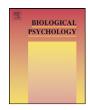
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The role of arousal in the preparation for voluntary movement

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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.

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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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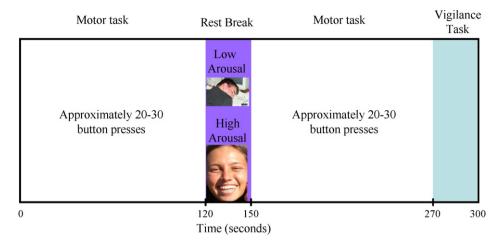


Fig. 1. Arousal manipulation in the experimental paradigm. High and low arousal conditions were performed in 5-min blocks. For the first 120 s, participants performed the motor task; next, participants received a 30 s rest break, during which the arousal manipulation was implemented (in high arousal 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 nonlinearly 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 distractionarousal 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

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