



The effect of conscious intention to act on the Bereitschaftspotential

Shiro Takashima¹ · André M. Cravo² · Koichi Sameshima³ · Renato T. Ramos^{1,4}

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Abstract

The current study investigated the effect of conscious intention to act on the Bereitschaftspotential. Situations in which the awareness of acting is minimally expressed were generated by asking 16 participants to press a button after performing a mental imagery task based on animal pictures (automatic condition). The affective responses induced by the pictures were controlled by selecting the animals according to different valences, threatening and neutral. The Bereitschaftspotential associated with the button presses was compared to the observed when similar movements were performed under the basic instructions of the self-paced movement paradigm (willed condition). Enhanced Bereitschaftspotential amplitudes were observed in the willed condition with respect to the automatic condition. This effect was manifested as a negative slope at medial frontocentral sites during the last 500 ms before movement onset. The valence of the pictures did not affect the motor preparatory potentials. The results suggest that significant part of the NS' subcomponent of the readiness potential is associated with the attention to—and, presumably, awareness of—intention to move, possibly reflecting cortical activation from supplementary motor areas. Secondly, our findings supports that the feeling of threat does not influence the Bereitschaftspotential associated with automatic movements. Regarding methodological issues, the behavioural model of spontaneous voluntary movements proposed in automatic condition can benefit investigations on purely motor (or non-cognitive) subcomponents of the Bereitschaftspotential.

Keywords Readiness potential · Bereitschaftspotential · EEG · Conscious intention · Volition

Introduction

The experience of an individual acting at his own will has puzzled scientists and philosophers for centuries. In physiology, an important issue on the theme consists of

understanding the brain processes underlying the genesis of voluntary movements, particularly those associated with the conscious intention to move. In the last decades, researchers have found evidences that brain processes that lead to voluntary movements are initiated unconsciously (Libet et al. 1983) and manifested in electroencephalography (EEG) as the Bereitschaftspotential (or readiness potential) (Kornhuber and Deecke 1965), a gradual decay of voltage over the vertex starting up to 2 s before the movement onset. Nevertheless, studies on the timing of conscious intention to move indicate that during the imminence of motor actions—at least 200 ms before (Libet et al. 1983; Haggard and Eimer 1999)—these subliminal processes can assume conscious representation, possibly enabling volitional mechanisms of action control, such as motor updating and inhibition (Schultze-Kraft et al. 2016). Regarding subcomponents of the Bereitschaftspotential manifested few hundreds of milliseconds before the motor act that could possibly correlate brain activities underlying the conscious intention to move, the NS'—marked by steeper negative slope starting at about 500 ms prior to the movement onset (Shibasaki et al.

✉ Shiro Takashima
takashima.shiro@gmail.com

¹ Department of Psychiatry, LIM23, Hospital das Clinicas HCFMUSP, Faculdade de Medicina, Universidade de Sao Paulo, Rua Doutor Ovídio Pires de Campos, 785-Cerqueira César, 05403010 Sao Paulo, SP, Brazil

² Centro de Matemática Computação e Cognição, Universidade Federal do ABC, R. Santa Adélia, 166-Bangu, 09210170 Santo André, SP, Brazil

³ Department of Radiology, Hospital das Clinicas HCFMUSP, Faculdade de Medicina, Universidade de Sao Paulo, Av. Dr. Arnaldo 455-Cerqueira César, 05403010 Sao Paulo, SP, Brazil

⁴ Frederick W. Thompson Anxiety Disorders Centre, Sunnybrook Health Sciences Centre, Department of Psychiatry, University of Toronto, Toronto, Canada

1980)—would be the most evident candidate. However, the association between the NS' and conscious processes lacks empirical support.

While being essential for motor actions that require any sort of volitional control, the conscious intention to move is often absent prior to simple movements, which can be reproduced automatically. Thus, it can be admitted that preliminary descriptions of the electrophysiology of the conscious experience of action control could stem from studies comparing movements which demand different levels of skill. In this way, previous works showed that relatively complex or discrete movements (which presumably demand more volitional control) are associated with higher amplitudes of the NS' than simple movements (Simonetta et al. 1991; Kitamura et al. 1993; Masaki et al. 1998). This effect was observed invariably in the medial, but also in the lateral regions of the vertex, probably reflecting enhanced cortical activity from, respectively, supplementary motor areas and primary motor areas (Shibasaki et al. 1993). Nevertheless, by varying the level of skill required to perform an action, researchers probably influenced more directly (or even exclusively) motor and cognitive processes (such as reasoning, attention, memory, timing and decision making) integrated with the volitional coordination of motor actions (property of consciousness to integrate several brain processes is discussed in Dehaene and Naccache 2001; Baars 2005; Tononi et al. 1998) rather than the very conscious experience of acting.

In an attempt to probe the effect of the conscious intention to move on the readiness potential, Keller and Heckhausen (1990) compared self-paced movements—obtained according to Libet's protocol (Libet et al. 1983)—with unconscious hand movements detected while individuals performed a mental task. According to their results, conscious movements were preceded by increased Bereitschaftspotential than unconscious ones, particularly within 500 ms prior to the movement, at medial sites. This finding may suggest that the conscious intention accounts for significant portion of the medial NS', albeit the reliability of this conclusion was challenged by some relevant methodological issues. First, the long duration of the experimental sessions (“three hours or until the subject got tired”) needed to record sufficient number of unconscious movements could induce psychological states, such as reduced arousal or demotivation, which could alone explain their main results (McAdam and Seales 1969; Dirnberger et al. 2004; Bortoletto et al. 2011). Second, the results can also be explained by differences in mechanical aspects of the movements across conditions, such as intensity (electromyographic activities underlying unconscious movements were consistently lower than those associated with conscious movements) and site (wrist, hand or finger movements were not discriminated) (Kutas and Donchin

1974; Oda et al. 1996; Jankelowitz and Colebatch 2002). Third, the rejection of large number of participants and the few number of unconscious movements per individual lead to low resolution of ERP curves (in which the early subcomponent of the readiness potential could not be identified) and challenged the consistency of the results.

Based on the studies discussed above, it can be hypothesised that brain processes associated with the conscious experience of action control account for at least part of the NS' subcomponent of the readiness potential. This hypothesis is to some extent supported by Haggard and Eimer (1999) which showed that the timing of the conscious intention to act correlates with the onset of the lateralized readiness potential (LRP), which is known to contribute to the lateral and asymmetric portion of the NS'. Regarding the present hypothesis, our study aims to investigate the effect of the conscious intention to move on the Bereitschaftspotential by comparing spontaneous voluntary movements executed under different levels of awareness. However, different from Keller and Heckhausen (1990), the current experiment is concerned with maintaining similar occurrence rates and mechanical features of the movements across conditions. To understand how a movement initiated under reduced awareness can be reproduced several times in a systematic way, one can remind of simple daily actions performed to fulfil ordinary goals, such as the act of leafing through a magazine. In this example, while individuals are distracted by the pages' content, standardized movements of turning the page are initiated with certain periodicity (after each page is satisfactorily inspected) and automatically, that is, without (or with minimum) conscious intention to act.

Inspired by the example above, in our first experiment (Experiment 1, named automatic condition), while pressing a button to display animal pictures, the participants were distracted from their motor actions by a mental imagery task based on the presented pictures. Because a previous study showed that the emotional content of images can affect the readiness potential associated with the self-exposure to the same images (Perri et al. 2014), putative affective responses induced by the pictures were controlled by selecting the animals according to two categories: threatening (automatic threat condition) and neutral (automatic neutral condition). The movement-related potentials recorded in Experiment 1 were compared to the obtained in a second experiment (Experiment 2, or willed condition), in which the same movements of pressing the button were performed under the basic instructions of the traditional self-paced movement paradigm. In this condition, under the explicit instruction to move at will and without distractors, the participants would be induced to attend to (and, thus, be aware of) their own intentions to move. Using this approach, the current study is concerned with analysing the effect of the conscious experience of acting on the Bereitschaftspotential,

particularly regarding the amplitude of its early and late (NS') subcomponents.

Methodology

Participants and experimental set up

18 healthy volunteers took part in the experiment, after providing informed consent in written form. The experimental protocol was approved by the University Research Ethics Committee. Because the EEG records from two individuals were too noisy, their data were rejected during the signal preprocessing stage. Thus, the study was based on data from 16 participants (7 males, 25.2 ± 7.6 years, mean \pm standard deviation), 14 right-handed according to self-report. Each participant was seated in a dark and noiseless room with their head supported on a chin rest located 60 cm from an LCD monitor screen (22 inches, 60 Hz). The responses (button press) were recorded with a commercial Cedrus^R response box RB-530. The Psychtoolbox version 3 (Brainard 1997) for GNU Octave v3.8.1 was used to generate the visual stimuli. The EEG signal was recorded using the actiCHamp (BrainVision^R) system with 64 electrodes placed according to the 10–10 system.

Stimuli and procedures

Experiment 1: automatic condition

A black disc (radius 0.2° , the fixation point) was presented on the centre of a grey screen. After the response button was pressed, the fixation point changed colour sequentially to yellow and red (remaining for 500 ms in each colour) and, then, an animal picture (70.4 cm^2 of area) was displayed. Immediately after its appearance, the picture gradually disappeared (for 1667 ms) and the black fixation point became visible again, remaining until a new response was given (sequence of events outlined in Fig. 1a). Each picture was repeated in five consecutive trials and, then, a screen announcing “next image” was displayed for a random interval from 1 to 2 s before the next trial.

The experiment consisted of two conditions: the automatic neutral, in which the presented pictures were 20 images of non-threatening animals (for instance, cat, puppy, rabbit, sheep, cow, hen, golden fish, all in resting stance); and the automatic threat, constituted by 20 photos of threatening animals (for example, wolf in threatening stance, shark, crocodile, lizard, snake, spider) (examples in Fig. 1a). The animals were selected according to their hedonic character. The two conditions were blocked (100 trials in each block) and the order of the blocks was counter-balanced across participants.

During the trial, the participants were required to (1) look at the fixation disc; (2) press the response button with the index finger of the right hand; (3) pay attention to the picture; (4) after the picture disappeared, while fixating at the black disc, imagine the presented animal as it were alive; (5) after the thought was performed “sufficiently” (we did not provide further descriptions about what “sufficiently” meant), start the next trial by pressing the response button with the index finger of the right hand. Noteworthy, the participants were instructed that the crucial moment of the experiment was the imagination period, so that the task should be executed carefully. No explicit instruction about when or how the button should be pressed was provided. Button presses delivered within 2 s after the complete disappearance of the picture were not accepted. Before the experiment, the subjects performed a training block of 20 trials.

Experiment 2: willed condition

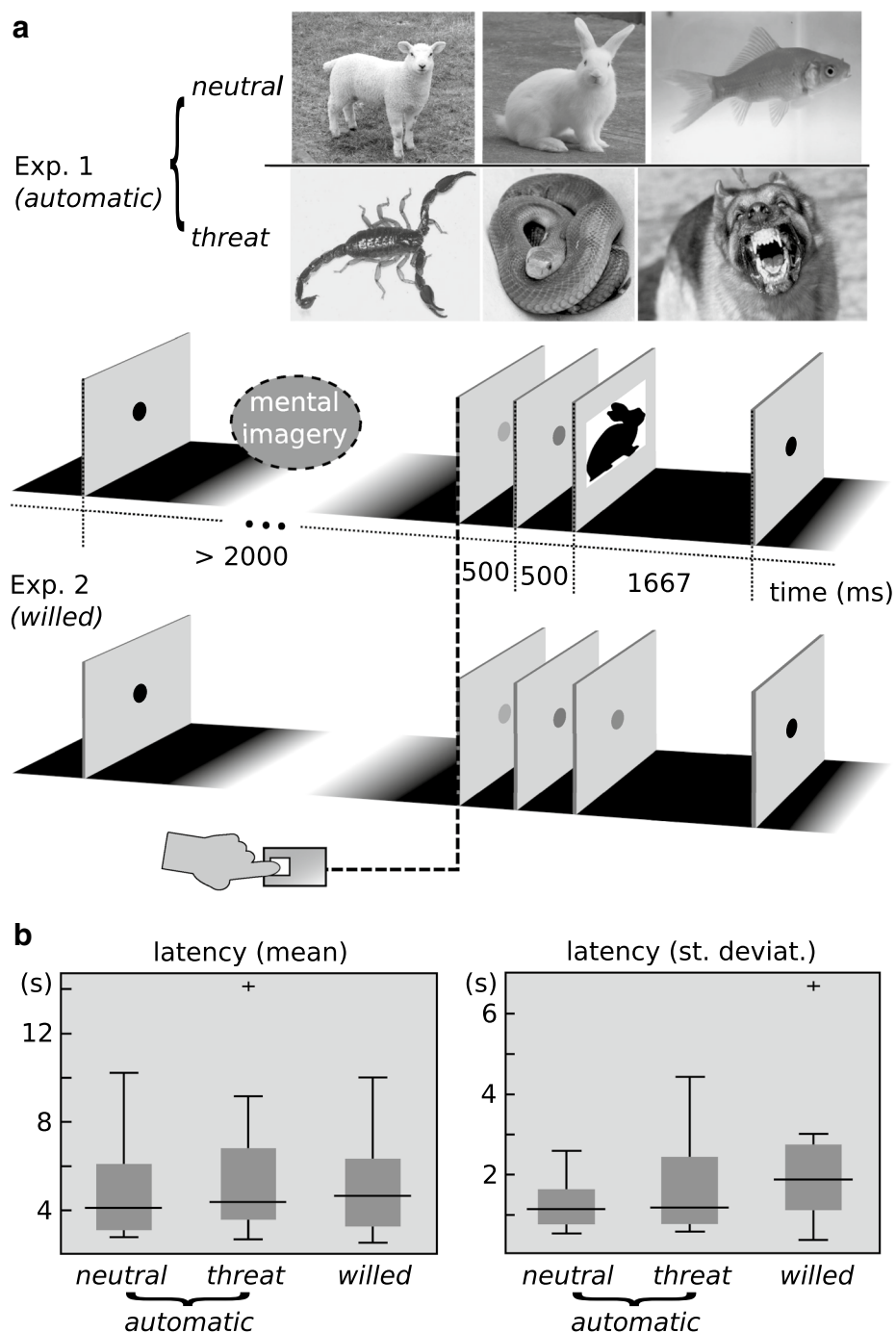
The sequence of events in Experiment 2 was almost identical as in Experiment 1, except that no picture was presented. In each trial, the fixation point was presented and after a button press it changed colour from black to yellow, from yellow to red (similar to Experiment 1), from red to blue, and then, gradually returning to black (for 1667 ms) (sequence of events outlined in Fig. 1a). The experiment was constituted of a single block of 100 trials, also addressed as the willed condition.

Instead of the imagination task, participants were instructed to look at the black fixation point and press the button when they wanted to do so, trying to be “as spontaneous as possible”, “without planning the movement”. Importantly, they were instructed that they should wait for at least 2 s after the fixation point returned to black to press the button (participants were instructed to not count during this period). Button presses delivered within this minimum waiting interval were not accepted. To avoid the influence of the attention to the act concerning the current task on the first experiment, experiments 1 and 2 were necessary performed in this order.

Rationale of the experimental protocol

At this point, one may still question why would automatic and willed conditions differ in terms of the conscious experience of acting. Our experience concerning most of daily actions shows that simple movements generated in response to ordinary action demands have strong tendency to initiate automatically (without awareness), especially when our attention is focused on any concern or attribution other than the movement execution. Based on this fact, in automatic condition, the automatic generation of button presses was induced by associating the movements with mere transition

Fig. 1 Scheme of the task and the Bereitschaftspotential. **a** Sequence of trial events in Experiments 1 and 2. **b** Boxplot of individual means (left) and standard deviations (right) of the latencies of button press



of trials and by distracting individual's attention to the mental imagery task. In contrast to this situation, in the willed condition, after being explicitly instructed to move "at will", participants were induced to be aware of their possibility of moving (or not moving) in the near future, fact that makes movements more willed, that is, associated with conscious choices of acting [concept of "will" as deliberate choice is discussed and adopted in Norman and Shallice (1986), Frith et al. (1991), Lau et al. (2004)]. It can also be observed that,

in similar situation, a movement may not be time locked to the conscious intention to act if the moment of its initiation was planned in advance, the reason why we discouraged the participants to "plan their movements".

In Experiment 1, one could ask what would be the exact role of the mental imagery task, since the simple presentation of the pictures would be enough to distract the individuals' awareness from their motor activities. Besides distracting the participants, the imagery task would make

them fixate gaze at the central point for few seconds before pressing the button, just as they would behave in Experiment 2. By simply asking the participants to look at the images and then pressing the button, during the time interval of Bereitschaftspotential occurrence, participants would exhibit voluntary eye movements and, also, be exposed to much more complex visual stimuli than in Experiment 2. These facts could not only influence motor preparatory processes underlying the readiness potential, but also add oculomotor artifacts and perceptual ERP components to the EEG signal.

Another element of the experimental design that is worthy explaining is the presentation of the yellow and red fixation circles (lasting for 1 s) just following the button presses in all trials. Previous studies show that task relevant stimuli that are predictable in time (such as the pictures in Experiment 1) can be preceded by an ERP component known as the contingent negative variation (CNV) (Walter et al. 1964), a negative slope resembling the Bereitschaftspotential in terms of overall time course and scalp distribution. Considering this fact, in Experiment 1, if the pictures were presented immediately after the button presses, the readiness potential could overlap with the putative CNV wave related to the picture onset. To avoid this, the yellow and red discs were introduced as warning signals, precueing the pictures appearance and, thus, positioning the putative CNV between the time interval from the button press to the picture onset.

Another potential confounding factor that we tried to cope with is the novelty effect associated with the visual stimuli in Experiment 1: before the presentation of a novel picture, individuals could express specific mental states not expected in Experiment 2, such as increased hesitation, arousal or motivation, that could influence the readiness potential (Bortolotto et al. 2011; McAdam and Seales 1969). To reduce such novelty effect, we adopted repetitions of the same picture in five subsequent trials, omitting from analyses the trials in which each picture was presented for the first time (immediately following the “next image” screen).

EEG acquisition and preprocessing

Electrode impedances were reduced below 20 k Ω and, recording was performed in DC mode at 1000 Hz, referenced to the Cz channel. The EMG electrode was located over the flexor digitorum superficialis muscle of the right forearm.

Preprocessing and data analysis were performed in Matlab^R R2009a (The MathWork^R). The EEG data were re-referenced to the averaged earlobes, and high-pass and low-pass filtered at 0.05 and 40 Hz (2th order, double-pass, Butterworth filter). EMG was filtered with a high-pass filter at 10 Hz (2th order, double-pass) and a notch filter at 60 Hz, and represented as unsigned value. Ocular artifacts were removed using independent component analysis (ICA,

infomax) available in EEGLAB toolbox (Jung et al. 1998; Delorme and Makeig 2004). Because ICA decomposition relies on stationary assumption, the ICA weight matrix was calculated from a copy of the EEG data which were high-pass filtered at 1 Hz (2th order, double-pass).

Movement onset was determined as the moment at which the cumulative EMG signal, calculated within 250 ms before the button press, reached 80% of its total value. Taking this movement onset as temporal reference (represented as the zero on time axis), the EEG data were epoched from –2300 to 600 ms. In each trial, electrodes were rejected according to the peak amplitude and kurtosis of the signal. Individual peak amplitude and kurtosis thresholds were, respectively, 61.25 ± 19.93 μ V and 4.09 ± 0.30 (z scored value equal to 1.8). Trials with more than 8 rejected electrodes were entirely rejected. The remaining rejected electrodes were interpolated using spherical spline interpolation (Perrin et al. 1989). The EMG signal was visually inspected and trials presenting clear EMG peak before –250 ms from button presses were rejected. In sum, rejected trials corresponded to an average of $15.40 \pm 5.93\%$ of trials per participant; $3.25 \pm 0.86\%$ of the channels per trial were interpolated. The individual ERPs from each condition were extracted by averaging the EEG epochs along the trials.

Data analysis

All data analyses were performed in Matlab^R R2009a (The MathWork^R). The baseline period for ERP analysis was from –2300 to –2000 ms with respect to the movement onset. For ERP analysis, three regions (medial and two lateral) and two time intervals (the peak of the early and late subcomponents of the readiness potential) were selected according to the spatio-temporal features of the Bereitschaftspotential. The comparisons of the readiness potential amplitudes across the three experimental conditions (namely, automatic neutral, automatic threat and willed) were performed with repeated measures ANOVA (with Greenhouse–Geisser correction). The post hoc comparisons were performed using the Tukey–Kramer method. To avoid the influence of expectancy to a new picture on the readiness potential, the first trial after the “next image” screen in Experiment 1 was rejected.

Results

Behavioural results

The distribution of the individual means and standard deviations of the latencies of button press—period in which the black fixation point remained unaltered waiting for the participant’s response—in each condition are displayed by

the boxplots in Fig. 1b. The latencies were similar across conditions in terms of means (median = 4.37 s; $\chi^2 = 0.78$, $p = 0.677$, Kruskal–Wallis ANOVA) and standard deviations (median = 1.25 s; $\chi^2 = 4$, $p = 0.135$). Regarding the intensity of movements, no significant difference was found in the averaged EMG amplitudes [200 ms window centred at the movement's onset, $F(1.94, 25.24) = 1.19$, $p = 0.320$, $\epsilon = 0.97$]. Despite the limited role of EMG in revealing the actual intensity of muscular activity, its homogeneous amplitude across conditions suggests that strength of button presses remained roughly uniform along the experiments. Together, the behavioural results suggest that putative condition effects on the motor preparatory potentials were not ascribed to physical aspects of motion.

Bereitschaftspotential analyses

The spatial distribution of the Bereitschaftspotential peak (within 300 ms before movement onset) during the experiment (conditions merged) is shown by the scalp map in Fig. 2a. The negativity was widely distributed over medial and lateral frontocentral sites, from which three pairs of electrodes were selected for analysis (FCz and Cz, FC3 and C3, FC4 and C4, scalp map in Fig. 2a). The time courses of the Bereitschaftspotential from the selected regions are

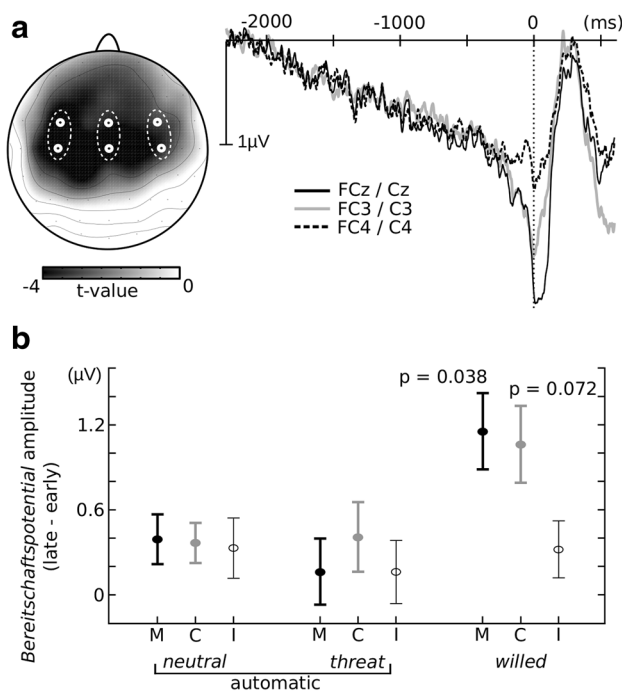


Fig. 2 The Bereitschaftspotential analysis. **a** Topography of the Bereitschaftspotential peak (conditions merged) within -300 to 0 ms (left) and the time course of the component (right). **b** Error bars of the increase of Bereitschaftspotential amplitude from the early to the late intervals in each region and condition

presented by the graphic in Fig. 2a. Accordingly with the general consensus, the component was manifested as a slow negative potential shift starting by -2000 ms and reaching maximum amplitude by the moment of movement onset. The curves clearly show the transition between the early and late (the NS') subcomponents, approximately at -500 ms.

The Bereitschaftspotential amplitudes from the early and late subcomponents (time factor, averaged potential from -800 to -500 ms and from -300 to 0 ms), three selected regions (region factor, left, medial and right frontocentral area) and three experimental conditions (condition factor, automatic neutral, automatic threat and willed) were compared with a repeated measures ANOVA. The results are summarized in Table 1. The significant time main effect [$F(1.00, 15.00) = 18.98$, $p = 0.001$, $\epsilon = 1.00$] indicates simply that the amplitude of the Bereitschaftspotential increased from the early to the late interval, as clearly observed in Fig. 2a. Accordingly with previous descriptions of the component, this increase was asymmetric, as supported by the time \times region interaction [$F(1.87, 28.07) = 4.20$, $p = 0.028$, $\epsilon = 0.94$], being higher in contralateral (left) than ipsilateral (right) electrodes [also shown in Fig. 2a, $t(15) = 3.09$, $p = 0.007$].

The significant time \times region \times condition interaction [$F(3.14, 47.17) = 3.55$, $p = 0.020$, $\epsilon = 0.79$] represents the main result of the current study. According to the post hoc analysis, this finding can be ascribed to significant increase of Bereitschaftspotential amplitude from the early to the late time interval specifically in willed condition at medial frontocentral sites [$t(15) = 4.29$, $p = 0.038$, Tukey–Kramer post hoc test, pairwise comparisons of all $2 \times 3 \times 3$ factors]. Similar time effect was marginally significant at contralateral (left) frontocentral electrodes, also in willed condition [$t(15) = 3.92$, $p = 0.072$]. These findings are shown by the errorbars in Fig. 2b and by the ERP curves in Fig. 3a. No other comparison in post hoc was shown

Table 1 The readiness potential amplitudes across time (-800 to -500 and -300 to 0 ms), regions (left, medial or right frontocentral areas) and condition (automatic neutral, automatic threat and willed) factors were compared with a repeated measures ANOVA

	<i>df</i> (<i>n</i> ₁ , <i>n</i> ₂)	<i>F</i>	<i>p</i>	ϵ
Time	1.00, 15.00	18.98	0.001**	1.00
Region	1.78, 26.66	0.30	0.715	0.89
Condition	1.96, 29.43	0.14	0.863	0.98
Time \times region	1.87, 28.07	4.20	0.028**	0.94
Time \times condition	1.49, 22.34	2.83	0.093	0.74
Region \times condition	2.66, 39.85	1.13	0.344	0.66
Time \times region \times condition	3.14, 47.17	3.55	0.020**	0.79

The degrees of freedom (*df*) were corrected according to the sphericity (ϵ) using Greenhouse–Geisser method. *p* values less than 0.05 are marked with **

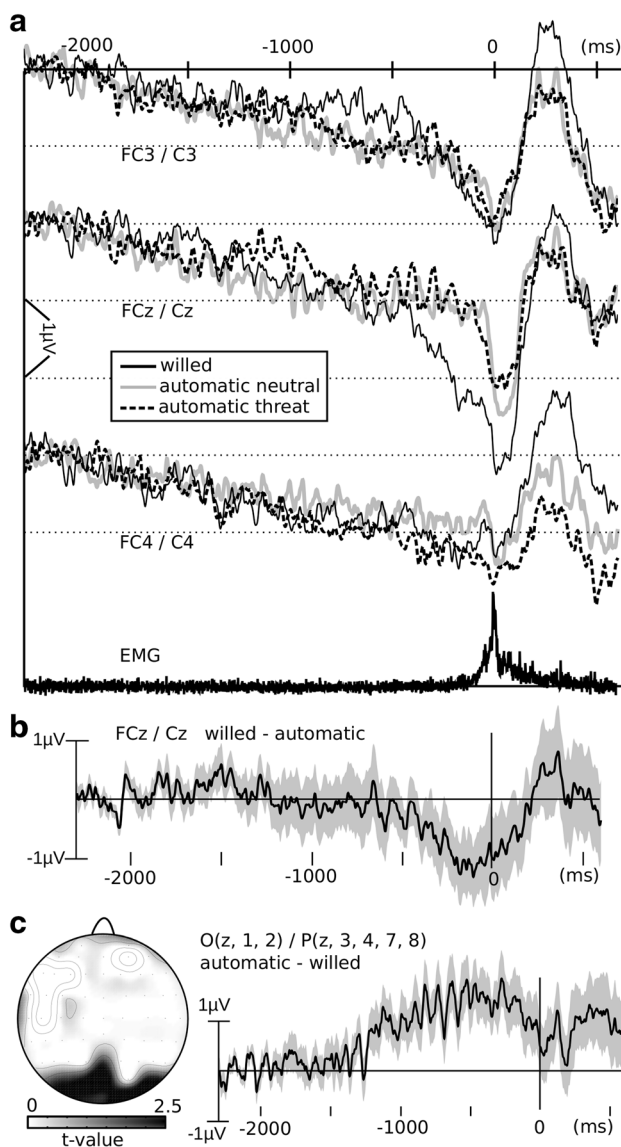


Fig. 3 The Bereitschaftspotential in the experimental conditions. **a** Time course of Bereitschaftspotential in each condition from left or contralateral (top), medial (middle) and right (bottom) frontocentral regions. The EMG activity (conditions merged) is depicted below the ERP curves. **b** Difference between the motor-related potentials from willed and automatic (threat and neutral merged) conditions at medial frontocentral sites. **c** Difference between the ERP curves from automatic (threat and neutral merged) and willed conditions expressed by the topographic map (averaged ERP within -1000 to -300 ms) (left) and time series (occipital and parieto-occipital electrodes) (right)

to be significant ($p > 0.164$). This fact suggests that the emotional valence of the mental imagery task in automatic conditions did not affect the readiness potential amplitudes significantly across time and region factors. To rule out the hypothesis that the present interaction was ascribed to differences of LRP peak amplitude (difference between left and right electrodes during the late interval) across

conditions, we compared them with a repeated measures ANOVA [$F(1.80, 27.00) = 0.55, p = 0.566, \epsilon = 0.90$].

To better evidence the time course of the condition effect on the readiness potential at medial frontocentral electrodes, we merged the response locked potentials in both automatic conditions and subtracted the resultant ERP from the one in willed condition. According to the difference wave depicted in Fig. 3b, the motor-related potentials concerning specifically the willed condition was manifested as a negative wave starting approximately at -500 ms and peaking just before the movement onset. This negativity shows to be consistent with the medial part of the NS' subcomponent, which was virtually absent in the automatic conditions (Fig. 3a).

Before interpreting the main results, it should be assured that the current condition effect on the readiness potential was not ascribed simply to the elapse of time, since the automatic conditions always preceded the willed condition. For this, we regressed the trial-by-trial Bereitschaftspotential amplitude (within late time interval, in medial frontocentral region) along Experiment 1 (automatic conditions, regardless threat or neutral) against the ordinal position of each trial and verified that the linear coefficient (-0.004) was not different from zero (R -square $< 0.00, F = 1.05, p = 0.305$).

Correlates of mental imagery

Taking into account the main objective of the study, the quality of mental imagery (for instance, vividness or sharpness) was not considered relevant to the analysis, since the mere attempt of the participants to execute the task, independently of their low or high performance, would suffice to distract them from their intention to move. Nevertheless, our first experiment relied on the assumption that participants were at least trying to perform the mental task. This fact was simply presumed—and not objectively checked or measured as commonly made in psychophysical tests—as we considered that the volunteers had no reason to neglect the mental task (presented as the main task of the experiment) and, instead, wait for a while before pressing the button. Nevertheless, it is worthwhile to check some evidences suggesting that participants actually performed the mental imagery task before pressing the button, because on the contrary, the reliability of the study could be compromised.

Previous ERP studies show that brain processes underlying visual mental imagery are manifested as a slow positive wave at occipital sites (Farah et al. 1989; Bosch et al. 2001). Considering this fact, the proposition that the individuals were actually imagining the animals before pressing the button was corroborated by the increased positivity in occipital electrodes observed in automatic condition in relation to willed condition [$t(15) = 2.96, p = 0.010$, considering all occipital and parieto-occipital electrodes and the time interval from -1000 to -300 ms (ERP segment at least 1000 ms

after the complete disappearance of the picture, thus, not directly affected by it)] (Fig. 3c). Noteworthy, this effect do not correspond to the condition effect on the NS', as shown by its clearly distinct spatio-temporal features (reaching maximum from -800 to -300 ms before the movement onset at occipital topography, as shown in Fig. 3c). It should be emphasised, however, that in Experiment 1, the act of mental imagery did not present precise moment to start or end, thus, any in depth analyses of associated ERP (which did not even present adequate baseline interval) would be too audacious.

Discussion

In the present study, we investigated ERP correlates of the conscious intention to act by comparing spontaneous voluntary movements executed under different levels of awareness. In Experiment 1, the main strategy to reduce the awareness associated with the execution of self-initiated movements was to shift participants' attention from their motor intentions to the mental task. Since the awareness of acting along the experiments could not be evaluated or measured (in automatic condition, individuals could not even know that their motor actions were being examined), the assumption of its modulation across willed and automatic conditions was based on theoretical and pragmatic arguments. Under the explicit instruction to initiate determined movement at will—as in willed condition—individuals experience some sort of responsibility for controlling their own actions and, congruently, the feeling of acting according to their own initiative. Nevertheless, it is easy to realize that such expression of will is absent in most of daily actions, specially simple movements evoked by ordinary contextual demands—such as opening the door, turning the light on, turning the page of a book and, presumably, starting a new trial in Experiment 1—which show strong tendency to initiate automatically, that is, without (or with minimum) awareness. As well-described by William James, this kind of movement (so-called *ideo-motor*) “follows unhesitatingly and immediately the notion of it in the mind”, so that we are “aware of nothing between the conception and the execution” of the movement, “we think the act, and it is done; and that is all that introspection tell us of the matter”.

In contrast to Experiment 2, the readiness potential in Experiment 1 showed relative reduction of amplitude within the last 500 ms before the movement onset, specially at medial frontocentral sites. In agreement with Keller and Heckhausen (1990), this result suggests that the attention to intention to move—which was considered a sufficient factor for individuals to become aware of their motor intentions—accounts for significant part of the *Bereitschaftspotential* peak over the medial frontal cortex. Apart from their

findings, our results take the investigation one step further supporting that the attention to motor intention is correlated specifically with the NS' subcomponent of the readiness potential. Considering that the supplementary motor complex (SMC, term which encompasses both supplementary motor area and pre-supplementary motor area) represents the main activation source of the medial NS' (Ikeda et al. 1992; Rektor et al. 1994; Yazawa et al. 1998), the present finding in line with the hypothesis that the SMC plays an essential role in the establishment of volitional mode of action control (Curtis et al. 2005; Aron and Poldrack 2006; Brass and Haggard 2007; Isoda and Hikosaka 2011). As a matter of fact, the association between NS' and volitional motor control is encouraged by previous evidences associating greater NS' with more complex or discrete movements (Simonetta et al. 1991; Kitamura et al. 1993; Masaki et al. 1998).

Considering these facts, it is important to discuss the scope of the present study in clarifying the precise physiological meaning of the NS'. Our results suggest that while being anyhow correlated with the attention to intention to move, brain processes underlying substantial part of the NS' are not necessary for the automatic execution of goal-directed movements. With regard to the possible factors underlying the expression of the medial NS' in the willed condition, it is noteworthy that while being instructed to move at will, the participants were induced not only to be aware of their actions, but also to volitionally control them—actually, to our knowledge, no experimental research in humans has succeeded in modulating the awareness of moving and the volitional motor control as independent factors. Although it can be presumed that cognitive functions specifically involved in the volitional coordination of skilled movements played a negligible role in the current NS' effect, the conscious initiation of even the simplest voluntary movements still relies on deliberate choices between moving or not along the time, phenomenon which presumably integrates multiple cognitive functions such as timing and time perception, working memory and decision making. Further studies would be necessary to verify the precise the role of volitional action control, as well as integrated cognitive functions, to the NS'.

In a previous study, Rektor et al. (2001) used intracerebral recording to analyse the *Bereitschaftspotential* in an experimental design similar to the adopted in the present study, obtaining, however, different results. In their study, participants performed movements of turning the pages of a book under two conditions: first, in a self-paced manner, ignoring the content of the book, and second, moving the pages at the moment they decided that the pictures on the page were sufficiently inspected. In contrast with our results, the experimental conditions did not affect the readiness potential associated with the act of turning the pages. In our view, this result can be ascribed to the fact that regardless condition,

the participants were instructed to maintain a uniform style of page turning, to initiate the movement with a brisk onset, as fast as possible, and to avoid blinks during the movement. Thus, in Rektor's experiment, instead of modulating the individuals' explicit attention to their motor acts across conditions, participants were clearly induced to attend and, thus, be aware of, the execution of their movements in both conditions.

Regarding alternative accounts for our results, one can hypothesise that the condition effect of the NS' was ascribed to specific brain processes underlying mental imagery which were not associated with the conscious intention to act. In particular, the condition effect on the NS' could result from deviation of working memory resources from motor planning to the imagination task. Accordingly, Baker and collaborators found reduction of the Bereitschaftspotential amplitude associated with self-paced button presses when these movements were performed concomitantly with a working memory task (Baker et al. 2011). However, apart from their study, in Experiment 1, the mental and motor assignments did not present a competitive relationship—observed when two or more tasks (which rely on limited processing resources) are forcibly carried at the same time, leading to mutual interference in respective performances (discussion and examples of competitive dual-tasks in Pashler 1994)—since individuals were informed to press the button naturally after the accomplishment of the imagination task. Nevertheless, an interaction between the readiness potential and brain processes specifically related to visual imagery can not be totally disclaimed, and replications of the current study using different mental tasks as distractors—as long as they are not associated to confounding ERP components at frontocentral sites—would be worthy to test this possibility.

From a methodological perspective, our findings suggest that the use of a distractor mental task before the evocation of voluntary movements can benefit future studies on the physiology of the Bereitschaftspotential. The conscious experience intrinsically associated with the performance of the self-paced movement paradigm (the most employed task to study the Bereitschaftspotential) often represents an important confound factor in studies on the readiness potential. As a matter of fact, in virtue of its integrative character, consciousness hypothetically enables complex interactions between motor planning and several cognitive, affective and emotional factors (Dehaene and Naccache 2001; Baars 2005; Tononi and Edelman 1998). For instance, the evaluation of the effect of muscular strength on the readiness potential is considered tricky, since the conscious experience of executing stronger muscular contractions can induce mental states such as increased awareness or motivation, which can, by itself, affect the readiness potential (McAdam and Seales 1969; Bortoletto et al. 2011). Because voluntary movements in Experiment 1 were generated under reduced awareness,

they probably represent more adequate behavioural model for studying purely motor (non-cognitive) components of the readiness potential in comparison with the self-paced movement paradigm.

As secondary finding, the emotional states associated with the mental task did not affect the Bereitschaftspotential preceding the automatic voluntary movements. Acute stress responses to threatening situations are known to privilege vigorous and fast movements in detriment of fine and skilled ones (Van Gemmert and Van Galen 1997; Metz et al. 2005; Navarro et al. 2012), probably reflecting increased excitability of both peripheral and central motor pathways (Metz et al. 2005; Metz 2007). The effect of such increased action tendencies on motor preparatory processes was little explored (Grecucci et al. 2009). Regarding this issue, our investigation suggests that the feeling of threat induced by images does not affect the readiness potential associated with the automatic execution of simple voluntary movements. Nevertheless, our results do not disclaim the possibility that the emotional responses triggered by the stimuli were not strong enough to affect the motor preparatory potentials.

For the main purpose of the study, the comparison between threat and neutral conditions provided reliable evidence that our main finding was not ascribed to affective states induced by the animal pictures. In a previous study, Perri et al. (2014) found that motor preparatory potentials preceding the self-administration of affectively arousing pictures are characterized by increased positivity at prefrontal sites. In the current study, comparing the motor-related potentials between neutral and threat conditions, we could observe that such positivity did not affect the readiness potential.

Conclusion

In the present study, we investigated ERP correlates of the conscious intention to move by comparing the Bereitschaftspotential associated with voluntary movements executed under different levels of awareness. By distracting participants' awareness from their motor acts to a mental task, the current study showed evidences that brain processes associated with the conscious experience of moving account for significant portion of the NS', specially at medial frontocentral sites. Indeed, our results show that the medial NS' is virtually absent prior to the automatic execution of voluntary movements. Secondarily, our study supports that the feeling of threat induced by visual images does not affect the readiness potential associated with automatic movements.

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References

- Aron AR, Poldrack RA (2006) Cortical and subcortical contributions to stop signal response inhibition: role of the subthalamic nucleus. *J Neurosci* 26(9):2424–2433
- Baars BJ (2005) Global workspace theory of consciousness: Toward a cognitive neuroscience of human experience. *Progr Brain Res* 150:45–53
- Baker KS, Mattingley JB, Chambers CD, Cunnington R (2011) Attention and the readiness for action. *Neuropsychologia* 49(12):3303–3313
- Bortoletto M, Lemonis MJ, Cunnington R (2011) The role of arousal in the preparation for voluntary movement. *Biol Psychol* 87(3):372–378
- Bosch V, Mecklinger A, Friederici AD (2001) Slow cortical potentials during retention of object, spatial, and verbal information. *Cogn Brain Res* 10(3):219–237
- Brainard DH (1997) The psychophysics toolbox. *Spatial Vis* 10:433–436
- Brass M, Haggard P (2007) To do or not to do: the neural signature of self-control. *J Neurosci* 27(34):9141–9145
- Curtis CE, Cole MW, Rao VY, D'Esposito M (2005) Canceling planned action: an fMRI study of countermanding saccades. *Cereb Cortex* 15(9):1281–1289
- Dehaene S, Naccache L (2001) Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition* 79(1–2):1–37
- Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 134(1):9–21
- Dirnberger G, Duregger C, Lindinger G, Lang W (2004) Habituation in a simple repetitive motor task: a study with movement-related cortical potentials. *Clin Neurophysiol* 115(2):378–384
- Farah MJ, Weisberg LL, Monheit M, Peronnet F (1989) Brain activity underlying mental imagery: event-related potentials during mental image generation. *J Cogn Neurosci* 1(4):302–316
- Frith CD, Friston K, Liddle PF, Frackowiak RSJ (1991) Willed action and the prefrontal cortex in man: a study with PET. *Proc R Soc London B Biol Sci* 244(1311):241–246
- Greccucci A, Balaban E, Buiatti T, Budai R, Rumiati RI (2009) The emotional control of action: ERP evidence. *Arch Ital Biol* 147(1–2):37–49
- Haggard P, Eimer M (1999) On the relation between brain potentials and the awareness of voluntary movements. *Exp Brain Res* 126(1):128–133
- Ikeda A, Lüders HO, Burgess RC, Shibasaki H (1992) Movement-related potentials recorded from supplementary motor area and primary motor area. *Brain* 115(4):1017–1043
- Isoda M, Hikosaka O (2011) Cortico-basal ganglia mechanisms for overcoming innate, habitual and motivational behaviors. *Eur J Neurosci* 33(11):2058–2069
- Jankelowitz S, Colebatch J (2002) Movement-related potentials associated with self-paced, cued and imagined arm movements. *Exp Brain Res* 147(1):98–107
- Jung TP, Humphries C, Lee TW, Makeig S, McKeown MJ, Iragui V, Sejnowski TJ (1998) Extended ICA removes artifacts from electroencephalographic recordings. In: *Advances in Neural Information Processing Systems*, pp 894–900
- Keller I, Heckhausen H (1990) Readiness potentials preceding spontaneous motor acts: voluntary vs. involuntary control. *Electroencephalogr Clin Neurophysiol* 76(4):351–361
- Kitamura J, Shibasaki H, Takagi A, Nabeshima H, Yamaguchi A (1993) Enhanced negative slope of cortical potentials before sequential as compared with simultaneous extensions of two fingers. *Electroencephalogr Clin Neurophysiol* 86:176–182
- Kornhuber HH, Deecke L (1965) Hirnpotentialänderungen bei Willkürbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und reafferente Potentiale. *Pflüger's Archiv für die Gesamte Physiologie des Menschen und der Tiere* 284(1):1–17
- Kutas M, Donchin E (1974) Studies of squeezing: handedness, responding hand, response force, and asymmetry of readiness potential. *Science* 186(4163):545–548
- Lau HC, Rogers RD, Ramnani N, Passingham RE (2004) Willed action and attention to the selection of action. *Neuroimage* 21(4):1407–1415
- Libet B, Gleason CA, Wright EW, Pearl DK (1983) Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). The unconscious initiation of a freely voluntary act. *Brain* 106(3):623–642
- Masaki H, Takasawa N, Yamazaki K (1998) Enhanced negative slope of the readiness potential preceding a target force production task. *Electroencephalogr Clin Neurophysiol* 108(4):390–397
- McAdam DW, Seales DM (1969) Bereitschaftspotential enhancement with increased level of motivation. *Electroencephalogr Clin Neurophysiol* 27(1):73–75
- Metz GA (2007) Stress as a modulator of motor system function and pathology. *Rev Neurosci* 18(3–4):209–222
- Metz GA, Jadavji NM, Smith LK (2005) Modulation of motor function by stress: a novel concept of the effects of stress and corticosterone on behavior. *Eur J Neurosci* 22(5):1190–1200
- Navarro M, Miyamoto N, van der Kamp J, Morya E, Ranvaud R, Savelsbergh GJP (2012) The effects of high pressure on the point of no return in simulated penalty kicks. *J Sport Exerc Psychol* 34(1):83–101
- Norman DA, Shallice T (1986) Attention to action: willed and automatic control of behavior. In: Davidson RJ, Schwartz GE, Shapiro D (eds) *Consciousness and self-regulation: advances in research and theory*, Springer, New York, Plenum, pp 1–18
- Oda S, Shibata M, Moritani T (1996) Force-dependent changes in movement-related cortical potentials. *J Electromyogr Kinesiol* 6(4):247–252
- Pashler H (1994) Dual-task interference in simple tasks: data and theory. *Psychol Bull* 116(2):220–244
- Perri RL, Berchicci M, Lucci G, Cimmino RL, Bello A, Di Russo F (2014) Getting ready for an emotion: specific premotor brain activities for self-administered emotional pictures. *Front Behav Neurosci* 8:197
- Perrin F, Pernier J, Bertrand O, Echallier JF (1989) Spherical splines for scalp potential and current density mapping. *Electroencephalogr Clin Neurophysiol* 72(2):184–187
- Rektor I, Fève A, Buser P, Bathien N, Lamarche M (1994) Intracerebral recording of movement related readiness potentials: an exploration in epileptic patients. *Electroencephalogr Clin Neurophysiol* 90(4):273–283
- Rektor I, Bareš M, Kaňovský P, Kukleta M (2001) Intracerebral recording of readiness potential induced by a complex motor task. *Mov Disord* 16(4):698–704
- Schultze-Kraft M, Birman D, Rusconi M, Allefeld C, Görden K, Dähne S, Blankertz B, Haynes JD (2016) The point of no return in vetoing self-initiated movements. *Proc Natl Acad Sci* 113(4):1080–1085
- Shibasaki H, Barrett G, Halliday E, Halliday AM (1980) Components of the movement-related cortical potential and their scalp topography. *Electroencephalogr Clin Neurophysiol* 49(3–4):213–226
- Shibasaki H, Sadato N, Lyshkow H, Yonekura Y, Honda M, Nagamine T, Suwazono S, Magata Y, Ikeda A, Miyazaki M, Fukuyama H, Asato R, Konishi J (1993) Both primary motor cortex and

- supplementary motor area play an important role in complex finger movement. *Brain* 116(6):1387–1398
- Simonetta M, Clanet M, Rascol O (1991) Bereitschaftspotential in a simple movement or in a motor sequence starting with the same simple movement. *Electroencephalogr Clin Neurophysiol* 81:129–134
- Tononi G, Edelman GM (1998) Consciousness and complexity. *Science* 282:1846–1851
- Van Gemmert AWA, Van Galen GP (1997) Stress, neuromotor noise, and human performance: a theoretical perspective. *J Exp Psychol Hum Percept Perform* 23(5):1299–1313
- Walter WG, Cooper R, Aldridge VJ, McCallum WC, Winter AL (1964) Contingent negative variation: an electric sign of sensorimotor association and expectancy in the human brain. *Nature* 203(4943):380
- Yazawa S, Ikeda A, Kunieda T, Mima T, Nagamine T, Ohara S, Terada K, Taki W, Kimura J, Shibasaki H (1998) Human supplementary motor area is active in preparation for both voluntary muscle relaxation and contraction: subdural recording of Bereitschaftspotential. *Neurosci Lett* 244(3):145–148