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The role of arousal in the preparation for voluntary movement

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ABSTRACT

Planning and readiness for action are associated with pre-movement brain activity reflected in the readiness potential (RP). Previous research suggests that RP is affected by higher-order cognitive functions. The present study investigated the relationship between arousal and RP. Twenty participants performed a RP paradigm in which they executed self-paced movements approximately every 4–5 s. Participants' arousal level was directly manipulated through interaction with the experimenter during the rest breaks preceding the movement task. Skin conductance level (SCL) differed between arousal conditions, indicating that the arousal manipulation was effective. RP was significantly higher under the low arousal than the high arousal condition. This arousal effect also changed depending on whether RP was measured at overall high or low levels of arousal. Our data indicate that arousal does not directly activate structures underlying action preparation. We suggest that the arousal effect may be mediated by the attentional resources allocated to the movement.

1. Introduction

Movement is the interface between our intentions and behavior. Understanding the role of physiological and cognitive systems in the planning and initiation of voluntary movements has both important theoretical and clinical implications. The aim of the present study is to investigate how neural processes underlying the preparation for volitional movement are modulated by arousal level. The study of arousal may be important to understand what are the physiological mechanisms involved in the activation of the motor regions, that ultimately enable us to prepare and execute voluntary self-initiated actions.

Voluntary self-generated movements are preceded by neural activity starting up to 2 s prior to movement execution. This activity is reflected in the readiness potential (RP), an event-related potential revealed by averaging EEG activity preceding the initiation of voluntary movement (Deecke et al., 1969). The RP has two main subcomponents, early RP and late RP, which are spatially, temporally, and morphologically unique (Kutas and Donchin, 1980; Shibasaki et al., 1980). The early RP is a slowly increasing negative potential with symmetrical distribution over the scalp and peak amplitude over midline fronto-central sites. The late RP is a steeper negative slope, predominant over the hemisphere contralateral to the movement. Early and late RP seem to represent functionally distinct processes: early RP has been associated with more abstract levels of the motor intention. Indeed, cognitive variables (including attention, motivation, and physiological states) influence the early RP to a greater extent than the late RP (for a review, see Shibasaki and Hallett, 2006). Late RP has been associated with the precise definition of the motor plan. Indeed, the late RP is modulated by basic movement parameters, such as force (Masaki et al., 1998; Siemionow et al., 2000), rate of force development (Ray et al., 2000; Siemionow et al., 2000), effector (Milliken et al., 1999), and by planning related to the structure of movement sequences (Bortoletto et al., 2011; Bortoletto and Cunnington, 2010).

Arousal is a general behavioral state characterized by sensory alertness, motor activity and emotional reactivity and produced by arousal electrophysiologic pathways of the nervous system (Pfaff, 2006). Cognitive research has almost entirely focused on how arousal modulates cognitive processes that are induced by external stimuli. Little is known about how arousal may influence the preparation and execution of endogenously initiated voluntary actions. The present study investigated whether arousal level modulates the neural processes underlying movement preparation, in order to understand the role of arousal in self-initiated behavior.

Based on the anatomy of the central nervous system and the structures that are involved in action programming, arousal may have a direct effect on movement preparation. Indeed, cortical areas employed in the planning of voluntary action and in the generation of the RP (Ball et al., 1999; Cunnington, 2003; Cunnington et al., 2002; Deiber et al., 1999), such as the cingulate motor area (CMA) and supplementary motor area (SMA), are directly inner-

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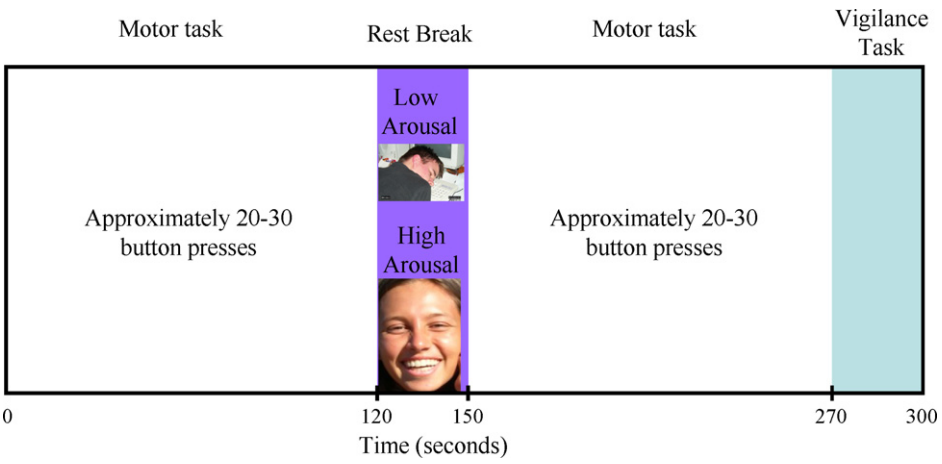

Fig. 1. Arousal manipulation in the experimental paradigm. High and low arousal conditions were performed in 5-min blocks. For the first 120 s, participants performed the motor task; next, participants received a 30 s rest break, during which the arousal manipulation was implemented (in high arousal blocks the experimenter engaged the participant in cheerful banter, in low arousal blocks the participant rested in isolation); after this, participants engaged in the motor task again for 120 s; finally, participants performed a 30-s vigilance task.

vated by arousal networks. In this case, arousal and RP amplitude would share a positive monotonic relationship, such that greater RP amplitudes would be observed under conditions of high arousal than low arousal.

In line with this hypothesis, reaction times (Bertelson and Tisseyre, 1969) and movement force (Ulrich and Mattes, 1996) studies have reported a direct relationship between phasic arousal and movement. Evidence suggests that phasic arousal speeds early processes of movement preparation and action selection (Hackley, 2009), as well as increasing activity in primary motor areas (Jepma et al., 2008). Nevertheless, the relationship between tonic and phasic arousal is unclear and they may play different roles in action preparation.

Alternatively, arousal may affect action preparation non-linearly via attentional mediation. The distraction-arousal hypothesis (Tecce and Cole, 1976) may explain the relationship between arousal, attention and premovement brain activity. According to this theory, increased arousal is associated with increased distractibility. Under conditions of heightened arousal, participants become overly distracted; consequently, less attention is allocated to preparatory processes related to the experimental task and the cortical potentials are reduced. Attention facilitates the execution of voluntary actions and increases brain activity in motor and premotor areas (Lau et al., 2004; Rowe et al., 2002); therefore, variations in attention allocation associated with arousal changes should affect premovement cortical activity. In summary, the distraction-arousal hypothesis implicates attention as a mediating variable in the relationship between arousal and slow cortical potentials amplitude and predicts that an inverted U-shaped function may describe the relationship between arousal and readiness potential.

Such a curvilinear relationship would have important implications for the interpretation of experimental results. For example, it is necessary to gauge the overall position of relative high and low arousal conditions within the greater arousal continuum. This is because, while at overall low arousal levels RP amplitudes may increase for the high compared with low arousal condition, at overall high levels of arousal RP amplitudes would decrease for the high compared with low arousal condition.

The only study to examine the role of arousal in action preparation has reported an inverted-U shaped relationship between arousal (monitored by skin potential level) and late RP amplitude (Masaki et al., 2000). However, in this study arousal was not directly manipulated and results may have been affected by potential confounds, such as increased fatigue in low arousal trials. For example, within each experimental block trials were classified into one of three arousal states based on skin potential level and arousal tends to decrease continuously through the experimental block. Therefore, it is likely that high arousal trials were obtained from the beginning of the block, medium arousal trials from the middle of the block, and low arousal trials from the end of the block. Consequently, the decreased amplitude in the low arousal condition, compared to high and medium arousal conditions, may have been related to increased fatigue towards the end of the block rather than to low arousal.

The present study extends upon previous research by comprehensively investigating the RP and the possible mechanisms underlying the interaction between arousal and voluntary movement preparation. Firstly, arousal was directly manipulated as an independent variable within a controlled paradigm. Moreover, in order to investigate the interaction between arousal and the various processes involved in readiness for action, RP was measured in different time frames and over different scalp regions.

2. Methods

2.1. Participants

Twenty healthy individuals (9 females, aged 22.24 ± 3.40 years) volunteered for this study. Data from two participants were excluded from analyses due to excessive EEG artefacts. All participants were right-handed as determined by the Edinburgh Handedness Inventory (Olfield, 1971), and had no history of psychiatric or neurological disease. Participants signed information consent forms. The study was approved by the Ethics Committee of the University of Queensland.

2.2. Procedure

The experiment was conducted in an air conditioned and dimly-lit Faraday room. Participants were seated in a comfortable chair, approximately 90 cm from the computer screen.

The experiment was run in blocks of 5 min each. Each block (see Fig. 1) consisted of a 2-min finger movement task, a 30-s rest break, another 2-min finger movement task and a 30-s rapid serial visual presentation task (data not reported). All blocks were identical except for the rest break occurring in the middle of the block, in which the arousal manipulation was implemented through social interaction. Previous studies have shown that social interaction increases physiological arousal (Vrana and Rollock, 1998; Zajonc, 1965). In high arousal blocks, the experimenter entered the room energetically at the beginning of the rest break and engaged the participant in light-hearted, cheerful conversation (the researcher used pre-scripted positive phrases such as "You are doing fantastic! How are you feeling?" and "Good job! Keep up the good work!"); in low arousal blocks, the participant spent the rest break in isolation. Importantly, participants were unaware that the study was specifically examining arousal level and that interaction during these rest breaks was used to manipulate arousal level (participants were debriefed following completion of the study). The experiment consisted of 12 blocks, 6 for the high arousal

condition and 6 for the low arousal condition. The presentation order of the high and low arousal blocks was counterbalanced across participants. Crucially, the RP was only measured from data in the period following the rest break, during which participants were in a state of relatively high or low arousal level.

During the finger movement task, participants were required to repeatedly perform a short sequence of button presses (right index-middle-index finger) approximately once every 4–5 s, in their own time, until the end of the 2 min period. Prior to commencing the experiment, participants were given detailed instructions and completed a 30-s practice block of the finger movement task. Participants were explicitly instructed not to count between movements, but rather to develop a natural movement rhythm. If the participant's movement pace was too fast or slow, the experimenter instructed the participant to adjust their rhythm. The aim of this instruction was to maintain movement spontaneity by preventing the movements from becoming cued via an unintentional counting process. On average the number of movements performed during the second 2-min block was 166 (±13.81) in the high arousal condition and 169 (±15.67) in the low arousal condition.

2.3. Electrophysiological recordings

EEG, EOG and skin conductance (SC) were recorded using a Biosemi Active-Two amplifying system. EEG was recorded from 64 electrodes distributed on the scalp according to the widening International 10–20 System. In order to monitor eye movement and blink, four EOG electrodes were placed 1 cm above and below the left eye, and 1 cm from the outer canthus of each eye. Signal offset from all channels, used as index of the quality of the contact between electrodes and skin, was less than ±50 mV. Skin conductance was measured with two Ag–AgCl electrodes placed on the palmar surfaces of the left middle finger and index finger-tips. These electrodes were filled with biologically inert gel (K-Y Lubricant Jelly, Johnson & Johnson Pacific, NSW, Australia). The data were digitized at a sampling rate of 512 Hz.

2.4. Analyses

2.4.1. Skin conductance

Mean SCL was calculated across the 2-min period following the rest break for each participant.

2.4.2. Movement-related potentials

EEG was referenced offline to linked mastoids, low-pass filtered at 50 Hz, corrected for blink artefacts using spatial filters implemented in the BESA software (Berg and Scherg, 1994) and detrended. Bad channels (no more than 2 channels in any subject) were visually inspected and interpolated using the spherical spline interpolation method implemented in BESA. Epochs were created around sequence onset: from 2500 ms before the first button-press to 500 ms after movement onset. Baseline was set between 2000 and 1600 ms before the beginning of the sequence. Epochs were excluded from the analyses if the amplitude of the signal exceeded the threshold of ±60 μV in any channel. Moreover, we visually inspected the EOG channels to avoid the presence of eye movements in the signal. For all participants included in the analysis, no more than 30% of epochs were rejected. RP for low and high arousal was then obtained by averaging the remaining epochs.

The recording sites were grouped into eight regions (Bortoletto et al., 2011; Bortoletto and Cunnington, 2010), namely: left frontal-lateral (F1, F3, FC1, FC3), frontal-medial (Fz, FCz), right frontal-lateral (F2, F4, FC2, FC4), left central-lateral (C1, C3, CP1, CP3), central-medial (Cz, CPz), right central-lateral (C2, C4, CP2, CP4), left parietal (P3, P5, PO3, PO7) and right parietal (P2, P4, P04, PO8).

Readiness potential in each area was segmented into eight 200-ms time periods, from −1600 ms to 0 ms. The average across all time points in each segment was used as a measure of readiness potential in the statistical analysis. In this way, we were able to investigate the time at which arousal state modulated action preparation with a resolution of 200 ms. We were able to determine whether arousal affected the RP in different areas at different times. Moreover we were able to distinguish between effects over the early RP and the late RP. Indeed, the first 5 time periods (from −1600 to −600 ms) correspond approximately to the early RP, the last 3 time periods (from −600 to 0 ms) correspond approximately to the late RP.

2.4.3. Statistics

To test the efficacy of our arousal manipulation, we ran a paired samples *t*-test on the SCL values in the high arousal condition compared with the low arousal condition.

To evaluate the effect of arousal on RP, a 3-way repeated-measures analysis of variance (ANOVA) was performed on the RP values using the following $3 \times 8 \times 8$ experimental design: *Arousal* (High, Low) × *Time* (8 segments) × *Region* (8 regions as described above). When appropriate, the Huynh–Feldt correction was applied. Post hoc comparisons were made using the Newman–Keuls test.

To further investigate whether arousal was the critical variable for the effect on RP, we ran linear regression analyses between the difference in SCL and the modulation of RP for high and low arousal. We calculated the normalized difference in SCL and the difference in RP amplitude during the last 400 ms on the three regions in which RP was most prominent: the frontal-medial, left frontal-lateral and central-medial regions. Then we separately tested the correlation between SCL and the three measures of RP.

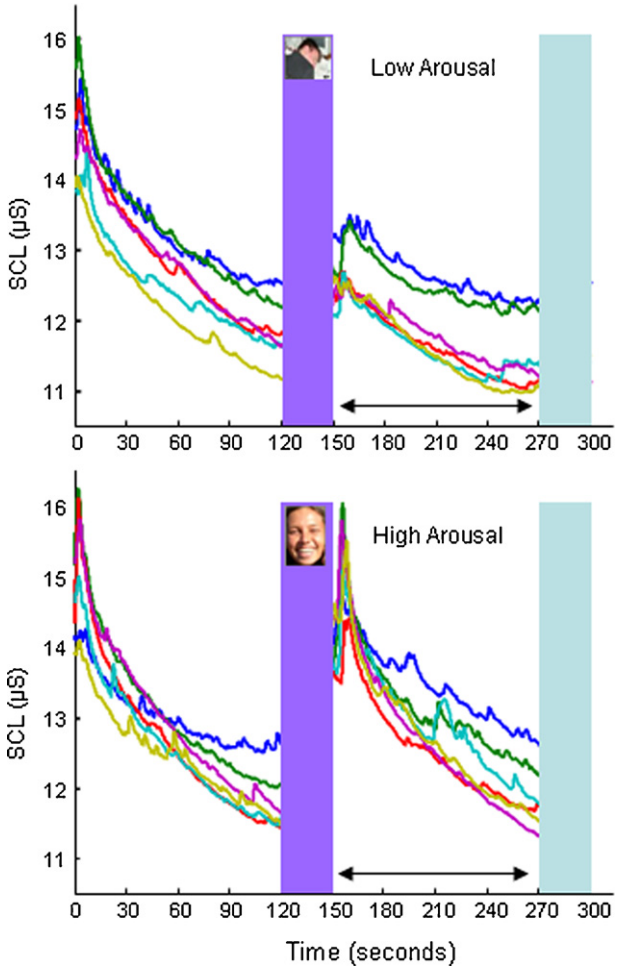

Fig. 2. Skin conductance level (SCL) across the 6 low arousal (top panel) and 6 high arousal blocks (bottom panel). It is apparent that the difference in SCL in the high arousal blocks is greater than in low arousal blocks during the second 2-min of the finger movement task (150–270 s, indicated by the black arrow).

Lastly, to more fully characterize the relationship between arousal level and RP amplitudes, we divided the data from the first minute and second minute of each block and compared high and low arousal conditions separately for the first half and second half of each block. SCL decreased rapidly within blocks as a function of time, but was still overall higher in high arousal than low arousal blocks (see Fig. 2). We were therefore able to compare differences between high and low arousal conditions at two different points of the arousal continuum: at a higher level of the arousal scale (first half of blocks) and at a lower level of the arousal scale (second half of blocks). We conducted paired *t*-tests on the SCL values for high compared with low arousal conditions, separately for the first minute and for the second minute of blocks. To examine effects of arousal on RP, we conducted separate 2-way repeated measures ANOVAs (Arousal, Time) for the first minute and second minute of blocks on the three regions in which RP was most prominent: the frontal-medial, left frontal-lateral and central-medial regions. With this analysis, we therefore investigated whether differences in RP amplitude between high and low arousal conditions would change depending on whether they are measured at the overall high or overall low levels of the arousal scale. We must stress that conducting analysis in this manner avoids any potential confounds of order or time on the task (e.g., effects of practice, fatigue, or change in electrodes over time). The statistical comparisons were always only between high and low arousal conditions which were parametrically manipulated across the experiment and fully counterbalanced to avoid any potential order effects.

2.4.4. Behavioral data

For the voluntary finger movement task, movement parameters related to the time of movement execution, i.e., inter-sequence interval and speed of sequence execution, were analyzed in order to ensure these variables did not confound results. Paired *t*-tests were conducted to compare the mean inter-sequence interval that was self-paced, by participants, as well as the speed of sequence execution (1–2–1; the

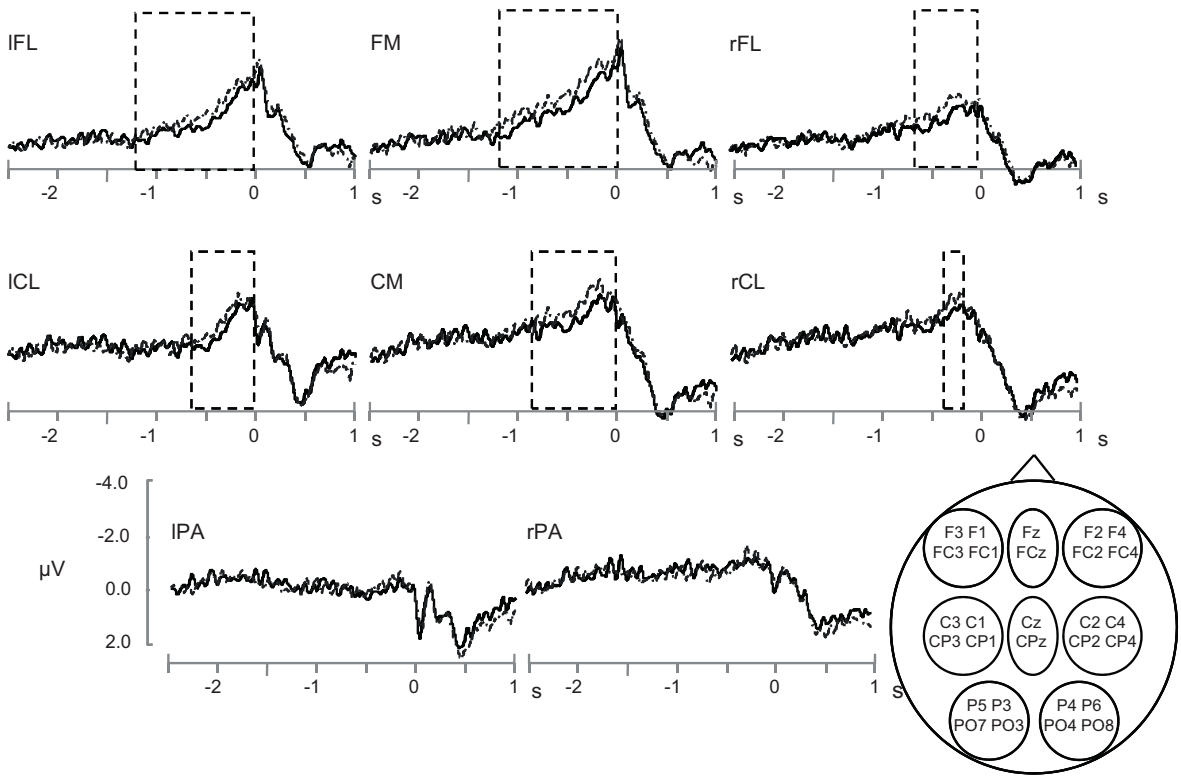

Fig. 3. Mean RP amplitude (μV) during high (black) and low (grey) arousal conditions. Time 0 ms indicates movement onset. Dashed squares indicate the time intervals where significant differences were found between high and low arousal conditions. The electrode cap on the bottom right corner shows how electrodes were grouped in different regions. lFL: left frontal-lateral (F1, F3, FC1, FC3), FM: frontal-medial (Fz, FCz), rFL: right frontal-lateral (F2, F4, FC2, FC4), lCL: left central-lateral (C1, C3, CP1, CP3), CM: central-medial (Cz, CPz), rCL: right central-lateral (C2, C4, CP2, CP4), lPA: left parietal (P3, P5, PO3, PO7), rPA: right parietal (P2, P4, P04, PO8).

mean interval between first and third button-presses) under conditions of high and low arousal.

3. Results

3.1. Skin conductance

Analyses of skin conductance level showed that the experimental manipulation implemented during the resting interval, before the movement task, effectively altered arousal state [$t(17) = 5.08$, $p < .001$]. Mean skin conductance level over the 2-min movement task block was significantly higher under conditions of high arousal (M: 12.96 μS, SD = 5.12) than low arousal (M: 12.07 μS, SD = 5.07).

Fig. 2 depicts SCL across the six high and six low arousal blocks. A clear increase in arousal level during the middle rest interval is evident for all six high arousal blocks. SCL also increases, but to a lesser extent, during the low arousal blocks' rest intervals.

3.2. Movement-related potentials

The readiness potential displayed its typical widespread distribution over the scalp. It appeared as a slow negative increase before movement execution [Main effect Time: $F(7, 119) = 4.04$, $\varepsilon = 0.25$, $p < .05$], and its amplitude was larger over frontal-medial, left frontal-lateral and central-medial areas [Main effect Region: $F(7,119) = 13.86$, $\varepsilon = 0.49$, $p < 0.001$]. Over these areas the rate of increment in the RP amplitude was higher than over the right frontolateral, centrolateral, and parietal regions [Interaction Time × Region: $F(49, 833) = 12.45$, $p < .001$]. Moreover, the transition from the early to the late component of the readiness potential was evident as an abrupt increase in the slope gradient over the left central-lateral area, starting approximately 600 ms before movement execution. This indicated that the time periods between 600 ms before movement to the movement execution (times: 6, 7, and 8) correspond to the late RP, whereas the time preceding 600 ms before the movement corresponds to the early RP.

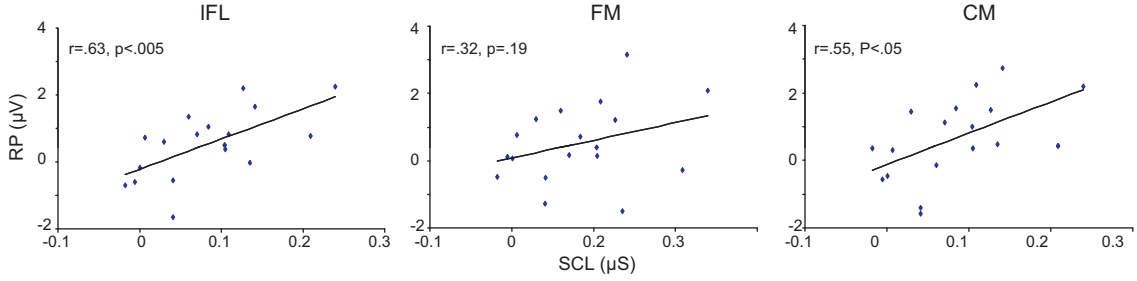

Fig. 4. Scatterplot of RP amplitude modulation versus difference in the SCL. SCL is calculated as the normalized difference between high and low arousal. RP is calculated as the difference between high and low arousal during the last 400 ms before movement execution. Graphs from left to right correspond to: lFL: left frontal-lateral, FM: frontal-medial, and CM: central-medial regions. Lines indicate fitted linear regression models.

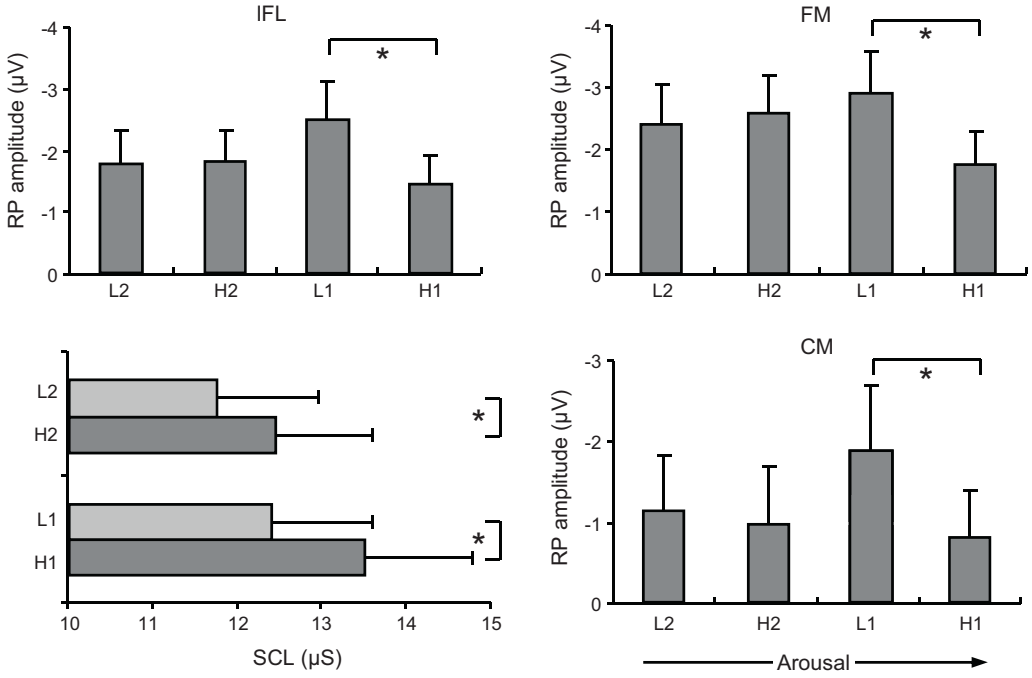

Fig. 5. Mean skin conductance level (bottom left panel) and readiness potential (RP) amplitude (measured in the last 400 ms before movement execution) for the first minute of the blocks and for the second minute of the blocks during high and low arousal conditions. H1: high arousal condition, first minute of the blocks, L1: low arousal condition, first minute of the blocks, H2: high arousal condition, second minute of the blocks, and L2: low arousal condition, second minute of the blocks. Stars indicate significant differences.

Arousal level modulated the amplitude of movement-related potentials preceding action execution. The readiness potential was greater for the low arousal condition than for the high arousal condition during both the early and the late component (Fig. 3). The time at which arousal affected the amplitude of the readiness potential varied across scalp areas [Interaction Arousal × Time × Region: $F(49, 833) = 1.41$, $p < .05$]. The decrease in RP amplitude with high arousal was detected earliest over the fronto-medial and left fronto-lateral regions (post hoc comparisons $p < .05$, from 1200 ms to 0 ms before movement) and over the central-medial region (post hoc comparisons $p < .05$, from 800 ms to 0 ms before movement). Then, it appeared during the late readiness potential in the left central-lateral region and in the right frontal-lateral region (post hoc comparisons $p < .05$, from 600 ms to 0 ms before movement), and lastly in the right central-lateral region (post hoc comparison $p < .05$, from 400 ms to 200 ms before movement). In the right parietal region, the RP was larger for high arousal than for low arousal between 1400 and 1200 ms before the movement and between 800 and 400 ms before the movement.

The regression analyses (Fig. 4) showed that the change in SCL, from high to low arousal conditions, was significantly correlated with the change in RP amplitudes measured over left frontal-lateral and central-medial regions (lFL: $r = .63$, $p < .005$; CM: $r = .55$, $p < .05$). Regression was not significant over the frontal-medial region (FM: $r = .32$, $p = .19$). Participants with the greatest change in SCL, with our arousal manipulation, were therefore also the ones who showed the greatest change in RP amplitudes between conditions, suggesting that the modulation of RP amplitudes with our experimental manipulation was indeed related to changes in arousal level and not some other factor.

In order to more fully characterize the relationship between arousal level and RP amplitudes, we further examined differences between high and low arousal conditions separately for the first half of each block and for the second half of each block. SCL was significantly higher in the high arousal condition than in the low arousal condition both in the first half of the block [$t(17) = 5.36$, $p < .001$] and in the second half of the block [$t(17) = 3.83$, $p < .005$]. Importantly, we found that the effect of arousal level on RP amplitudes changed depending on whether they were measured at the overall high level of the arousal scale (first half of blocks) or at the overall low level of the arousal scale (second half of blocks). In the first minute of blocks, at overall high levels of arousal, RP amplitude decreased for high compared with low arousal conditions in all analyzed regions [significant effects in the last 600 ms before movement execution in the frontal-medial region, Interaction Arousal × Time: $F(7, 119) = 3.55$, $p < .005$, and the left frontal-lateral region, Interaction Arousal × Time: $F(7, 119) = 4.7776$, $p < .001$, and in the last 400 ms in the central-medial region, Interaction Arousal × Time: $F(7, 119) = 3.36$, $p < .005$]. In the second half of blocks, at overall lower levels of arousal, RP amplitudes did not differ between high and low arousal conditions in any areas [for all main effects Arousal and Interactions Arousal × Time, $p > .05$]. Fig. 5 shows the SCL for first and second minute of the blocks and the mean RP in the last 400 ms before movement execution. Taken together, it appears that the RP amplitude does not change linearly with arousal level. Rather, the effect of arousal on the RP depends on the overall arousal level.

3.3. Behavioral data

Basic movement parameters did not differ significantly between arousal conditions. The inter-sequence interval, i.e., the interval between the end of a sequence and the beginning of the following one, was shorter than 2500 ms (the epoch length) in less than 2% of trials, and was not significantly different in the high ($M = 3772$ ms, SD = 432) and low ($M = 3705$ ms, SD = 444) arousal conditions [$t(19) = 2.04$, $p = .056$]. Also, speed of sequence execution did not differ significantly between the high ($M = 502$ ms, SD = 152) and low ($M = 497$ ms, SD = 148) arousal conditions [$t(19) = 0.83$, $p = .417$].

4. Discussion

The aim of this study was to examine the role of arousal in the preparation and execution of voluntary action. The data support the hypothesis that arousal indirectly affects action preparation. Interpreting our results in conjunction with previous research, we suggest that arousal may influence action preparation by modulating the cognitive and attentional resources allocated to the movement.

The experimental paradigm effectively manipulated arousal level between conditions and controlled for possible confounding variables, such as practice and fatigue. Arousal was manipulated by social interaction between the experimenter and participant. According to Zajonc's social facilitation hypothesis (Zajonc, 1965), social interaction increases physiological arousal. Measures of skin conductance level showed that the experimental manipulation was effective: on average, autonomic arousal was greater during the 2 min movement task in the high arousal compared to the low arousal condition. Analysis of movement rate and speed of movement indicated that basic movement parameters remained constant between conditions.

Increased RP amplitudes were observed under the low compared to the high arousal conditions. Furthermore, across participants there was a significant correlation between change in arousal level and RP amplitudes; those participants with the greatest skin conductance change between high/low conditions also showed the greatest RP amplitude difference. This suggests that our arousal manipulation was the critical variable affecting the amplitude of readiness potential. The direction of this arousal effect, however, was the opposite of what would be expected if arousal networks had directly activated the structures of the motor system during action preparation; increased arousal and skin conductance level was associated with decreased RP amplitudes. Therefore, the main conclusion drawn from our results is that, despite a relationship between arousal and RP amplitude, arousal does not play a direct role in action preparation.

Our results may be better explained by changes in the attentional resources allocated to task execution, associated with different arousal levels (Tecce, 1972; Tecce and Cole, 1976). In our experiment, decreased RP amplitude under conditions of high arousal may be the direct result of heightened distractibility, which prevented participants from fully attending to movement preparation and execution. Indeed, it is likely that a state of low arousal and relaxation better meets the cognitive requirement of simple RP paradigms, in which attentional demands are very low. Further studies could investigate this issue by collecting subjective data assessing arousal, concentration and stress of sustained attention during motor tasks.

The role of attention in motor control has been previously investigated, and evidence consistently shows that attention facilitates execution of voluntary actions and increases premovement brain activity. fMRI studies have reported higher activation in prefrontal, premotor and parietal regions when participants are instructed to attend to their intention to move (Lau et al., 2004; Rowe et al., 2002). Moreover, when attention is directed to specific characteristics of movement, such as motor timing and motor sequencing, premovement brain activity is selectively increased in areas contributing to those specific aspects of actions (Bortoletto et al., 2011; Bortoletto and Cunnington, 2010). Our recent studies have also shown that when attention is distracted away from movement preparation, by a secondary attentional load task, RP amplitudes are significantly decreased (Baker and Cunnington, 2010). Lastly, when complex movement sequences are practiced so that they become overlearned, the RP (Niemann et al., 1991) and activity in the prefrontal, premotor and parietal areas decreases (Jueptner et al., 1997; Poldrack et al., 2005; Wu et al., 2004). In line with these studies, if low arousal leads to increased task engagement and less distractibility, then enhanced RP amplitudes in the low arousal condition may be due to changes in attentional resources.

An inverted U-shaped function has been previously suggested to describe the relationship between arousal, attention and slow cortical potentials. Studies on readiness and anticipation of cued responses have reported an inverted U-shaped function between arousal and the Contingent Negative Variation (CNV), a slow EEG potential that occurs in anticipation of a cued target (Fischer et al., 2008; Higuchi et al., 1997; Kamijo et al., 2004; Tecce, 1972). Although the CNV is generated before the response to external cues, it is thought to share critical features with processes of self-initiated movement preparation (Brunia and Damen, 1988; Brunia and van Boxtel, 2001). Our results are not inconsistent with these studies. Indeed, our data show that the relationship between RP amplitude and arousal changes over different ranges of the arousal continuum. We cannot make firm conclusions about an inverted U-shaped relationship from our data alone, however, since we found a decrement in RP amplitude with increasing arousal only at the high end of the arousal scale, but no significant differences at the lower range of arousal level. Perhaps at even lower levels of arousal, the relationship with RP amplitude would be reversed, but such effects were not statistically significant at the lowest levels of arousal achieved in our study. Future studies should parametrically modulate arousal to several levels. Although such a controlled experimental manipulation would be complex, parametric modulation of arousal level is the only way to avoid potential confounding effects of fatigue, practice, or order.

Another interesting result of this study is that both the early and late RP components were modulated by arousal state. This result is at odds with the suggestion that arousal is implicated only in the moderation of voluntary movement execution and with a previous study that reported arousal effects only for the late RP, but not the early RP (Masaki et al., 2000). A possible reason for this discrepancy may be that in the study reported by Masaki et al. the level of arousal varied with the level of fatigue. Therefore their data may have been confounded by this variable. In contrast, we matched high and low arousal conditions for fatigue and found that arousal influences multiple aspects of readiness for action: from early movement preparation through to movement execution. In particular, the timing at which arousal affected the RP over different scalp regions matched the timing at which RP was recorded in each region: first in the fronto-medial and left fronto-lateral area, followed by centro-medial areas, left central area and right fronto-lateral area. Therefore, the order of activation we recorded on the scalp and the appearance of the arousal effect on scalp regions corresponded to the temporal sequence in which premotor and motor regions contribute to movement preparation, as shown in fMRI studies (Ball et al., 1999; Cunnington, 2003). Therefore, the effect of arousal was unspecific and generalized for all areas involved in action preparation, and was related to both early movement preparation and late movement execution.

Finally, our results suggest that tonic and phasic arousal can independently interact with the motor system and may play unique roles in action preparation. Indeed, warning signal studies have shown that phasic arousal can increase the cortical excitability of motor areas (Jepma et al., 2008), suggesting that phasic arousal may directly activate the motor system. In contrast, our study has shown that tonic arousal does not increase movement-related cortical activity. Future research in this field should focus on the possible instrumental role of phasic arousal in self-initiated action preparation.

In conclusion, the present study has found that RP amplitude is larger under conditions of low arousal than high arousal. This is an important finding because it indicates that tonic arousal and RP amplitude do not share a monotonically increasing linear rela-

tionship; thereby suggesting that tonic arousal does not directly activate the motor regions underlying voluntary movement preparation and execution. We suggest that cognitive processes, such as attention, may play an instrumental role in mediating the relationship between arousal and readiness for action. However, further research is needed to understand the intricate cognitive and psychological mechanisms through which arousal and attention modulate voluntary movement preparation and execution.

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