



Readiness potentials driven by non-motoric processes



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ABSTRACT

An increase in brain activity known as the “readiness potential” (RP) can be seen over central scalp locations in the seconds leading up to a volitionally timed movement. This activity precedes awareness of the ensuing movement by as much as two seconds and has been hypothesized to reflect preconscious planning and/or preparation of the movement. Using a novel experimental design, we teased apart the relative contribution of motor-related and non-motor-related processes to the RP. The results of our experiment reveal that robust RPs occurred in the absence of movement and that motor-related processes did not significantly modulate the RP. This suggests that the RP measured here is unlikely to reflect preconscious motor planning or preparation of an ensuing movement, and instead may reflect decision-related or anticipatory processes that are non-motoric in nature.

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1. Introduction

In a series of studies of volitional action beginning in 1965, Kornhuber and Deecke described an event-related potential (ERP) now known widely as the ‘readiness potential’ (RP) (Kornhuber & Deecke, 1990). In the following decades, a great deal of work in psychology, neuroscience, and philosophy has attempted to understand the relationship between the RP and volition (e.g. Haggard & Eimer, 1999; Libet, Gleason, Wright, & Pearl, 1983) and between the RP and action (e.g. Böcker, Brunia, & Cluitmans, 1994; Shibasaki, Barrett, Halliday, & Halliday, 1980). Despite this, it is not known whether the RP reflects processes related solely to movement or whether some components of the RP reflect non-motor processes such as general preparation or anticipation. This distinction is important because some arguments in the debate surrounding free will rely on an assumption that the RP reflects specific neural processes associated with unconscious motor preparation. Our goal here is to determine empirically whether the RP occurs solely in the context of motor processes or whether it also occurs in the context of non-motor processes.

The RP is known as a slow negative event-related potential waveform seen in the surface recorded electroencephalogram (EEG) at centrally-located electrodes during the seconds leading up to a temporally unconstrained, freely-chosen bodily movement. When the EEG signals from many trials are time-locked relative to the movement and averaged together to reduce noise, the RP is seen as an increase in EEG amplitude as the time of movement approaches. A number of tasks have been used to elicit RPs. In some experiments, the time between volitional movements is instructed to fall within a range as

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specified by the experimenter (Deecke, Grzinger, & Kornhuber, 1976), while in others, subjects can wait as long as they like before freely moving (Libet et al., 1983; Schlegel et al., 2013). However, all RP paradigms to date have involved a movement of some kind that subjects must execute at a time of their choosing, typically an extension or flexion of one or multiple digits or limbs (cf. Brunia & Van den Bosch, 1984; Ikeda, Lders, Burgess, & Shibasaki, 1993).

While RP paradigms employ a movement as the time-locking event, other centrally measured negative ERPs with similar waveforms occur even in the absence of an overt motor response. For example, the 'contingent negative variation' (CNV; Walter, Cooper, Aldridge, McCallum, & Winter, 1964) arises during the interval between a warning stimulus and a subsequent imperative stimulus that instructs the subject to respond or act in some way. The CNV can occur even when the instructed action is purely cognitive (Cui et al., 2000; Donchin, Gerbrandt, Leifer, & Tucker, 1972; Ruchkin, Sutton, Mahaffey, & Glaser, 1986; van Boxtel & Brunia, 1994). Another similar ERP, the 'stimulus preceding negativity' (SPN; Damen & Brunia, 1987), precedes an anticipated stimulus that provides performance feedback or other task relevant information. Like the CNV, the SPN can also occur without any concomitant movement (Brunia, 1988; Chwilla & Brunia, 1991a).

Given that the CNV and SPN are not uniquely motor-related, we asked whether the RP could likewise be elicited in the absence of a motor response. The central difficulty in addressing this question is that, without an observable response, there is no externally measurable event to which the data can be time-locked for averaging to derive an ERP such as the RP. Studies of the CNV and SPN can avoid this conundrum by time-locking to the arrival of an external stimulus. However, a similar tactic would not work with the RP, since subjects spontaneously choose the timing of the time-locking event in an RP paradigm on each trial (for a review of the relationship between RP, CNV, and SPN see Brunia, Van Boxtel, & Böcker, 2012).

Previous attempts to investigate non-motor contributions to the RP have been unable to completely control for movement. For example, Freude, Ullsperger, Krüger, and Pietschmann (1988) showed that the amplitude of the RP varies with the difficulty of a subsequent non-motor task. However, in their design a movement was used to elicit the RP, and electromyography was used to measure the consistency of the muscle recruitment across conditions in only one subject. Thus, their result shows the effect of additional anticipation on the RP, but does not address the degree to which the RP itself may be driven by motor-related processes. Likewise, the work of Praamstra, Stegeman, Horstink, Brunia, and Cools (1995) and Dirnberger, Fickel, Lindinger, Lang, and Jahanshahi (1998) has shown that the amplitude of the RP is modulated by non-motor factors such as the endogenous versus exogenous control of movement timing. However, in each study a movement was used as the time-locking event, thus leaving open the question of the degree to which movement may have contributed to the RPs that they observed. In sum, showing that the RP is modulated by non-motor factors does not address the question of whether an RP would still be observed if volitional movements were removed entirely from the process of volitional decision making. That is the novel question that we address here.

Trevena and Miller (2010) attempted to address the contribution of motor action to the RP using a different paradigm in which subjects heard tones presented at random intervals and had to decide, upon hearing a tone, whether or not to move. Their task was quite dissimilar from those usually used to elicit an RP, since subjects did not choose the timing of their movements. A close inspection of their data shows that little if any RP is discernible—the "RP" at Cz never appears to exceed $-2 \mu\text{V}$ while its amplitude in the classic Libet task is usually around $-10 \mu\text{V}$ (cf. Haggard & Eimer, 1999; Libet et al., 1983; Schlegel et al., 2013). While their task appears to successfully isolate the motor contribution to the ERP that they observed, it lacks the principal characteristic of RP paradigms, namely that choices to act be volitionally generated and endogenously timed (Kornhuber & Deecke, 1965). Furthermore, recent electrophysiological work has shown that some neurons in motor cortex activate both when a movement is made and when a movement is withheld (Bonini, Maranesi, Livi, Fogassi, & Rizzolatti, 2014), suggesting that withholding a movement entails similar neural activity to a motoric action. Thus, to fully control for the contribution of motor-related processes to the RP, we devised a task that excluded both the production of and the withholding of any movement.

Our solution to this problem was to use a modified version of the classic Libet clock task. In his original experiment, Libet presented subjects with a rotating analog clock stimulus and instructed them to make a simple finger movement at a time of their choosing while noting the position of the clock hand when "the subjective experience of 'wanting' or intending to act" first appeared in their conscious experience (Libet et al., 1983: p.623). In our modified version of this task, subjects made a simple cognitive decision (choosing one of four presented letters) at a time of their choosing. They noted the time when they made their decision, and they either pressed a button as soon as they decided (50% of trials) or made no overt response (50% of trials). In both cases, subjects reported their time of decision after the trial had ended. We then time-locked each trial to the subject's reported time of decision, thereby allowing us to compare neural signatures of decision-making in both motor and non-motor contexts within subjects.

2. Methods

2.1. Subjects

17 subjects (9 female, 16 right handed, mean age 23.27 years [SD 3.24 years]) gave written consent according to the guidelines of the Dartmouth Committee for the Protection of Human Subjects. Data from one subject were excluded due to experiment interruption.

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