglia (ellipse), seem to modulate the ERN and fERN in gambling and error-monitoring tasks. Modified with permission from Nature Publishing Group (Gleichgerrcht et al., 2010).

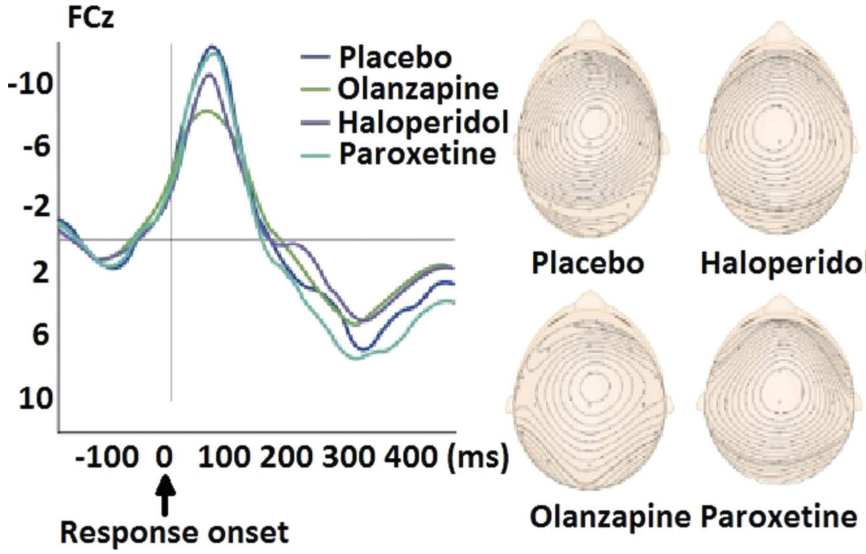

Figure 4. Reduction of ERN by haloperidol, but even more so by olanzapine. Effects of paroxetine were absent. ERN topographies were similar in the four drug conditions. Adapted with permission from de Bruijn et al. (2006).

hyperactivity disorder (ADHD) participants showed a normalized ERP modulation of performance monitoring compared with nonmedicated participants (Groen et al., 2008). Haloperidol and olanzapine also reduce ERN amplitude (de Bruijn, Sabbe, Hulstijn, Ruigt, & Verkes, 2006) (see Figure 4). Given their frontal–basal connection and modulation based on neurotransmitters, frontostriatal circuits seem to be essential for behavior regulation, particularly for self-action monitoring (Menzies et al., 2008). According to the stated results, the ERN and the fERN are generic, high-level processing systems related to error learning and reward processing (Holroyd & Coles, 2002; Ridderinkhof et al., 2004).

COMPLEMENTARY ISSUES

Intracraneal recordings

Local field potentials (LFPs) and electrocorticography (ECoG) in patients with surgically implanted electrodes (Figure 5) have provided new methods for studying spatiotemporal brain dynamics of cognition. Intracranial recordings help diagnose and treat neurological conditions such as epilepsy, Parkinson's disease, and tumors. LFP and ECoG measure direct brain activity with the highest quality of combined temporo-spatial resolution than any other human neuroscience method. Compared to scalp ERP, LFP and ECoG provide a better spatial resolution (mm vs. cm) and higher frequency domains (0–500 Hz vs. 0–40 Hz) (Ritaccio et al., 2010) and are less influenced by ocular and muscular artifacts. Intracranial ERP assessment and evoked oscillatory activity have provided important insights into working memory, episodic memory, language, face processing, consciousness, and spatial cognition (Jacobs & Kahana, 2010).

An important issue in decision-making cognition is the role of corticobasal ganglia communication and its effect on conflictive decision processes. Usually, theoretical models accentuate the role of cortical areas in decision making (e.g., orbitofrontal area), but they tend to overemphasize the influence of subcortical areas. In a study done by Cavanagh et al. (2011), direct intracranial stimulation and recordings in humans during a choice conflict task evidenced that subthalamic nucleus stimulation reverses mediofrontal influence over the decision threshold. The study also evidenced a parallel temporal corticostriatal mechanism for facilitating high-value actions and reducing decision thresholds (see Figure 6).

Source location in dense arrays

The current use of dense arrays of electrodes (from 64 to 256 channels) allows a better measurement of field potentials and improves the estimation of ERPs' brain sources. The source estimation reduces the spatial imprecision of ERPs and links temporal information with low-resolution anatomical measures. Important advances on parametric and nonparametric

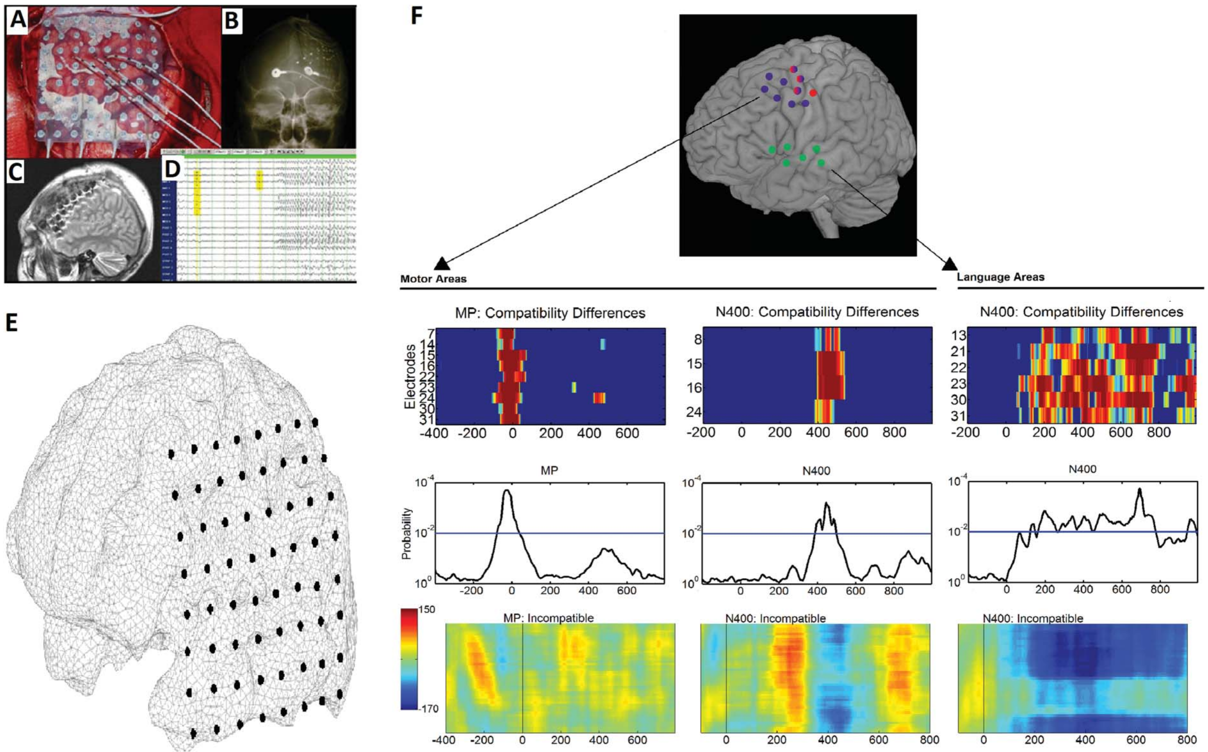

Figure 5. Intracranial recordings. (a) Grid of 63 electrodes for ECoG in a patient with refractory epilepsy. (b) X-ray computed tomography (CT) and (c) MRI showing the electrode grid and deep electrodes for LFPs. (d) Intracranial EEG. (e) Coordinates where the electrodes were situated over a brain surface reconstruction. (f) Motor and language areas modulated by coupling of action and semantic process during an action–sentence compatibility effect. Normalized position of the electrodes superimposed in a render three-dimensional map of the canonical CH2bet from MRIcron software, BSD License. Time–probability charts showing the significant effects at MP in premotor/motor areas and temporal areas. Point-by-point *p*-value waveform of statistical comparison between two categories. Single trial power activity for intracranial ERP. Modified and reproduced with permission from Cortex (Ibanez, Cardona, et al., 2012).

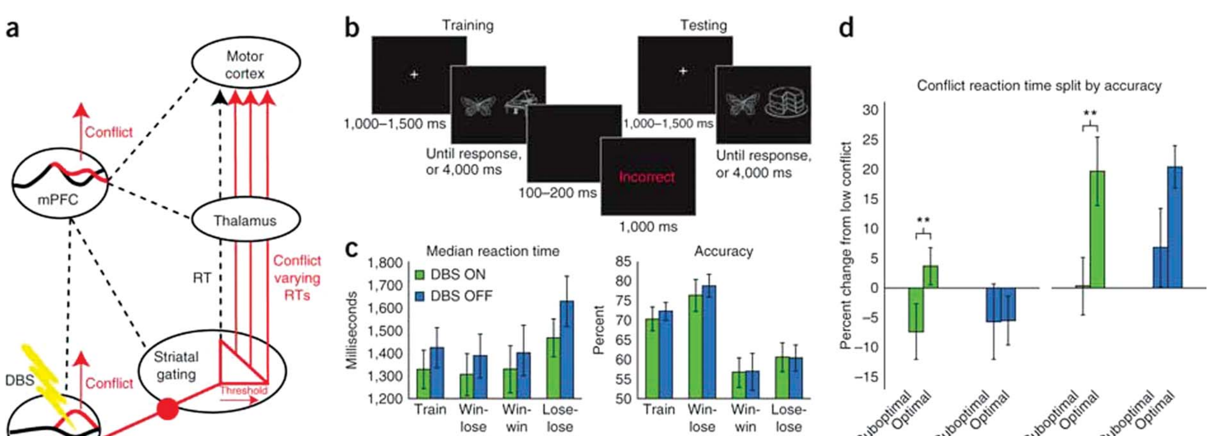

Figure 6. Cortical–subcortical interaction in decision making. (a) Proposed model of medial prefrontal cortex and subthalamic nucleus (mPFC–STN) gating of decision threshold. Action plans are gated in a corticostriatal loop (dashed line). In the presence of mPFC-detected conflict, the STN inhibits behavioral output by raising the threshold required for the striatum to gate action plans. This results in conflict-varying response times (solid lines). DBS to the STN interrupts this process, resulting in a disruption of the ability of mPFC to regulate control. RT, response time. (b) Task dynamics. During training, participants learned to choose one item in each pair (termed A/B and C/D) that was reinforced more often (A/B, 100%/0%; C/D, 75%/25%). In this example, the butterfly might be A and the piano might be B. During testing, participants had to choose the better stimulus, leading to high-conflict choices for win–win (A/C) and lose–lose (B/D) as well as low-conflict choices (A/D, C/B). For example, if the cake was C in training, this would reflect a high-conflict win–win cue. (c) Study I performance data (mean ± SEM). (d) Study I conflict adaptation split by accuracy (mean ± SEM). Suboptimal trials were relatively speeded compared with correct trials ON (but not OFF) DBS. Reproduced with permission from Nature Publishing Group (Cavanagh et al., 2011).

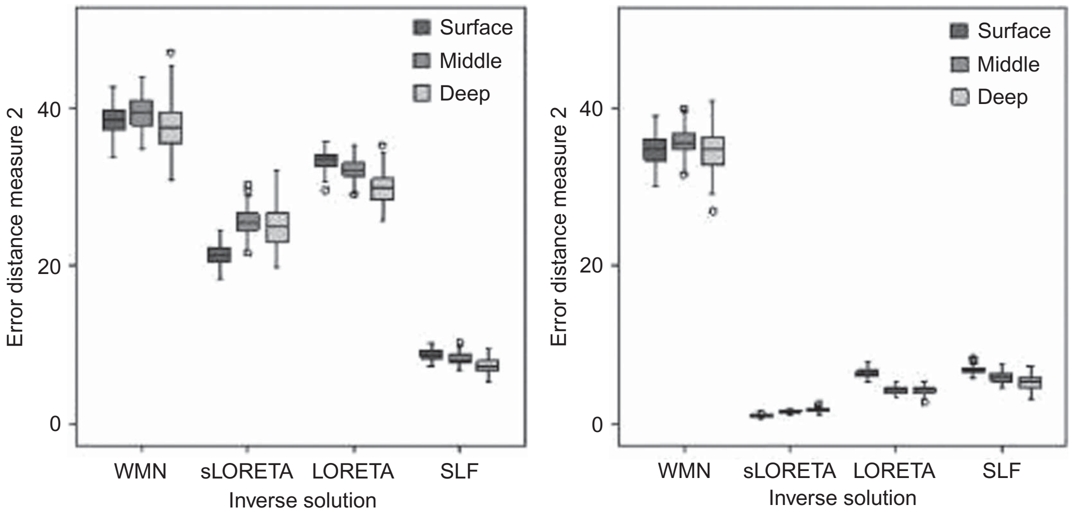

Figure 7. Comparison of different source estimation models. The box–whisker diagrams show the median (horizontal line within each box), the interquartile range (between the bottom and the top of each box), and the range of scores (shown by the whiskers). Circles represent outliers. Plots (a) and (b) show the results for each of the four inverse solutions (horizontal axis) for error measure (ED2) with anSNR (defined as the ratio of source variance to noise variance) of 5 dB. (a) The results without regularization and (b) the results with regularization. Regularized sLORETA has the lowest errors in terms of localization error. Reproduced with permission from BioMed Central Ltd (Grech et al., 2008).

methods exist (Grech et al., 2008). Several engineering solutions to find ERP sources using inverse problems with parametric and nonparametric methods are available (e.g., LORETA, sLORETA, VARETA, S-MAP, ST-MAP, Backus–Gilbert, LAURA, SLF, SSLOFO, and ALF; BESA, MUSIC, and FINES, reviewed in Grech et al. 2008). Methods of distributed sources (e.g., sLORETA, see Figure 7) combined with enhanced spatial constraints (e.g., photometry) can produce more relevant results. Finally, principal component analysis (PCA) and independent component analysis (ICA) are now accessible for ERP source localization. Distributed EEG/MEG source analysis using statistical parametric mapping of magnetic resonance imaging (MRI) promises further advances in social and affective neuroscience (Junghofer, Peyk, Flaisch, & Schupp, 2006).

The use of source location to improve social neuroscience research has been demonstrated in theory of mind (ToM) research. Human social interactions depend on having a ToM, ability to infer thoughts, beliefs, intentions, and desires in other people's minds. Although several fMRI reports of neural networks involved in ToM performed in the last decade exist, little is known about the temporal dynamics of these networks. Leuthold, Filik, Murphy, and Mackenzie (2012) used dense-array ERPs to show that a right N270-400 component followed by a larger positivity at frontal sites is activated when decoding mental states from images of eyes. Moreover, source estimation of N270-400 and the frontal positivity yielded two different sources at anterior temporal and orbitofrontal regions, respectively. Thus, anterior temporal lobe activation may reflect increased demands of integrating general social knowledge and specific contextual information. Orbitofrontal activation would later reflect high-level mind-reading functions. These findings suggest that ToM components may rely on partially dissociable mid-latency neural mechanisms.

The use of a high number of dense arrays (improving the source estimation), complementary techniques for electrode location (e.g., photometry), and the recent development of source localization algorithms can provide measures of improved spatial resolution for further social and cognitive research.

fMRI–ERP simultaneous recordings

fMRI provides an accurate spatial resolution but measures indirect brain signatures (hemodynamic response) and has poor temporal resolution. ERPs are a direct measure of cortical activity but have poor spatial resolution. Combining fMRI and ERPs provides a spatial and temporal fine ground resolution of cognitive brain activity (Gore, Horovitz, Cannistraci, & Skudlarski, 2006). Recently, removal algorithms of fMRI artifacts on ERPs have been developed, facilitating the combination of the two methods. For instance, ERP/fMRI co-recording allows an enhanced study of origins and locations of ERP neural generators.

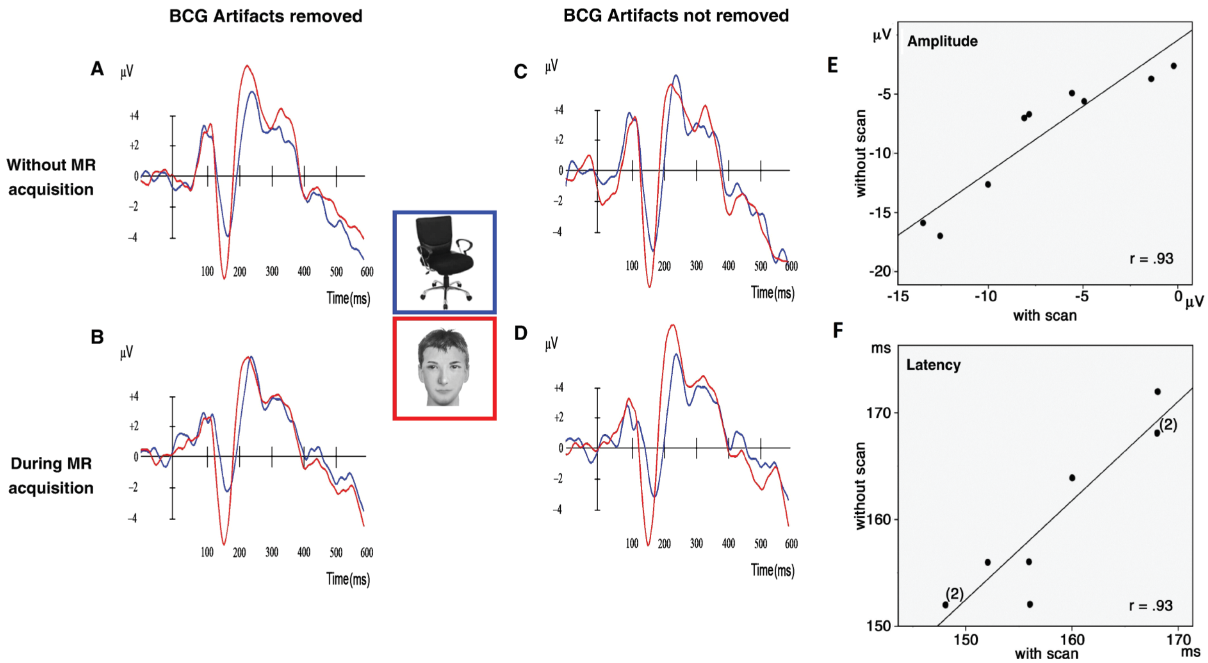

Figure 8. Simultaneous ERP–fMRI recordings of N170 component. (I) Grand average ERP of nine subjects at a representative temporal–occipital electrode P8, without (a, c) and with (b, d) MR acquisition when BCG artifacts are removed (a, b) or not removed (c, d). (II) Correlations across subjects for the N170 peak amplitude (a) and latency (b) to faces at electrode P8 reveal very high correlations between data collected with and without MR acquisition. The symbol "(2)" indicates a dot representing overlapping data points of two subjects. Reproduced with permission from NeuroImage (Sadeh et al., 2008).

For example, the intertwined spatial (fusiform areas) and temporal brain dynamics (N170) of face processing in the human brain have been measured with this methodology (Sadeh, Zhdanov, Podlipsky, Hendler, & Yovel, 2008). This study confirmed the specific functionality of N170 facial processing and linked its temporal dynamics with neuroanatomical face-processing areas (fusiform cortex). Moreover, face-selective characteristics of the N170 (e.g., N170 peak amplitude, latency, selectivity to faces, laterality to faces) are preserved during simultaneous fMRI data acquisition, allowing further cross-talk research (figure 8). Integrating fMRI and ERP recordings shows promising insights into social neuroscience.

WHAT DO ERPS CONTRIBUTE TO SOCIAL NEUROSCIENCE?

The genuine advantage of ERP studies

In the previous sections, we highlighted the specific contribution of ERP processing in emotional processing, contextual effects in speech, empathy, and decision making. Here, we summarize the wide-ranging benefits of ERP research. The temporal precision of the ERP allows assessing several matters: (a) short and transient brain changes, (b) behavioral correlates and task modulation in a stage-by-stage sequentiation, and (c) bottom-up and top-down cognitive interactions.

ERP tracks the fine temporal dynamic changes of cognitive processes. Multiple cognitive events are transient and restricted to short time windows. Subtle changes between trials can also be studied with recent approaches to single trial dynamics (Makeig et al., 2002). The ERP technique assesses cognitive stages from early windows (e.g., 80 ms after stimulus onset or 700 ms before subject response) to successive dynamical changes over time.

ERPs can be considered the "reaction time for the twenty-first century" (Luck, 2005). A multilevel measure of cognitive processes can be achieved using trial-by-trial analysis and behavioral responses. Even without a behavioral response (e.g., passive paradigms) or task-modulated behavior, ERPs can still record the processing stages affected by experimental manipulations.

Current ERP research in social neuroscience (e.g., attention–emotion interaction, facial processing, empathy, prejudice and attitudes, decision making) highlights the role of early and late cortical dynamics. Early responses (e.g., 80–200 ms after stimulus onset) usually index bottom-up sensory mechanisms sensitive to stimulus salience. For instance, early modulation refers to the facilitation of early automatic and pre-attentional discrimination of salient stimuli. Later stages (300–800 ms) may be considered a marker of top-down control mechanisms that support the processing of task-relevant stimuli. The late process can be interpreted as a correlate of arousal, control, and awareness. Thus, the early/late processes can be understood as an early automatic and late controlled parallel process. Time dynamics is crucial to the interaction of these processes, especially because neuroimaging studies sometimes provide imprecise information. Several neuroimaging studies, for example, suggest that the rapid detection of salient targets is a pure bottom-up process (e.g., Wardak, Vanduffel, & Orban, 2010). The influence of the dorsal attention network (lateral prefrontal cortex and the ACC), however, during both bottom-up and top-down processing (Ossandón et al., 2012) was revealed using spatial–temporal dynamics of intracranial single trial ERP. Given the limited temporal resolution, previous neuroimaging studies failed to find active top-down processes in visual search paradigms.

Thus, ERP measures present important advantages: (a) temporal dynamic and transient changes of cognitive events, (b) modulation of experimental manipulations and its combination with behavioral outcome, and (c) differentiation and interaction between early bottom-up/automatic and late top-down/controlled events. The combination of ERP research with intracranial procedures, source location algorithms, and fMRI co-recordings reduces spatial resolution limitations and offers a more complete picture of social and cognitive brain processes.

Limitations of ERP paradigms

There are also several methodological limitations often present when assessing questions of social neuroscience with ERP assessment.

Current inferences about spatial resolution of the brain, neuroanatomical questions, or issues regarding clear origins and functional significance of neural ERP generators should be avoided. ERPs used in source localization do not provide specific information in relation to biophysical events that underlie different components (Luck, 2005; except under certain conditions, such as ERP–fMRI simultaneous recordings; some components with relatively unitary neural generators as the occipital P1, the N170, or the ERN/fERN; or during intracranial recordings).

Further, several steps during signal preprocessing may yield inconsistent results when poorly controlled and when using different processing strategies. Multiple preprocessing stages (e.g., filtering and artifact rejection) and different measures for statistical analysis (e.g., single trial vs. subject average comparisons; peak latency vs. peak amplitude vs. mean amplitude analysis; electrode selection and region of interests criteria) should be more explicitly described and compared in ERP research. A meticulous report of preprocessing steps (e.g., Duncan et al., 2009) would make ERP studies more comparable and reliable.

For example, the number of trials after artifact rejection tends to be dissimilar between subjects and conditions, yielding SNR differences. The percentage of trial rejections are often not reported and not statistically contrasted. Analysis of independent components (ICA) is an adequate method for artifact deletion without trial rejection. Nevertheless, the ICA has its drawbacks, as residue of the artifact still remains in the EEG after component removal (Shackman, McMenamin, Maxwell, Greischar, & Davidson, 2010), and direct removal of ICA components might lead to EEG data loss (Lindsen & Bhattacharya, 2010). Given these concerns, the use of likelihood/mutual information based on ICA methods is recommended (Delorme, Palmer, Onton, Oostenveld, & Makeig, 2012)

With regard to analysis, there are no explicit rules for electrode selection. The selection of the regions of interest (ROIs) varies across studies. Some authors select different electrodes depending on each subject to optimize task manipulation (Rousselet & Pernet, 2011). This strategy may result in an invalid procedure because it compares the electrodes with maximum amplitudes of one subject and condition with other electrodes of another subject and condition. As in fMRI studies (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009), nonselective criteria for ROIs analysis should be considered.

With regard to statistical comparisons, single-trial analysis is a more sophisticated procedure than mean amplitude or mean latency analysis, but is not always performed in ERP studies (Rousselet & Pernet, 2011). However, the dynamics of single-trial analysis is not well known and varies across tasks. Conversely, in some paradigms the subject average signal provides a simple and adequate measurement. Problems with classic group statistics and categorical designs should be replaced by reverse correlation techniques and statistical modeling approaches (Liu, Agam, Madsen, & Kreiman, 2009).

In summary, ERP studies have a number of dissimilar (and usually not well-documented) results in preprocessing stages, in addition to arbitrary or inappropriate statistical analyses. These caveats increase noisy results and reduce comparability among studies. Inconsistencies, however, are not restricted to ERP studies. The use of inadequate analysis strategies (Nieuwenhuis, Forstmann, & Wagenmakers, 2011), arbitrary selective data criteria (Kriegeskorte et al., 2009), or incorrect multivariate comparisons (Edward, Christine, Piotr, & Harold, 2009) is frequent in neuroimaging studies. Improving ERP research demands producing explicit and detailed reports, consensus among data preprocessing and analysis, ICA methods, correlation techniques, statistical modeling approaches, and nonselective criteria for ROIs analysis.

Some theoretical remarks

The fields of social neuroscience reviewed in this study suggest that basic social cognition (e.g., emotion, empathy, speech, decision making) is a highly situated phenomenon (Amoruso et al., 2011; Barrett et al., 2007; de Gelder et al., 2010; Ibanez & Manes, 2012). An experimental object may be processed differently because of contextual information or intrinsic motivation. This result can occur at neurophysiological and behavioral levels. Cognitive process seems to be a very ecological phenomenon dependent on external (world) and internal (mind) micrological circumstances. Thus, multilevel approaches (from neuroscience, psychology, and social sciences) combining ERP research and social cognition may have certain advantages: theoretical co-construction, interlevel cross-evidence, and combined explanatory strategies. The future of multilevel approaches to social neuroscience should rely on the adequate interplay between ecological approaches and rigorous experimental designs. The role of ERPs in assessing time dynamics of social processes in the brain is essential for these future studies.

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