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The emotional control of action: ERP evidence

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ABSTRACT

It is known that unpleasant emotions can modulate the speed of involuntary movements, yet the effects of aversive stimulation on voluntary motor acts have not been systematically investigated. The effects of aversive stimulation on subsequent movement-related cortical activity were examined using a task involving compatible and incompatible movements. Negative shifts in the timing of two motor event-related potentials were found subsequent to aversive stimulation for compatible movements only. With analogy to the Fear-Potentiated Startle Reflex, a reactive mechanism affecting covert action, these Fear-Potentiated Movement-Related Potentials (FPMPs) reflect preparation for overt actions performed to cope with particular types of danger. Further analysis revealed a positive deflection in the left frontal cortex prior the execution of incompatible movements, which may reflect inhibitory suppression of externally-triggered imitative tendencies.

Key words

Fear-potentiated movement related potential • Readiness Potential • Motor Potential • Unpleasant emotions • Stimulus response compatibility • Defensive system • Imitation

Despite extensive investigations in the domain of emotions such as fear conditioning, facial expression recognition, autonomic activation, and emotional memory, the relationship between emotions and the action system is still not well understood (Zhu and Thagard, 2002). The emotions elicited by potentially life-threatening aversive stimuli have been found to produce, after an initial fear reaction, subsequent defensive reactions that help in coping with different types of threats (Mineka and Ohman, 2002; McNaughton and Corr, 2004). How this critical shift from reaction to action in fearful situations is accomplished by organisms is to date little understood (LeDoux, 1996).

In the perspective we favour, an aversive situation (such as a human or animal attack) causes the engagement of a hypothetical defensive system (Lang et al., 1997; see also the "fear module" of Mineka and Ohman, 2002) whose function is to select a set of potential actions that can keep individuals away from danger. The studies testing this hypothesis all employ the fear-potentiated startle reflex paradigm with human subjects (Lang et al., 2000). In these studies, threat cues evoked emotions that are viewed as a preparatory state that is usually elicited by very unpleasant pictures, and is indexed by changes in the amplitude of electromyographic signals recorded from muscles involved in the startle reflex (Brown et al., 1951). These covert motor responses may not be representative of the larger domain of overt action. When we face a threat, this type of reflex is only the first step; to effectively cope with imminent danger a more complex overt action must also be taken.

Most studies have failed to find an effect of aversive stimuli on overt voluntary action. Lemke et al. (2005), for example, have recently developed a paradigm to simultaneously study the influence of

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emotions on involuntary (classic startle eye-blink reflex) and voluntary movements, using an infrared kinematic tracking analysis of the subjects' reaching hand movements. Although an emotional modulation of the involuntary movement was observed, no significant differences were found between the recorded parameters (i.e. duration of finger movement, duration of hand movement, peak velocity of finger, finger's movement curve, length of the hand movement curve and peak velocity of finger and hand) of the voluntary movement in the emotional condition and in the neutral condition.

In contrast, Rumiati et al. (submitted) have showed a modulatory effect of emotional pictures on voluntary motor performance. They used a modified paradigm originally developed by Brass and colleagues (Brass et al., 2000; Brass et al., 2001a). Brass et al. (2001), for instance, subjects were pre-instructed to either lift or tap the index finger, as soon as they saw a lifting or a tapping movement. When seen and performed movements were the same (i.e. compatible trials), RTs were faster than when they were different (i.e. incompatible trials). The authors concluded that human adults have a strong tendency to imitate and suggested that action imitation is a special case of S-R compatibility. In Rumiati et al. (submitted), subjects observed a tapping or a lifting movement preceded by an unpleasant, a positive or a neutral picture, and then they performed either a compatible or incompatible movement (Experiment 1). They found that the emotional content of primes interacted with the compatibility between seen and performed movements, and that compatible movements were faster after unpleasant than after positive or neutral primes. They also showed that the facilitation of the compatible movements after the unpleasant emotional primes was influenced by the level of the subjects' anxiety (Experiment 2 in Rumiati et al.). In the compatible trials, the more anxious the subjects were, as established on an anxiety scale, the slower they were to respond, and *vice versa*, the less anxious they were, the faster they responded.

The present experiment was designed to examine possible electroencephalographic correlates of the influence of negative emotions on imitation by using previously characterized cortical movement-related potentials to see if the neural signal differs in the emotional condition with respect to the neutral one. We predicted that during the execution of the motor task in the emotional condition, enhanced cortical activity should be found in two movement-related components: the Readiness Potential (RP), and the Motor Potential (MP), the first preceding the execution of the movement, and the second accompanying it.

Difference in performance between compatible and incompatible movements is of particular importance for the present study. As recent studied have suggested (Brass et al., 2000, 2001a), simply observing a finger movement evokes a tendency to execute that action but, since evoked imitations are not always adaptive in everyday situations, they are usually inhibited. However Brass et al. (2003) showed that patients with frontal lesions produced significantly stronger imitative response tendencies than a control group, suggesting a critical role of these brain regions in inhibiting these responses. Luria (1966), Lhermitte et al. (1986), and De Renzi et al. (1996) had previously provided similar observations.

To investigate the neural structures involved in the inhibition of imitative responses, Brass et al. (2001b) carried out an fMRI experiment in which subjects executed a pre-instructed finger movement (tapping), while viewing compatible (tapping) or incompatible (lifting) movements. When contrasting the incongruent with the congruent trials, the right middle frontal gyrus (MFG), the banks of the superior frontal sulcus, as well as the right superior frontal gyrus (SFG), the right anterior parietal cortex, the posterior precuneus bilaterally and the parieto-occipital sulcus were found activated. They argued that these areas are associated with the conflict between the externally triggered imitative response, and the intention of the to-be-executed willed action (Brass et al., 2001b). They also claimed that prefrontal cortex (especially the MFG) plays a role in inhibiting the externally triggered imitative response. Coherently with this data, we aspect frontal electrodes activation in comparing incompatible with compatible trials signals.

Methods

Participants

Fifteen subjects (seven males) all right-handed, with normal or corrected-to-normal vision (mean age: 25 years; education: 16 years), took part in the study after providing written informed consent. They were

naïve to the study and were paid 10 euros for their participation. Subjects were interviewed to assess their medical and psychological condition, and were administered two tests to assess anxiety-related personality traits that potentially affect reactions to emotional stimuli: 'negative affectivity' (PANAS, Watson and Clark, 1994). However, as all subjects scored within normal range, no analysis of these questionnaires will be reported. Prior to the experiment proper, subjects a familiarization phase (20-trials, later excluded from the analysis). Those who did not perform the task adequately were asked to perform additional 20 trials to reach standard performance. Subjects were monitored via a unidirectional mirror during the experiment.

Stimuli

Neutral and emotional pictures and short movies of a moving hand were employed as stimuli. Two sets of pictures from the International Affective Picture System (IAPS, Lang et al., 2005) were used as primes. The IAPS, developed to provide a set of normative emotional stimuli for experimental investigations of emotion, contains a large set of emotionally-standardized, color photographs distributed in a two-dimensional affective space formed by "valence" and "arousal" ratings. Based on our previous work suggesting that only negative, unpleasant emotions affect the imitation task, we used only emotionally-negative pictures and neutral ones. Emotionally-negative pictures had a mean valence of 2.28, and mean arousal of 6.05, and neutral stimuli had a mean valence of 5.08 and mean arousal of 2.76, which were generally judged to be very unpleasant. Fear-relevant stimuli depicted dangerous objects, animal attacks, human attacks, scenes of calamities and accidents, bloody scenes, human and animal mutilations, self-defence, pollution and corpses, known to elicit defensive reactions. Perceptual (from simple objects to complex images) and semantic features (grouped in four categories: objects, animals, humans and landscapes) of the stimuli were balanced across conditions. A total of 100 pictures (50 neutral and 50 negatively emotional) were selected. There were two repetitions for each image, so the subjects saw a total of 100 negative and 100 neutral pictures.

To control for perceptual differences in terms of colors, brightness and complexity between the emotional pictures and the neutral ones, we analyzed the "entropy" of the intensity of the images (used to characterize their texture), the "inertia" (mean contrast between each pixel and its neighbour over the whole image), the "uniformity" (summation of squared elements in the grey level co-occurrence matrix), the "homogeneity" (closeness of the distribution of elements in the grey level co-occurrence matrix to the same matrix diagonal), the brightness and the percentage of the three fundamental colours using functions provided in the Matlab Image Processing Toolbox. Each stimulus was analyzed independently, and the values of the two sets (neutral vs. emotional) were compared using ANOVA. None of these parameters differed significantly between the two sets of stimuli (Entropy $F(1,98) = 2.06$, $p = 0.155$; Inertia $F(1,98) = 0.66$, $p = 0.42$; Uniformity $F(1,98) = 0.88$, $p = 0.35$; Homogeneity $F(1,98) = 2.29$, $p = 0.133$; Brightness $F(1,98) = 1.14$, $p = 275$; Percentage of Red: $F(1,98) = 3.829$, $p = 0.053$; Percentage of Blue: $F(1,98) = 0.659$, $p = 0.419$), except for the Percentage of Green ($F(1,98) = 9.776$, $p < 0.01$). Picture complexity must be balanced to avoid effects due to different amounts of novel information (Buodo et al., 2002). Other studies using the same kind of pictures have shown that perceptual features such as colors, and brightness (measured with subjective ratings) and compression format do not seem to be relevant. We suggest that the difference in green color percentage has little direct effect on the ERP components measured in this study, which occur later than visual potentials affected by color parameters**.**

After each prime (emotional or neutral), subjects saw the movement of an animated hand. The animated hand mirrored the participant's right hand which was kept on the table in front of them. The video sequence consisted of five frames, the first of which showed the index finger in a middle, resting position, identical for both movements (lifting and tapping), which remained visible for 300 ms; the subsequent three frames flashed for about 30 ms each. The last frame contained an image of the final finger position and remained on the screen for 210 ms (Fig. 1).

Experimental procedure

All procedures were approved by the SISSA ethical research committee. Participants sat in a recliner in a sound-attenuated, dimly lit room. The scalp

and peripheral electrodes (EMG and EOG) were applied, and computerized task instructions were given. To prevent excessive eye-blink artefacts, participants were also asked to blink their eyes as much as possible while viewing the fixation point and to avoid eyeblinks during other parts of the trial. A Pentium IV computer controlled the experiment (E-prime software) and the data acquisition. The visual stimuli were projected on a 19-inch white screen located approximately 1.1 m from the participant's eyes (≈ 22° of visual angle).

We adapted the paradigm used by Grecucci et al. (submitted) in order to accommodate the ERP recordings. Each trial consisted of the following events (Fig. 1): first a fixation point appeared, lasting for 200 ms, followed by a black screen for 200 ms. Then the prime pictures were presented for 1 second, followed by a digitized video-sequence of the animated hand for 600 ms, at the end of which subjects were required to execute the pre-instructed movement. The images of the moving hand were positioned in the centre of the screen, and were of approximately life size (13 x 16 cm); IAPS pictures covered the whole screen. Each experiment contained 200 trials, 100 in the emotional and 100 in the neutral condition.

The type of stimulus (i.e. lifting or tapping) was varied within each block in a compatible or incompatible fashion. Thus the subjects performed the finger-tapping task while both randomly compatible and incompatible finger movements were shown (lifting and tapping). All IAPS pictures were randomized as well as the coupling of compatible-incompatible events with the pictures across trials.

Subjects had a maximum of 3000 ms to respond, after which a black screen was presented for another 3000 ms as an interstimulus interval. To record reaction times participants were asked to tap on the bar of a computer keyboard. To facilitate the position and the movement of the hand and to prevent fatigue of the muscles, a rigid platform was built. During training trials, participants were instructed to perform the movement in a precise way according to the following procedure: the hand was positioned on the platform with all the fingers in a resting position except the index finger which was rigidly kept up 6.5 cm upon the bar of the computer keyboard. The required movement was a downward motion of the index finger of about 60 degrees, similar to the observed tapping movement of the animated hand.

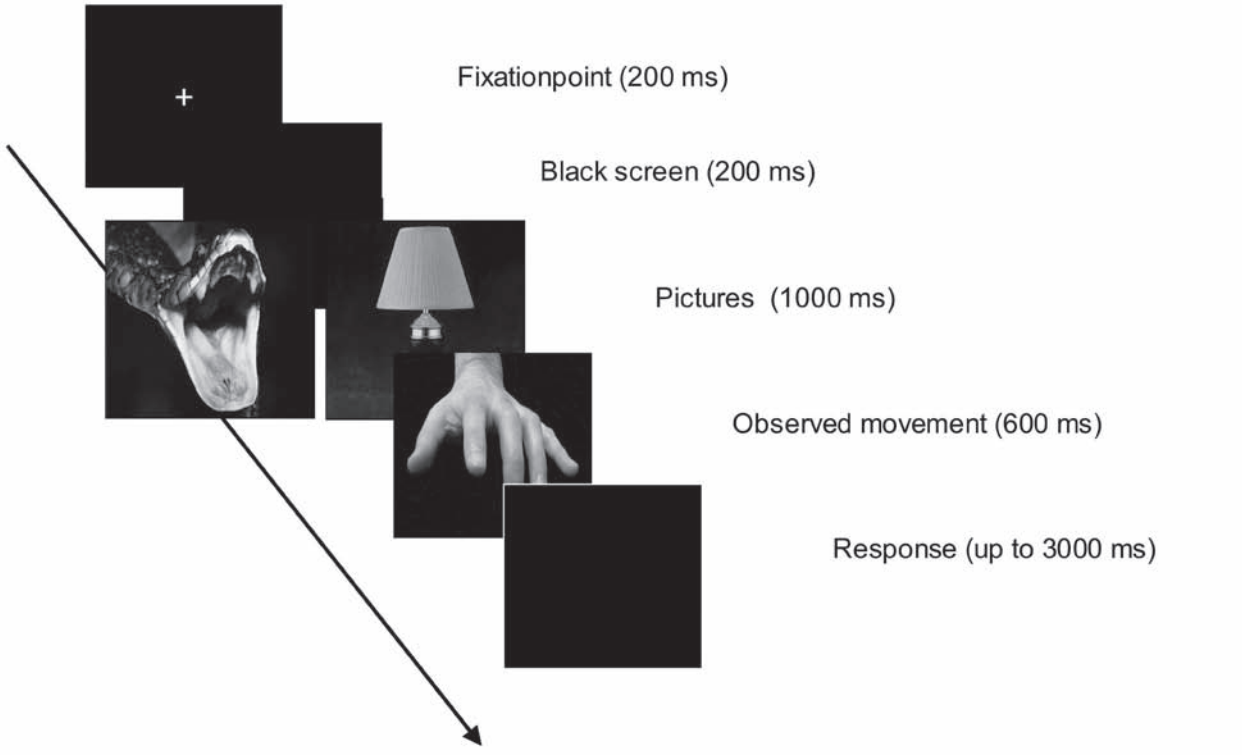

Fig. 1. - The experimental procedure.

Apparatus and data analysis

Electrophysiological data were recorded from the scalp using a 32-channel system (Neuroscan), with two channels used for the oculogram (HEOG and VEOG), and one for the Electromyogram (EMG). Nonpolarizable Ag/AgCl electrodes were positioned in a standard precabled cap (10/20 international system). Scalp impedance for each electrode was kept below 5 kΩ. The electronencephalogram (EEG) was recorded continuously with a sampling rate of 1000 Hz, with left mastoid as a reference and right mastoid as ground, and DC acquisition with HF at 200 Hz (12 db impedance). The signal was filtered offline (bandpassed between 0.05 Hz - 30 Hz). A baseline correction was applied by subtracting the mean of the signal from 100 ms before the fixation point to the stimulus onset from the recording of each trial.

The active EMG electrode was positioned on the extensor digitorum muscle of the arm performing the movement and referenced to an electrode placed 3 cm proximally on the same arm. The EMG channels were filtered with HF at 1500 Hz. Horizontal EOG (HEOG) was recorded bipolarly from the outer canthi of both eyes, while the Vertical EOG (VEOG) was recorded by placing the electrodes on an imaginary vertical line traversing the pupil of the eye, with the lower electrode 14 mm above the upper border of the eyebrow. The surface electrodes were filled with conductive gel after abrasion of the corresponding skin.

The signals were epoched and analyzed using Scan 4.2 software (EMS s.r.l.). Averaged data were statistically analyzed in SPSS, with further analyses run in Matlab 7.14 (graphics and interpolations. Raw EEG epochs were first visually inspected for artefact rejection. Trials with horizontal and vertical eye blink artefacts were manually rejected; the number of eliminated trials was less than 20% of all trials. The signal was average re-referenced only for the dipole-fitting analysis.

Repeated measures ANOVAs were used to test for differential cortical processing of the emotional conditions, with the Bonferroni-corrected t-test used for post-hoc tests. Individual waveform analyses of each sensor served to identify the temporal and spatial characteristics of the signal. This exploratory analysis served to further collapse the data across meaningful dimensions. After the exploratory analysis, the scalp was divided into three regions: anterior, central and posterior; each of these regions was subdivided in turn into left, mid and right areas. The electrodes belonging to each region were averaged; giving nine scalp regions-of-interest (three electrodes per region, except two temporal regions including four electrodes). See Table I for details.

Based on exploratory analyses, trials were divided into two time windows of interest, one covering the emotional stimulation, the other concerning the motor part of the task. For the emotional part of the task (from fixation point to emotional/neutral pictures), *stimulus locked* epochs were extracted from 100 ms before until 1400 ms after fixation point onset, covering the presentation of the IAPS pictures. The late-positive potential (LPP), a large positive deflection lasting for the duration of the emotional image over occipito-parietal sensors (Shupp et al., 2004; Sabatinelli et al., 2007), was scored as mean activity in the time interval of 400-800 ms after picture onset (corresponding to 800 ms - 1200

Table I. - Electrode groupings.

Region	Laterality	Electrodes
Anterior	Left	F1, F3, FC5
	Mid	FP1, FP2, Fz
	Right	F8, F4, FC6
Central	Left	T3, C3, CP1, CP5
	Mid	FC1, FC2, CZ
	Right	T4, C4, CP2, CP6
Posterior	Left	T5, P3, 01
	Mid	PO3, PO4, PZ
	Right	T6, P4, O2

ms after fixation point onset). The LPP has previously been used as a physiological marker for the allocation of perceptual and attentional resources to emotionally- relevant stimuli, and as an index of the engagement of basic defensive and appetitive circuits in the brain (Lang et al., 1997).

The motor part of the task (movement observation and execution) involved *response-locked* epochs extracted from 1000 ms before to 200 ms after muscle burst onset, using the standard back-averaging procedure usually employed to study motor related potentials. This procedure comprised the following steps: the EMG was full-wave rectified, and trigger signals indicating the beginnings of the movement (defined by the onset of electromyogram compound muscle action potential (CMAP) activity), were inserted by visually reviewing the continuous recordings for each trial. A threshold level (30% of the peak value) was defined to mark in a non-biased way the beginning of each CMAP. This served to indicate the onset of movement-related cortical activity, calculated by averaging the signal across trials from the CMAP backward.

For statistical purposes the resulting signal was further divided into two different movement-related potentials: the Readiness Potential (RP), scored as mean activity in the time interval ranging from -500 ms to 0 ms before the trigger, and the Motor Potential (MP), scored as mean activity from 1 ms to 200 ms after the trigger. Separate average waveforms were calculated for each condition (compatible versus incompatible and emotional versus neutral), for each subject and for each electrode.

The RP is a negative wave starting 1 sec before the movement, which has a site of maximum activity in the precentral area extending to the parietal and frontal regions, contralateral to the movement (Shibasaki et al., 1980). This potential is thought to result from activity in large frontal motor areas, and in primary and secondary sensory areas extending more parietally (Green et al., 2003). Two main epochs of the RP have been distinguished, an earlier symmetrical component followed by a lateral asymmetric one that starts about 500 ms before movement onset. Our analysis will use only this second phase of the RP which some authors refer to as the "negative slope" (Shibasaki et al., 1980). The Motor potential (MP) is the last stage of the motor-related potentials characterized by the maximum negative peak accompanying the executed movement. Its scalp distribution is more asymmetrical (contralaterally) and fronto-central (Shibasaki et al., 1980) and it typically accompanies the execution of the movement from the muscle burst to the end of the movement. In addition to these potentials we also measured the EMG signal recorded from the arm executing the movement. Data were analyzed using ANOVA including Category (emotion vs. neutral), Region (Anterior, Central, Posterior) and Laterality (Left, Mid, Right), as factors for each of the three time windows (covering the LPP, the RP and the MP).

The behavioural data were collected from the keyboard of the computer projecting the stimuli. Reaction times were analyzed using an ANOVA with all fifteen subjects, with two within-subjects factors, Compatibility (compatible vs. incompatible movements), and Category (neutral vs. emotional). Only trials with correct responses were included in the analysis; trials with response times below and above two standard deviations from the mean were excluded.

Results

Behavioral data

Subjects' accuracy was high (97%). The ANOVA revealed main effects of Compatibility ($F(1,14) = 19.325$, $p < 0.001$) and of Category ($F(1,14) = 6.859$, $p < 0.05$). Subjects were faster in responding in the compatible condition and after the negative emotional trigger. The interaction was also significant ($F(1,14) = 5.369$, $p < 0.05$). Results are reported in Fig. 2. Post-hoc analyses showed that, within compatible trials, the emotional vs. neutral trials differ significantly ($F(1,14) = 8.607$, $p < 0.05$), while within the incompatible trials they did not ($F(1,14) = 0.403$, $p = 0.532$). Post-hoc analyses also showed that the compatible trials were significantly different from the incompatible trials in both the neutral ($F(1,14) = 6.120$, $p < 0.05$) and the emotional condition ($F(1,14) = 9.680$, $p < 0.01$). Importantly, this pattern replicates the effects found in Rumiati et al. (submitted), except that the effect size was smaller (possibly due to the smaller sample size) and RTs slower (possibly due to the uncomfortable position of the subjects undergoing ERP recording).

Subjects obtained normal scores on negative and positive affectivity (as scored by the PANAS self

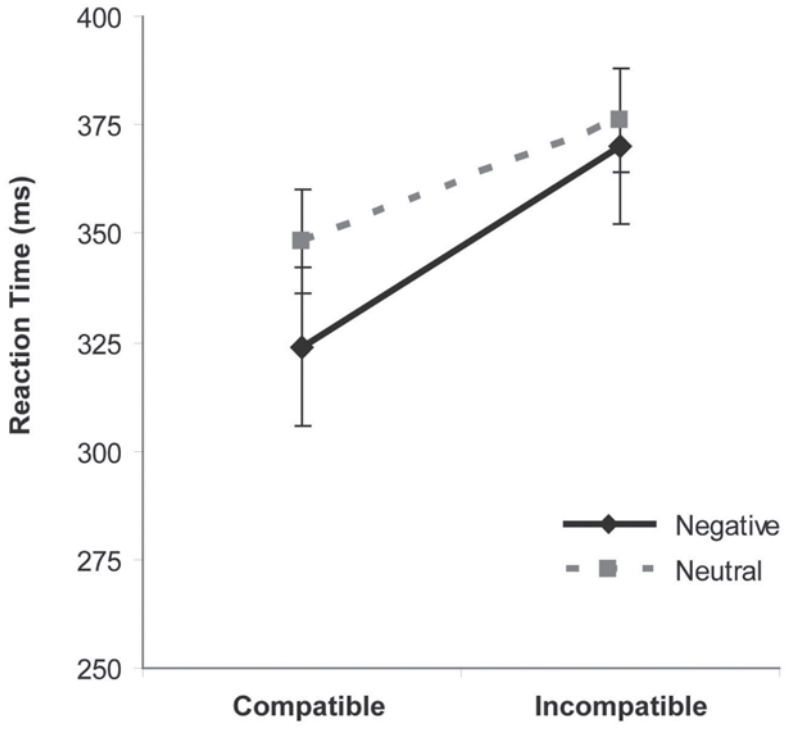

Fig. 2. - Behavioural results.
Subjects were faster responding after emotional stimuli than after neutral stimuli in the compatible condition. Subjects were also faster in the compatible condition than in the neutral condition (a response compatibility effect).

administered questionnaire), and normal scores on the Behavioural Inhibition and Behavioural Activation test, suggesting that they were not affected by that emotional disorders (which could have potentially affected the measures employed in this study).

Analysis of ERP data

Late positive potential

The emotional pictures elicited a larger Late Positive Potential (starting from 400 ms after picture onset, not shown), consistent with previous findings using IAPS images (Schupp et al., 2000). Mean amplitudes from the time window of interest (400-800 ms after picture onset where LPP is visible) were entered into the analysis. To correct violations of sphericity, Greenhouse-Geisser adjustment was applied. The ANOVAs confirmed that the LPP was modulated as a function of the emotional content of pictures (main effect of Category: $F(1,14) = 9.778$, $p < 0.01$); had differing scalp distributions (main effect of Region: $F(2,28) = 60.476$, $p < 0.001$); and different lateralization patterns (main effect of Laterality: $F(2,28) = 12.393$, $p < 0.001$). The only significant interaction was Region x Laterality ($F(4,56) = 8.379$, $p < 0.001$) [insignificant interactions included Category x Region ($F(2,28) = 0.503$, $p = 0.61$), Category x Laterality ($F(2,28) = 0.766$, $p = 0.48$), and Category x Region x Laterality ($F(4,56) = 1.931$, $p = 0.122$)]. Post-hoc contrasts revealed significant differences between emotional and neutral conditions in seven out of nine regions of the scalp (see Table I): left posterior ($p < 0.001$), mid posterior ($p < 0.001$), right posterior ($p < 0.001$), left central ($p < 0.05$), mid central ($p < 0.05$), right central ($p < 0.01$), and left anterior ($p < 0.05$). These data indicate that stimulus processing was modulated by the emotional content of the stimuli.

An early modulation of ERP due to emotions was also visible, starting from about 70 ms after picture onset. This component, known as Early Posterior Negativity (Schupp et al., 2004), was not formally

analyzed because we were not strictly interested in emotional components *per se*, but rather on how emotions modulate motor responses.

Motor-related potentials

Statistical analyses were conducted separately according to whether responses occurred in the compatible or the incompatible movement condition, because our previous analyses indicated that reaction times after viewing emotional vs. neutral stimuli differ significantly only in the compatible movement condition.

Analyses from the compatible movement condition

Readiness potential data

In the compatible condition, the amplitude of the RP (the wave associated with the preparation of the movement) increased in the emotional condition (see Fig. 3, on the left), consistent with our hypothesis of a fear-potentiated overt motor response after aversive emotional stimulation. The ANOVA confirmed that the RP was modulated by the emotional trigger (main effect of Category: $F(1,14) = 6.753$, $p < 0.05$), and that different emotional conditions were associated with different scalp distributions (main effect of Region: $F(2,28) = 8.814$, $p < 0.005$) and differently lateralization patterns (main effect of Laterality: $F(2,28) = 6.320$, $p < 0.05$). Only the Region x Category interaction was significant ($F(2,28) = 4.423$, $p < 0.05$) [non-significant interactions included Region x Laterality ($F(4,56) = 0.765$, $p = 0.55$), Category x Laterality ($F(2,28) = 1.862$, $p = 0.170$), and Category x Region x Laterality ($F(4,56) = 1.107$, $p = 0.36$)]. Greenhouse-Geisser adjustment was applied. Post-hoc contrasts revealed significant differences between emotional and neutral conditions in three out of nine regions of the scalp (see Table I), left central ($p < 0.001$), mid central ($p < 0.001$) and left posterior ($p < 0.05$). These findings indicate that motor planning is modulated by the emotional content of the trigger. The posterior differential activity might have less to do with the RP and be more connected to the perception of the moving hand.

Motor potential data

The MP (the wave accompanying the execution of the movement) in the emotional condition was associated with a stronger negative shift as shown in Fig. 3, consistent with our hypothesis of a fear-potentiated overt motor response following negative emotional stimulation. The ANOVA confirmed that the amplitude of the MP was modulated by the emotional trigger (main effect of Category: $F(1,14) = 14.750$, $p < 0.005$), but neither its scalp distribution (main effect of Region: $F(2,28) = 1.953$, $p = 0.168$) nor the lateralization pattern (main effect of Laterality: $F(2,28) = 0.475$, $p = 0.628$) showed any modulation. Only the Category x Region interaction was significant ($F(2,28) = 4.138$, $p < 0.01$) as well as the three-way interaction Category x Region x Laterality ($F(4,56) = 7.386$, $p < 0.001$), [insignificant interactions included Region x Laterality ($F(4,56) = 1.056$, $p = 0.389$), Category x Laterality ($F(2,28) = 0.483$, $p = 0.623$)]. Greenhouse-Geisser adjustment was applied. Post-hoc contrasts revealed significant differences between emotional and neutral conditions in seven out of nine regions of the scalp (see Table I), left posterior ($p < 0.05$), mid posterior ($p < 0.05$), right posterior ($p < 0.05$), left central ($p < 0.01$), mid central ($p < 0.01$), and left and right anterior ($p < 0.01$). These results indicate that motor execution is also modulated by the emotional content of the trigger. The MP appears to show a larger effect size between conditions relative to the RP, suggesting that these increased motor potentials are not a simple carryover effect of the LPP. In fact, if this were the case, a larger RP (earlier) relative to the MP (later) should be observed.

C3 and EMG latency analysis

We carried out further analyses on the peak latency of the EMG (the signal recorded from the extensor digitorum of the arm performing the movement), and of C3 (the site near the contralateral motor areas most involved in the execution of the movement). Since the actual timing of the waveforms in the different conditions is not detectable using the back-averaging technique, these measurements were taken from the whole trial (from 0 to 3000 ms) in order to preserve the real timing of events. Wilcoxon matched-pairs sign-rank tests were used to assess the significance of the signal latencies in the two conditions (emotional and neutral trials). The EMG latencies differed significantly ($z = -2,478$, N-ties = 13, $p < 0.05$, two-tailed), with the muscle burst arriving 25 ms earlier in the emotional relative to

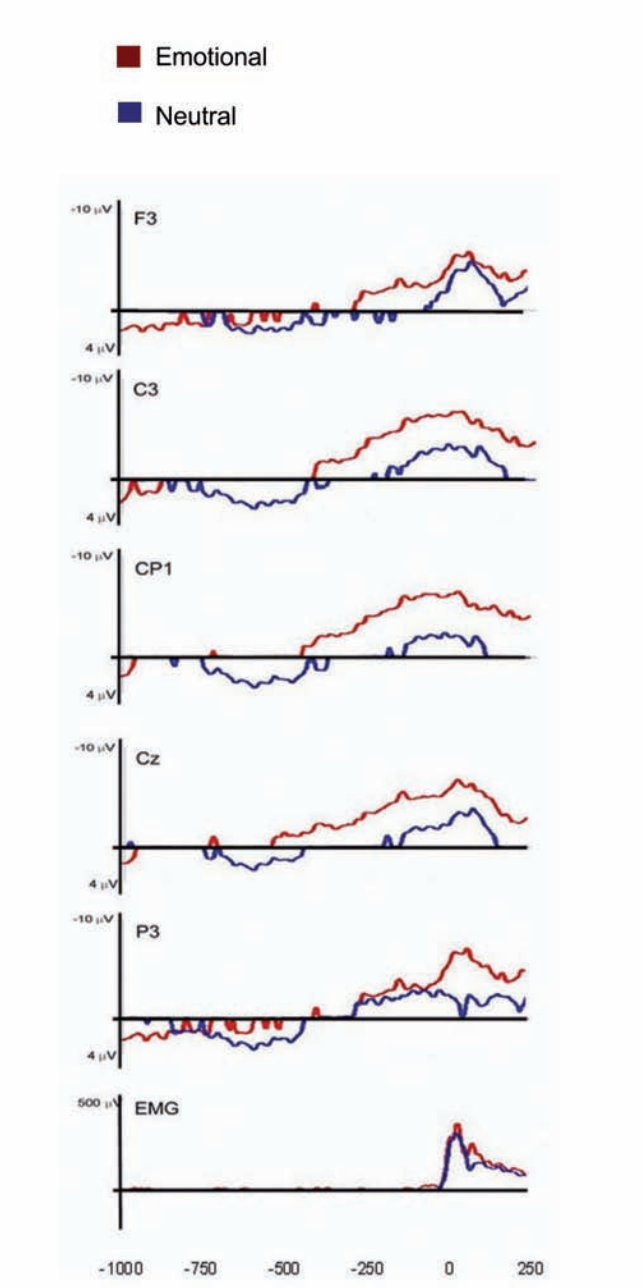

Fig. 3. - ERP for the emotional vs. neutral trials.
The grand average ERP waveforms for the emotional vs. neutral compatible conditions, showing the Readiness and Motor potentials. Sensors contralateral to the hand used for the motor response were selected based on enhanced RP and MP amplitudes in the emotional condition. Negativity is up.

the neutral condition, while waveforms' latencies in C3 did not differ (z = -1,584, N-ties = 13, p = 0.113, two-tailed). Additional analyses were run for mean peak amplitude in the EMG signal, which did not differ significantly (z = -1,542, N-ties = 13, p = 0.81, two-tailed).

Analyses from the incompatible movement condition

In the incompatible condition (Fig. 4), no significant emotional modulation of the amplitude of the Readiness Potential (F(1,14) = 1.897, p = 0.206) was found, while Region and Laterality effects were

significant (respectively $F(2,28) = 9.134$, $p < 0.005$, and $F(2,28) = 4.829$, $p < 0.05$). The interactions were not significant (Category x Region $F(2,28) = 0.724$, $p = 0.5$; Category x Laterality $F(2,28) = 2.272$, $p = 0.116$; Region x Laterality $F(4,56) = 1.893$, $p = 0.136$), nor was the triple interaction ($F(4,56) = 1.454$, $p = 0.239$). In the time window of the Motor Potential the modulation of emotion was not significant (main effect of Category: $F(1,14) = 1.924$, $p = 0.232$), nor was the lateralization distribution (main effect of Laterality: $F(2,28) = 3.457$, $p = 0.9$), but the scalp distribution was significant (main effect of Region: $F(1,14) = 6.012$, $p < 0.05$). The two-way and three-way interactions were not significant [Category x Region $F(2,28) = 0.585$, $p = 0.582$; Category x Laterality $F(2,28) = 3.646$, $p = 0.082$; Region x Laterality $F(4,56) = 0.801$, $p = 0.573$, Category x Region x Laterality $F(4,56) = 2.810$, $p = 0.144$].

An ANOVA, with Greenhouse-Geisser correction, on the incompatible and compatible trials in the neutral condition confirmed that the motor potentials significantly differed between the two sets of trials ($F(1,14) = 6.066$, $p < 0.05$); these were associated with different scalp distributions ($F(2,28) = 7.918$, $p < 0.005$), and a trend for different lateralization patterns (main effect of Laterality: $F(2,28) = 2.926$, $p = 0.075$). No interaction was found to be significant. The motor related potentials showed a positive deflection in the incompatible condition, while in the compatible condition we observed the typical negative deflection associated with the preparation and execution of the movement (the readiness and the motor potentials).

The scalp was further analyzed for the following electrodes: Fp1 (left prefrontal), F3 (left frontal), C3 (left central), P3 (left parietal), Fz (mid frontal), Cz (mid central), Pz (mid parietal), Fp2 (right prefrontal), F4 (right frontal), C4 (right central), P4 (right parietal). Post-hoc contrasts revealed significant differences between compatible and incompatible conditions in five out of 11 electrodes, Fp1 ($p < 0.01$), F3 ($p < 0.05$), F4 ($p < 0.05$), C4 ($p < 0.05$), P4 ($p < 0.05$). These results indicate that the incompatible condition modulated the cortical response.

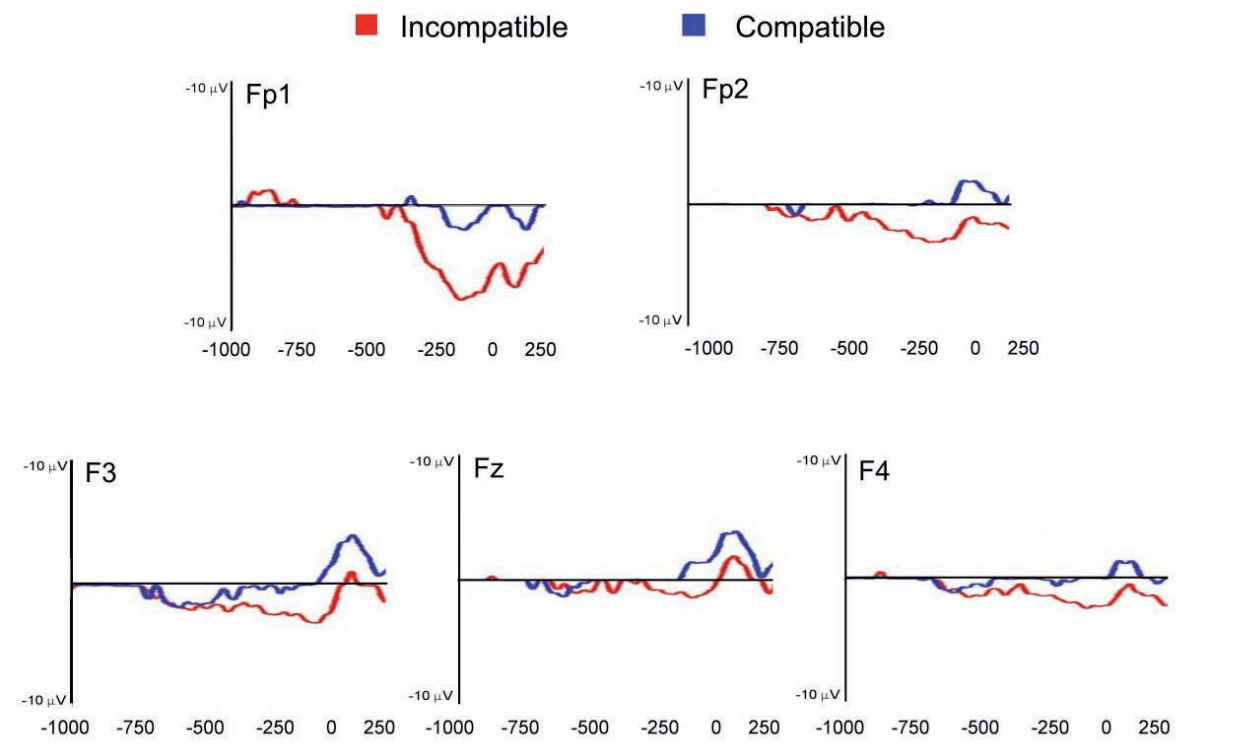

Fig. 4. - ERP for the incompatible vs. compatible trials.
The grand average ERP waveforms over frontal regions for incompatible and compatible conditions during neutral stimuli. Negativity is up.

Further analyses

Motor and perceptual enhancement

To test whether activity associated with the LPP could account for the enhancement of potentials over motor areas when subjects saw emotional pictures in the compatible trials, the correlation peak amplitudes of each subject for the three potentials (LPP, RP, MP) were compared using Pearson partial correlations (see Table II). There was a nonsignificant positive trend between RP and MP magnitudes, when controlling for the correlation of each with LPP ($r = 0.637$, $n = 10$, $p = 0.065$, two-tailed). However, there were no significant correlations between LPP and RP magnitudes controlling for MP ($r = 0.248$, $n = 10$, $p = 0.519$, two-tailed), nor between LPP and MP magnitudes controlling for RP ($r = -0.041$, $n = 10$, $p = 0.917$, two-tailed). Since a general increase in arousal should have produced positive correlations between the two motor potentials and LPP, this analysis suggests that a single mechanism such as arousal is not responsible for the pattern of brain potential results obtained in this study.

Discussion

The purpose of this study was to examine the influence of fearful emotions on overt voluntary action and its encepha. The enhancement of action as a consequence of emotional stimulation is a part of many theories of emotions (Frijda, 1987; Fanselow, 1994; Lang et al., 1997; Ohman and Mineka, 2001; Mineka and Ohman, 2002; McNaughton and Corr, 2004), but experimental studies have previously failed to convinsingly detect it (Lemke et al., 2005; Grecucci et al., 2007; Rumiati et al., submitted).

The present study provides evidence for enhanced processing of motor responses in the emotional condition relative to the neutral condition, as indexed by the Readiness potential and the Motor potential amplitude. The Readiness potential was strongly augmented in the emotional condition over the central electrodes contralateral to the hand performing the movement (see electrodes FC1, C3, Cz, CP1 in Fig. 3, left column). The signals from the two conditions began to differentiate starting about -750 ms before the muscle burst.

The potentiation of the RP, a signal considered to reflect intentional planning and preparation of movements prior to their execution (Kristeva-Feige et al., 1997), may be interpreted as a stronger preparation to act after fearful stimulation, in accordance with previous theories (Frijda, 1987). The Motor Potential that represents the final cortico-spinal outflow (Kristeva-Feige et al., 1997), also increased in the emotional condition, suggesting that motor responses are potentiated after emotionally-negative stimulation. To our knowledge, this is the first demonstration of the effect of emotions on voluntary overt action. With analogy to the Fear-Potentiated Startle Reflex (referring to covert action), these Fear-Potentiated Movement-Related Potentials (FPMPs) affect overt action, in which an organism must effectively face or escape from danger. This enhancement of the motor-related potentials cannot be explained as a carryover effect of the LPP (a signal with a positive polarity). The RP has a negative polarity; if the RP was affected by the LPP, it should have been less negative with respect to the neutral condition, and not more negative as we found.

Since the LPP usually lasts for the duration of the emotional stimulus (Bradley et al., 2003), its effect is likely to have been minimal when subjects started their movements. The lack of any significant difference in the motor-related potentials for the incom-

Table II. - Partial correlation matrix between Late positive potential (LPP), Readiness potential (RP), and Motor potential (MP). The Pearson product-moment correlation coefficient (above the diagonal), partial correlation coefficient (below the diagonal), degrees of freedom and 2-tailed significance are reported.

	LPP	RP	MP
LPP	-	0.2488 (10) p = 0.519	-0.0406 (10) p = 0.917
RP	0.2488 (10) p = 0.519	-	0.6376 (10) p = 0.065
MP	-0.0406 (10) p = 0.917	0.6376 (10) p = 0.065	-

patible condition further suggests that the increased negativity of the RP and MP cannot be explained as an effect of the positive wave elicited by the emotional stimuli. Moreover, positive arousal balanced pictures did not show any effect on RTs (Grecucci et al., submitted), and the EMG was not modulated by emotions, which indicates that our effect is poorly related with a general increase of the arousal.

Taken together these results confirmed our hypothesis that after the emotional stimulation there is a larger engagement of resources for motor programming and execution, and demonstrates that there is an important modulation of voluntary actions when we are required to respond after having clearly perceived and attended to motivationally-relevant stimuli.

This study also suggests that inhibitory effects of imitative responses can be seen both at a behavioural and at a neural level. Executing a movement incompatible with the one previously observed causes an interference that leads to longer response latencies (Fig. 2). Brass et al. (2001b) postulated a need for inhibiting the natural tendency to imitate movements, an interpretation which this work strongly supports. The classic negativity associated with movement-related potentials is also smaller for incompatible movements, which may be a physiological correlate of the slower RTs observed in this condition (Fig. 4).

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