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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 occured 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 $-2\ \mu V$ while its amplitude in the classic Libet task is usually around $-10\ \mu V$ (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.

2.2. Procedure

The task was a modified version of the classic Libet clock task (Libet et al., 1983). Subjects sat 50 cm from a computer monitor on which an analog clock with a radius of 2° visual angle was displayed (Fig. 1). Clock positions were labeled with the numbers 1 through 12, and a circle (radius of 1.5° visual angle) divided into four sections was shown inside the clock. Before each trial, the clock appeared as shown in Fig. 1: Trial Start. Once the subject initiated a trial by pressing a button, a triangular pointer began to rotate clockwise around the circumference of the quartered circle with a period of 10,200 ms (approximately four times the period of the standard Libet clock). Additionally, a small rapid serial visual presentation (RSVP) stream of randomly selected letters, each of which was in turn randomly colored, appeared inside each quadrant of the circle. Each letter was presented for 150 ms (6.67 Hz) with no interstimulus interval before the next letter replaced it. The four RSVP streams continued until the pointer reached the 3 o'clock position (2550 ms; Fig. 1: Waiting Phase). The letter identities stopped changing once the clock reached 3 o'clock, but the color of each of the four letters, one in each quadrant, continued to change randomly at the same frequency. The changing colors served to mitigate the otherwise abrupt change in the visual stimulus that occurred when the identity of the letters stopped changing, thus maintaining some degree of periodic change in the stimulus throughout each trial. At any time between the 3 o'clock and 12 o'clock positions, subjects freely chose one of the four letters and noted the clock position at the moment of their choice (Fig. 1: Decision Phase). The pointer always continued to rotate until it reached the 1 o'clock position (11,050 ms total for the trial). In order to boost motivation and attention, subjects were told that each section of the circle was a door behind which a small amount of money was 'hidden'. On each trial, subjects were told that they won the amount of money that was behind their chosen door. In actuality, however, all subjects were paid $15 per hour of participation. Subjects completed two types of trials: 'decision only' trials (50%) in which subjects chose a letter but made no overt motoric response, and 'decision plus movement' trials (50%) in which subjects both chose a letter and pressed a button at the "the moment when they made their decision." Trials were organized into four blocks (2 'decision only' and 2 'decision plus movement') of 20 trials each. Subjects responded with their right hand on one block of 'decision plus movement' trials and with their left hand on the other block. Block order was randomized across subjects. After each trial, subjects reported both the position of the pointer at the moment they made their decision and the letter that they had chosen. All stimuli were generated, and behavioral responses collected, using MATLAB (The MathWorks, Inc., Natick, MA) and the Psychophysics Toolbox (Brainard, 1997).

2.3. Data acquisition and analysis

EEG data were recorded from 64 scalp locations (10–10 system; Chatrian, Lettich, & Nelson, 1985) as well as from left and right mastoids. Electrooculographic (EOG) data were recorded from above and below the right eye and electromyographic (EMG) data were recorded from two pairs of electrodes placed in series over the flexor digitorum superficialis and/or flexor carpi radialis muscle of each forearm (one pair of electrodes for each forearm). All recordings were made at 2048 Hz using BioSemi ActiveTwo Ag/AgCl electrodes. Data were re-referenced offline to the average of the mastoid channels.

The data were preprocessed twice, once using a 0.016–70 Hz bandpass filter to identify and remove epochs containing eyeblink or eye-movement artifact, and once using a 0.016–15 Hz bandpass filter for averaging. 'Decision-aligned' epochs were defined from 2600 ms before to 500 ms after the reported decision time on each trial and baseline corrected using the mean signal between 2600 ms and 2500 ms before the decision. In order to minimize noise, epochs containing signal fluctuations exceeding 80 μV at FPz or Pz or during which the participant made an error were rejected (mean 26.09% rejected [SD 13.85%]). RPs were calculated at Cz separately for 'decision only' and 'decision plus movement' trials. Mean amplitude of the RP was determined by taking the average value of each subject's RP between the end of the baseline period and the time of decision (−2500 ms through 0 ms relative to the reported time of decision). Peak amplitude of the RP was determined as the largest (most negative) value that occurred between 600 ms and 100 ms prior to the reported time of decision (−600 ms through −100 ms relative to the reported time of decision). This window was chosen to encompass the peak of the RP waveform while excluding the movement-induced collapse, which, due to latency differences between the reported time of decision and the movement, begins before the reported time of decision (see Fig. 3).

Scalp topographies of the grand average data for each condition were constructed using the FieldTrip toolbox for MATLAB (Oostenveld, Fries, Maris, & Schoffelen, 2010). Data were interpolated between electrode locations using biharmonic splines as implemented in the MATLAB function "griddata".

In order to verify that the 'decision plus movement' condition resulted in a typical RP, another set of 'movement-aligned' epochs were defined relative to the button press on 'decision plus movement' trials only. This set of epochs was preprocessed identically to the 'decision-aligned' epochs except for the different time-locking event.

3. Results

Our main goal was to investigate the extent to which non-motoric processes contribute to the RP. To that end, we modified the classic Libet task so that it could be completed with or without the involvement of a motoric movement, allowing for a direct comparison between movement and non-movement-related decisions in the same subject. In one condition,
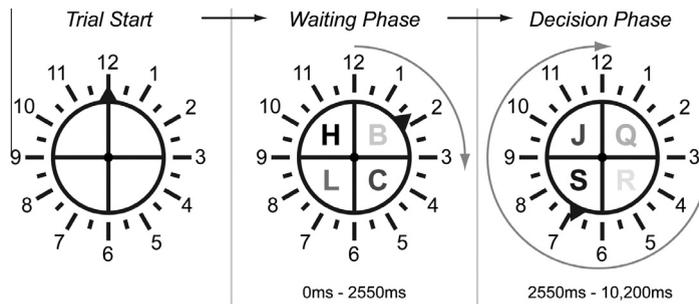
Fig. 1. The modified version of the classic Libet clock task (Libet et al., 1983) used in this experiment. A trial began when subject pressed a button, causing the clock pointer to begin rotating and an RSVP stream to appear within each quadrant (Waiting Phase). When the clock pointer reached the 3 o'clock position (2550 ms) the RSVP streams stopped, allowing subjects to choose one of the remaining letters at a time of their choosing before the pointer reached the 12 o'clock position. See main text for details.

subjects completed a cognitive task only ('decision only' condition), while in the other condition subjects also pressed a button simultaneously with the execution of the cognitive task ('decision plus movement' condition). Mean decision times, relative to the start of each trial, were 7996 ms (SE 294 ms) and 7976 ms (SE 270 ms) for the 'decision only' and 'decision plus movement' conditions, respectively [two-tailed $t(15) = 0.0994$, $p = 0.922$]. The distribution of decision times across subjects for each condition is shown in Fig. S1.

In order to verify that the purely cognitive 'choose-a-letter' task did not affect the RP adversely, we calculated movement-aligned RPs for the 'decision plus movement' condition. The movement-aligned RPs showed a typical RP shape (Fig. 2). Mean RP amplitude between the end of baseline (2500 ms before their reported time of decision, see Methods) and the time of button press was -3.16 μV (SE 0.995 μV) and average peak amplitude was -9.27 μV (SE 2.08 μV). Thus, the RP amplitude and shape are comparable to what is typically seen in the classic Libet task (cf. Haggard & Eimer, 1999; Schlegel et al., 2013).

In order to compare the EEG response between the 'decision only' and the 'decision plus movement' conditions, we could not time-lock each trial to a movement or button press as is typically done, because there was no movement on 'decision only' trials. Instead, we aligned the data to the subject's reported decision time on each trial (decision-aligned), thereby allowing us to isolate any additional motor contributions to the RP. Critically, 'decision only' and 'decision plus movement' tasks were identical except for the presence of a motor response on 'decision plus movement' trials. Average decision-aligned RPs for the 'decision only' and 'decision plus movement' conditions were not significantly different (Fig. 3). Mean RP amplitude was -2.07 μV (SE 1.17 μV) for the 'decision only' condition and -2.39 μV (SE 1.31 μV) for the 'decision plus movement' condition [two-tailed $t(15) = 0.269$, $p = 0.792$]. Likewise, peak amplitude was -7.10 μV (SE 2.01 μV) for the 'decision only' condition and -7.40 μV (SE 2.37 μV) for the 'decision plus movement' condition [two-tailed $t(15) = 0.172$, $p = 0.896$]. The mean amplitude of the RP during the same time window as used to calculate peak amplitude (-600 ms to -100 ms) was also not different between conditions (mean amplitude: -3.85 [SE 1.98] for the 'decision only' and -3.93 [SE 2.51] for 'decision plus movement' conditions; [$t(15) = 0.0434$, $p = 0.966$]). Scalp topographies for the RP from each condition are displayed in Fig. 4A. Fig. 3B shows the average difference wave between the two conditions and Fig. 4B shows the corresponding scalp topography.

While 'decision only' and 'decision plus movement' RPs were not significantly different based on any of the analyses that we performed, the failure to find a significant difference does not necessarily support the null hypothesis that no difference exists between conditions. We may have failed to detect a difference that exists if, for example, our study was underpowered. Thus, we performed a paired-samples Bayes-factor t test, with the scale factor set to 1.0, on the average RP amplitude data from each condition (Rouder, Speckman, Sun, Morey, & Iverson, 2009). The resulting JZS Bayes-factor (null/alternative) was 5.12, which can be considered positive evidence in favor of the null hypothesis (Kass & Raftery, 1995). Using the peak or average RP amplitude between -600 ms and -100 ms (relative to the reported time of decision) led to similar results (all JZS Bayes-factors [null/alternative] > 4.5).

In order to address the possibility that differences between 'decision only' and 'decision plus movement' RPs could have been present prior to, or during, the defined baseline window (-2600 ms to -2500 ms relative to the reported time of decision) we repeated the above analyses without performing baseline correction. If such early differences existed, performing baseline correction (subtraction of the average signal amplitude within the baseline window) would cause the differences to appear later in time (i.e. closer to the reported time of decision), and of the opposite sign simply as a result of the subtraction. The results of all analyses performed without baseline correction are consistent with the results reported above. Neither average RP amplitude nor peak RP amplitude were significantly different between 'decision only' and 'decision plus movement' conditions (all $p > 0.5$, all JZS Bayes-factors [null/alternative] > 4).

One potential drawback to our design was that any inaccuracies in subjects' reported decision times could introduce a temporal jitter in the time-locking event and thus potentially reduce the amplitude of the resultant decision-aligned RP compared to a movement-aligned RP. However, the 'decision plus movement' condition allowed us to compare subjects' reported decision time to the actual time of their button press on each trial, and thus to assess their ability to retrospectively report
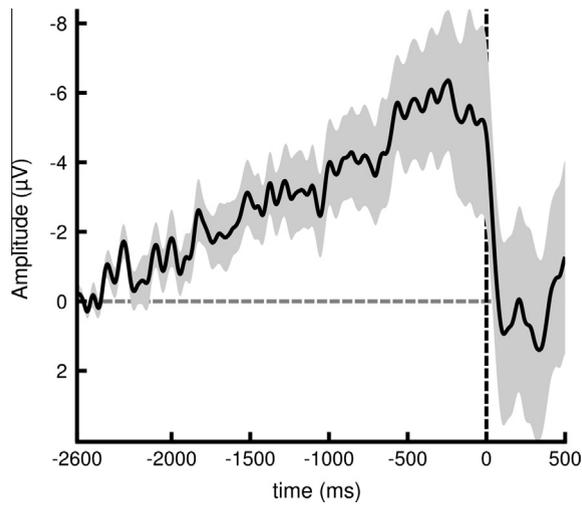
Fig. 2. Average response-aligned RP for the decision plus movement condition ($n = 16$). Time 0 indicates the time of button press on each trial. Shading represents standard error of the mean (S.E.M.).
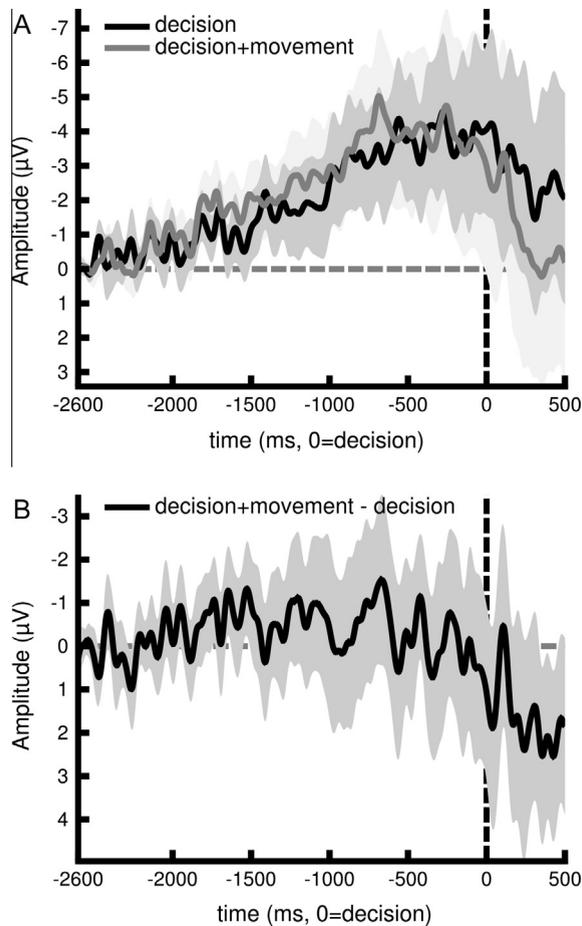

Fig. 3. Comparison between 'decision only' and 'decision plus movement' conditions ($n = 16$). A. Average decision-aligned RPs for the 'decision only' (grey) and 'decision plus movement' (black) conditions. B. Difference wave for decision-aligned RPs (decision plus movement – decision only). Time 0 indicates the reported time of decision on each trial. Shading represents S.E.M.
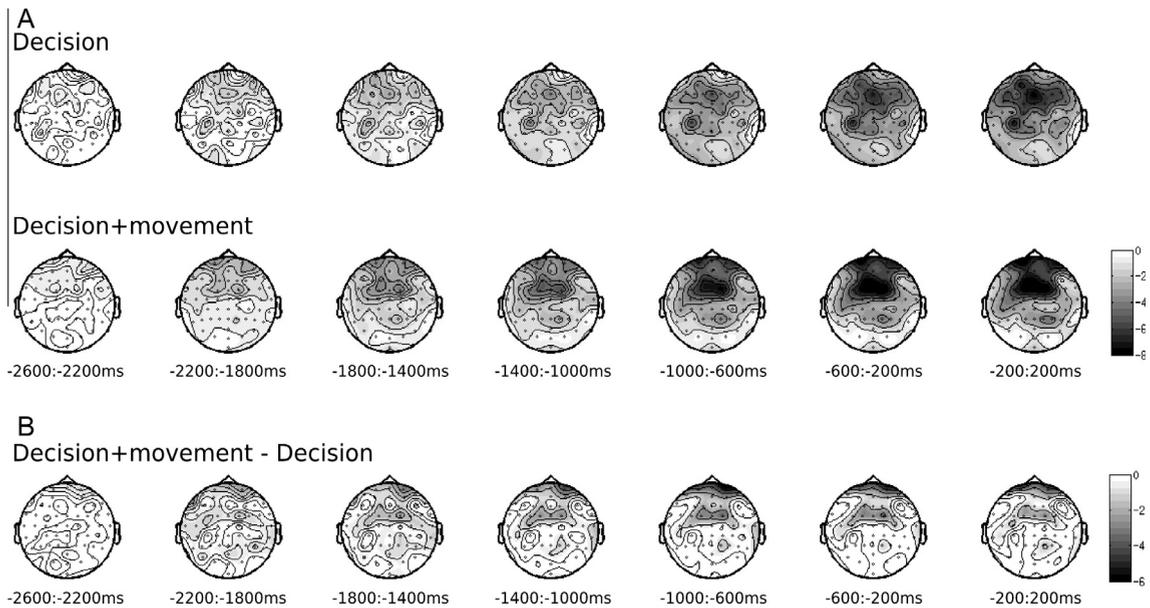
Fig. 4. Scalp topographies of decision-aligned RPs. A. Scalp topographies for the 'decision only' and 'decision plus movement' conditions that were presented in Fig. 3A. B. Scalp topography of the difference wave (decision plus movement – decision only) that was presented in Fig. 3B.

their time of decision. As subjects were instructed to simultaneously note the position of the clock pointer and press a button when they made their decision, any discrepancy between the two times is likely to reflect the imprecise nature of the judgment and the attentional load from the dual task ('choose a letter' task and pointer monitoring). Our data show that subjects were in fact quite accurate, reporting to have made their decision on average 41.72 ms (SE 34.61 ms) before they pressed the button. There was no significant difference between the reported decision time and actual button press time [two-tailed t (15) = 1.62, $p = 0.127$]. Given this lack of difference and the fact that robust RP amplitudes were observed in both the movement-aligned and decision-aligned data ($-9.27\ \mu V$ and $-7.40\ \mu V$ respectively, see Fig. S2), we can be confident that the RPs seen in the 'decision only' and 'decision plus movement' conditions reflect the cognitive and cognitive plus motor contributions to the RP, respectively.

4. Discussion

The goal of the current study was to determine the extent to which processes independent of movement contribute to the RP using a novel experimental design whereby RPs could be compared with and without a concomitant movement. Several different components of the RP have been identified (cf. Shibasaki & Hallett, 2006; Shibasaki et al., 1980). However, the extent to which any part of the RP is uniquely related to motor activity has not been shown previously. Our results suggest that the RP, at least in the paradigm considered here, is not unique to motor processes, as the 'decision only' condition showed robust RPs despite the fact that possible temporal jitter introduced by timelocking each trial to the subject's reported decision time could have led to a reduced RP amplitude.

The presence of RPs in the 'decision only' condition that were not significantly different from those in the 'decision plus movement' condition suggests that motor processes may only contribute minimally, if at all, to the RP. While the addition of movement may be a possible cause of the observed non-significant trend toward larger amplitude RPs in the 'decision plus movement' condition, this is not the only possibility. On 'decision plus movement' trials, there were more events for subjects to anticipate, prepare for, and attend to, as they had to make a button press simultaneously with their decision. They also may have felt compelled to make particularly fast button presses in order to minimize any potential delay between decision and movement, although no explicit instructions for speeded responses were given. As it has been shown that movement speed, movement force, and attention all modulate RP amplitude (Baker, Piriyapunyaporn, & Cunnington, 2012; Becker, Iwase, Jurgens, & Kornhuber, 1976; Becker & Kristeva, 1980; Miller, Shepherdson, & Trevena, 2011), a difference in implicit speed demands could have led to the observed trend. Thus, our data should be interpreted as an upper bound on the possible motor contribution to the RP since a stronger control of implicit speed demands would likely decrease the amplitude difference between motor and non-motor RPs.

An objection to the above argument could be that the 'decision only' RPs may still be contaminated by movement-related activity, even though no button presses were made. However, careful examination of the EOG and EMG traces (see Methods) revealed no detectable muscle or eye movement activity preceding decisions on trials that were included in the 'decision only' condition RPs (see Figs. S3 and S4 for average EOG and EMG traces). Additionally, subjects were explicitly instructed

to avoid making any movements along with their decisions on 'decision only' trials, as the crucial difference between 'decision only' and 'decision plus movement' trials was the movement. Still, we cannot rule out the possibility that subjects may have, for example, stiffened their posture or perhaps exhaled together with each decision. However, there are only two conceivable scenarios involving such inadvertent movements that are consistent with the lack of difference between 'decision only' and 'decision plus movement' RPs. The first possibility is that these inadvertent movements were present only on 'decision only' trials, and had a similar effect on the RP as the button press in 'decision plus movement' trials. The second possibility is that the inadvertent movements were present in both conditions and the RPs in both conditions reflect those movements, thus implying that the button press in the 'decision plus movement' condition did not further modulate the RP beyond the inadvertent movements. Both possibilities are unlikely given that the RP is known to be greatly affected by movement parameters such as force and speed (Becker & Kristeva, 1980; Becker et al., 1976). Had the inadvertent movements resembled the button press in terms of force or speed, they would have been detected in the EMG or as muscle artifact in the EEG. For these reasons, it is unlikely that the present finding can be explained by similar muscle activities across "decision only" and "decision plus movement" conditions.

In addition to overt and covert movements, the possibility exists that premotor, or pre-saccadic, activity could have contributed to the 'decision only' RPs as the spatial displacement of the letters in the present task would likely cause covert shifts in spatial attention toward the to-be-chosen letter. As spatial attention is closely linked with pre-saccadic circuitry (Rizzolatti, Riggio, & Sheliga, 1994), the RPs observed in the 'decision only' condition could thus be a product of premotor activation. However, decision-aligned activity did not show the lateralization that would be expected if premotor activation contributed to the observed RPs (see Fig. S5).

If the RP does not primarily reflect processes directly related to movement, what then might the RP reflect? Past findings suggest that three likely processes are action preparation, general anticipation, and spontaneous neural fluctuations. We discuss each of these processes below.

4.1. Does the RP reflect action preparation?

We define action preparation as the sequence of neural processes immediately preceding a temporally unconstrained action that are necessary, though not necessarily sufficient, to produce an action such as a bodily movement or a covert decision. This is essentially the interpretation of the RP suggested by Libet and colleagues within the domain of motor movements (Libet et al., 1983). They concluded that the activity reflected by the RP represents the brain deciding "to initiate or, at the least, prepare to initiate the act at a time before there is any reportable subjective awareness that such a decision has taken place" (Libet et al., 1983: p.640). Libet and colleagues based this interpretation on their finding that the RP begins on average several hundred milliseconds before W, defined as subjects' reported time of awareness of 'willing' or 'wanting' to move. Our data are consistent with this interpretation if expanded to include purely mental actions, such as covert decisions, since what mattered to Libet was the relative timing of the RP and W. However, our data rule out the possibility that the majority of the RP reflects uniquely motor-related processing. If we had found that the RP is unique to motor actions, it would have provided strong reason to doubt Libet's interpretation of the RP and the importance of his finding, since it is the freedom of the decision to move, and not the movement itself, that has broader implications for the debate surrounding free will.

While our data are consistent with Libet's interpretation, they rule out purely motoric models of the RP. Recent work by Fried, Mukamel, and Kreiman (2011), building on the historic association between the RP and movement, has raised the possibility that the slow rise of the RP reflects a buildup of activity within the motor or pre-motor circuits responsible for the generation of the ensuing movement. According to this model, once the activity in these circuits reaches a threshold, the motor command is transmitted to its effectors. Our data, however, provide evidence that the majority of the RP is not related uniquely to a specific response domain. Instead, the RP appears to reflect primarily non-motor activity that requires further processing before it can lead to a specific action sequence as suggested by more general accumulation-to-bound models of decision making (Jo, Hinterberger, Wittmann, Borghardt, & Schmidt, 2013; Murakami, Vicente, Costa, & Mainen, 2014; Schurger, Sitt, & Dehaene, 2012).

4.2. Does the RP reflect general anticipation?

By general anticipation, we mean the conscious experience that an event will soon occur, whether or not the precise nature or timing of it is known. Just as subjects anticipate the arrival of a stimulus in a CNV or SPN paradigm, they may also anticipate an upcoming movement or decision in an RP paradigm. While in many RP experiments, including ours, subjects are instructed not to plan their movements in advance (e.g. Haggard & Eimer, 1999; Libet et al., 1983; Schlegel et al., 2013), they may nonetheless experience a general sense that they will soon decide to move. Libet and colleagues asked subjects to report "the time of appearance of [their] conscious awareness of 'wanting' to perform a given self-initiated movement" (Libet et al., 1983: p.627). Since a non-specific, general sense of anticipation would not meet this criterion, it would therefore likely go unreported. Because the events targeted by Libet's instructions ('wanting', 'preparing', etc.) are specifically associated with the actual execution of the movement, reports of their occurrence would necessarily come closer to the movement time than a slowly building, general sense of anticipation, which may have no clear onset. This problem is not addressed easily by changing the wording of the instructions, since asking subjects to report the time at which they first became aware that they

were anticipating a movement may lead to such judgments occurring very soon after the trial commenced (in the Libet task, subjects know that they will move on every trial). If subjects do experience a building sense of anticipation, a possibility that has, to the best of our knowledge, not been tested, then the onset and shape of the early RP could presumably reflect that anticipation just as it does in CNV and SPN paradigms. There is evidence that the RP and CNV share neural sources (van Boxtel & Brunia, 1994), but some studies have found them to be dissociable (Ikeda et al., 1994, 1997). However, given the evidence that the CNV is not motor dependent (Cui et al., 2000; Donchin et al., 1972; Ruchkin et al., 1986; van Boxtel & Brunia, 1994) our finding that the majority of the RP likewise does not reflect uniquely motor-related processes is consistent with the possibility that the two event-related potentials are generated by shared neural sources. Note that the CNV or SPN, unlike the RP, is generated within an experimental paradigm that does not afford the subject free choice. To the extent that these event-related potentials are generated by shared neural sources, the neural sources that generate the RP may also not specifically be associated with free choice. The RP, or at least its early components, may simply reflect a buildup of anticipation analogous to that seen in the CNV or SPN (Chwilla & Brunia, 1991b; van Boxtel & Böcker, 2004).

4.3. Does the RP reflect spontaneous neural fluctuations?

Schurger et al. (2012) recently proposed an alternative explanation for the neural basis of the RP. Their interpretation posits that the shape of the average RP can be explained by a leaky stochastic accumulator model, wherein the timing of the movement is determined by the crossing of a threshold set on spontaneous fluctuations in neural activity. According to this model, a movement only occurs following a threshold crossing. Thus, time-locking the data to the movement is effectively time-locking to the threshold crossing and guarantees that the average RP will resemble a slow rise towards the threshold because only positive outcomes (instances where the threshold was actually crossed) would contribute to the average. This model suggests that the RP does not reflect any specific type of processing but instead is the by-product of a drift–diffusion process that has been time-locked to a threshold crossing. While the present paradigm does not afford a direct test of this alternative explanation, it remains possible that the RPs observed here are products of such a process. Schurger's model also suggests that the RP does not reflect processing within a specific action domain. Our finding that movement does not significantly modulate RP amplitude supports this aspect of their claim by extending the RP to the domain of covert decisions.

Another important implication of Schurger's model is that it suggests that the 'neural decision' to move at a specific time happens much later than the Libet interpretation claims. According to the model, the long, slow rise of the RP merely reflects the average of many spontaneous fluctuations, not the buildup of action or movement preparation or general anticipation. Recent work by Jo et al. (2013) has offered empirical support for this aspect of the model using EEG. If accurate, this model implies that the 'neural decision' to move does not occur until the threshold is crossed, on the order of 150 ms before movement. Consistent with this idea, single-unit recordings from rodents have found a population of neurons in pre-motor cortex that display ramp-to-threshold firing patterns preceding self-timed decisions in which the time of threshold crossing is highly correlated with the time of movement initiation, some 150 ms later (Murakami et al., 2014). While more empirical studies that explicitly test this model are needed, the model nonetheless offers a novel perspective on the neural basis of the RP that may prove useful moving forward.

5. Conclusion

Once an event-related potential is discovered, it is tempting to study its properties and relationships under the assumption that it reflects neural processing that is directly related to the original task that elicited it (e.g. that an ERP evoked by a movement task reflects motor-related processes). Our results show the usefulness of studying ERPs such as the RP outside of the paradigm in which they were initially discovered and defined. The current study shows that, although the RP has historically been considered a motor-related potential, the RP does not primarily reflect processes unique to motor execution or preparation, and may not even be primarily generated by the neural activity involved in making a free choice. Instead, it may reflect more general processes such as anticipation or those proposed by Schurger et al. (2012). Future research should test these possibilities directly and bring greater clarity to this half-century of scientific and philosophical debate.

Conflict of interest

The authors declare no conflict of interest.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.concog.2015.11.011.

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