

Feeling ready: neural bases of prospective motor readiness judgements

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Abstract

The idea that human agents voluntarily control their actions, including their spontaneous movements, strongly implies an anticipatory awareness of action. That is, agents should be aware they are about to act before actually executing a movement. Previous research has identified neural signals that could underpin prospective conscious access to motor preparation, including the readiness potential and the beta-band event-related desynchronization. In this study, we ran two experiments to test whether these two neural precursors of action also track a subjective feeling of readiness. In Experiment 1, we combined a self-paced action task with an intention-probing design where participants gave binary responses to indicate whether they felt they had been about to move when a probe was presented. In Experiment 2, participants reported their feeling of readiness on a graded scale. We found that the feeling of readiness reliably correlates with the beta-band amplitude, but not with the readiness potential.

Keywords: action; intention; awareness; readiness potential; beta; EEG

Introduction

Imagine that you have decided to try bungee jumping. Picture the moment right before you jump off the cliff. You vividly feel that you are about to jump, and the strength of this ‘readiness’ feeling keeps growing—perhaps it even comes and goes as you consider whether to jump or to change your mind and call it off. This feeling of ‘being about to move’ is a conscious experience of motor intention. While many people recognize the experience described above, some authors have questioned whether a conscious experience is informed by the preparation processes that precede voluntary action, arguing that it might be an illusion driven by a retrospective inference rather than a *bona fide* experience (Wegner 2002).

Identifying the relative contributions of prospective and retrospective information to intention awareness is not straightforward. Methods for studying prospective intentions must obtain reports before any action has been executed: if people provide intention judgements after a movement, there is a potential for *post hoc* confabulation (Kühn and Brass 2009; Schultze-Kraft et al. 2020). Here, we ran two complementary experiments to test whether prospective motor intention awareness can be predicted from two specific neural signals: the readiness potential (RP) and beta-band oscillations.

The RP is a characteristic ramping up electroencephalography (EEG) negativity over the motor cortex that precedes self-paced voluntary movements (Deecke and Kornhuber 1978). The RP has been reported as a reliable neural precursor of spontaneous actions in multiple studies (e.g. Vaez Mousavi and Barry 1993; Khalighinejad et al. 2018) and is typically visualized as the average of multiple self-paced actions. A prominent model suggests that the typical trial-averaged RP may result from stochastic fluctuations in neural activity that trigger a movement upon a threshold-crossing event (Schurger et al. 2012). Recent efforts have attempted to better understand the relationship between single-trial RP-like fluctuations and movement triggering. For example, RP detection has been successfully used to predict self-paced movements on a single-trial basis in real time (Schultze-Kraft et al. 2016, 2020). However, the presence of an RP only probabilistically predicts a subsequent movement, and the factors determining whether a given RP instance will be followed by a movement or not are not fully understood. The RP has further been suggested to correlate with reports of prospective awareness of intention (Parés-Pujolràs et al. 2019) and to contribute to delayed intention reports (Schultze-Kraft et al. 2020).

Event-related desynchronization (ERD) refers to a decrease in the frequency band-specific EEG power relative to a baseline

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period, and it is classically interpreted as a corresponding increase in cortical excitability (Kalcher and Pfurtscheller 1995; Pfurtscheller and Lopes da Silva 1999). ERD in the beta frequency range (~13–30 Hz) is present in sensorimotor areas during motor preparation and motor imagery tasks (Stancák and Pfurtscheller 1995; Leocani et al. 1997), and it reaches stereotyped amplitudes at the time of action irrespective of reaction times in perceptual decision making tasks (e.g. O’Connell, et al., 2012). It has been proposed that such a fixed level might reflect an action-triggering threshold [see O’Connell and Kelly (2021) for a review]. Beta-ERD is known to lateralize contralateral to the moving limb shortly before action, and it has been used to decode motor intention (Bai et al. 2011; Schneider et al. 2013; Salvaris and Haggard 2014). Further, single-trial changes in beta burst dynamics — short high-amplitude bursts in the beta-band frequency range — have been shown to underpin these classical cross-trial averages (Little et al. 2019). High beta burst rates have been associated with inhibitory control (Schulz et al. 2014; Hannah et al. 2020; Wessel 2020) and, consistent with a disinhibition process, single trials exhibit a gradual decrease in beta burst rates that lateralizes shortly before movement initiation (Little et al. 2019; Wessel 2020).

In this study, we investigated whether these two neural correlates of motor preparation also predict the prospective subjective experience of motor intention on a trial-by-trial basis and in the absence of any overt cues such as action itself. We hypothesized that, if participants have some insight into their motor preparation processes before action execution, these motor preparation-related signals might be informing their reports. That is, we hypothesized that the neural mechanisms involved in action generation may also be related to the conscious experience of such preparation. In our set-up, participants performed a self-paced movement task while watching a sequence of letters. Occasionally, the letter stream was interrupted with a visual cue that acted as an intention probe, and participants were asked to report whether they felt they were about to move when the cue appeared (Experiment 1) or how ready they felt they were on a continuous scale (Experiment 2). Importantly, reports were provided before any overt movement was executed, therefore precluding the possibility that subjective reports could have been informed by *post hoc* confabulation. We found that beta-band power was a significant predictor of subjective readiness, while the amplitude of the RP was not.

Materials and methods

Participants

Twenty-three subjects for Experiment 1 and 21 different subjects for Experiment 2 were recruited from the Institute of Cognitive Neuroscience Subject Database. All participants were healthy, right-handed, young adults with normal or corrected to normal vision, no known disabilities, and no history of neurological or psychological disorder. The studies were approved by the University College London Research Ethics Committee and written informed consent was obtained from all participants before beginning the experiment. All participants were invited to a single EEG session and were paid £7.50 per hour.

In Experiment 1, four participants were excluded because they did not produce a sufficient number of awareness reports (i.e. they reported being aware of an intention to move in <15 trials). Nineteen participants (10 female) were included for beta-band analysis ($M_{\text{age}} = 25.8$, $SD = 4.05$). We excluded one additional participant from the RP analysis because no RP was observed prior to self-paced actions (for RP analysis, $N = 18$; see [Supplementary Fig. S4](#)).

A canonical RP was defined as a decrease of at least $1 \mu\text{V}$ in the interval from 50 ms immediately after the baseline to 50 ms around the premovement RP peak (Trovò et al. 2021). The fact that some individuals do not exhibit an RP prior to self-paced movements is a well-known phenomenon that has previously been reported (Schurger et al. 2012; Parés-Pujolràs et al. 2019; Trovò et al. 2021), although its cause remains unknown (Schurger et al. 2021). The precaution to exclude participants who did not exhibit a clear RP from the analysis where the RP was the key dependent variable was also taken in our previous work (Parés-Pujolràs et al. 2019). The experimental design, sample size, exclusion criteria and key comparisons for Experiment 1 were pre-registered (<https://osf.io/zwsmp>).

In Experiment 2, a visual inspection of the data revealed that four participants exhibited excessive noise throughout the whole EEG time course across all channels due to technical problems during the recording session and were excluded from further analysis. Seventeen participants (13 female) were therefore included in the final Experiment 2 dataset ($M_{\text{age}} = 23.76$, $SD = 3.45$).

Procedure

Participants sat in a quiet room and viewed the stimuli on a computer monitor. The task instructions were first displayed on the computer screen and then verbally repeated by the experimenter before the beginning of the experiment.

Participants performed a simple self-paced motor task in both experiments. The tasks were programmed in Matlab R2014b and Psychophysics Toolbox v3 (Brainard 1997). In Experiment 1, subjects made self-paced actions and awareness reports by pressing designated keys (left/right arrow) on a standard computer keyboard with index fingers. In Experiment 2, they made self-paced actions by pressing the space bar with the right hand and reported ‘readiness’ judgements by pressing the numbers on the keyboard numeric pad.

Task

In both experiments, participants were instructed to fixate on a rapid letter stream and to make self-paced keypresses whenever they felt like it. They were specifically told not to predecide to respond to a specific letter and to try to be as spontaneous as possible (e.g. not to make keypresses after a fixed interval). Occasionally, one letter was presented in orange rather than in black font (see ‘Stimuli’). Both experiments were designed to obtain awareness reports before any movement had been executed to avoid the possibility of *post hoc* confabulation.

Experiment 1 (Fig. 1a) was adapted from the design of Parés-Pujolràs et al. (2019). Participants performed self-paced movements with the index finger of either the right hand (9 participants) or the left hand (11 participants). When they saw an orange letter, they were instructed to evaluate whether they felt they were about to execute their next self-paced movement. If they felt like the orange letter did not interrupt their preparation to move, they were instructed to ignore the orange letter and continue performing the task. Alternatively, if they felt like the orange letter had interrupted their preparation to move, they were instructed to abort the self-paced movement and instead report their awareness of movement intention by pressing a key with the hand contralateral to that with which they were executing self-paced actions. Responses to orange letters were measured during the 2-s response interval after the orange letter presentation, following the experimental protocol in a previous study (Parés-Pujolràs et al. 2019).

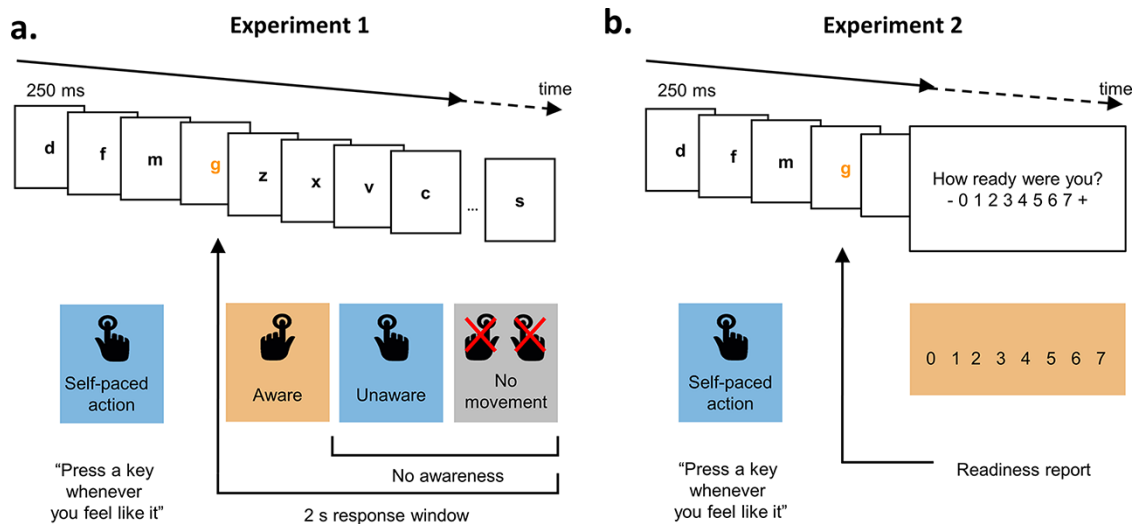


Figure 1. Experimental designs. Participants were asked to press a key whenever they felt like it (Self-paced) while fixating on a sequence of letters. Most letters were black, but occasionally, an orange letter would appear on the screen. The orange letter acted as an awareness probe, and participants were instructed to respond to it according to their momentary motor preparation state. (a) In Experiment 1, participants were instructed to report if they were about to move at the time the orange letter appeared. Thus, during the 2-s response interval following an orange letter, participants might do any of the following: (i) ignore the orange letter and not press any key (No movement), (ii) press a key with their other hand to indicate that they were aware of an intention to move when the orange letter appeared (Aware) or (iii) perform a self-paced movement with the designated hand if they were unaware of any intention to move at the time of the orange cue (Unaware). (b) In Experiment 2, the letter sequence would stop immediately after an orange letter was presented. Participants were then asked to rate how ready they were to move when the orange letter appeared (Readiness rating) on a scale from 0 ('not ready at all') to 7 ('about to move') using the computer keyboard

In Experiment 2 (Fig. 1b), the letter stream always stopped after the presentation of each orange letter, and a scale with numbers 0 to 7 was presented on the screen with the question 'How ready were you to move?'. Participants were asked to indicate how ready they felt they were at the time of the orange letter probe to execute the next self-paced movement, by pressing the corresponding number key on the keyboard (0 meant 'Not ready at all', 7 meant 'I was about to move'). There was no time limit for the response rating. There was a 2-s intertrial interval, after which the next letter stream started.

Stimuli

In Experiment 1, the task was divided into 6 blocks of 20 letter streams each. The letter streams were pseudo-random sequences of lower-case consonants (b, c, d, f, g, h, j, k, l, m, n, p, q, r, s, t, v, w, x and z). Any letter repetitions were separated by at least seven other letters. Letters were either black or orange and were presented on a light grey background without any blank intervals. Each letter was presented for 250 ms.

In Experiment 1, orange letters could appear multiple times during an uninterrupted letter stream. The time of the orange letters was drawn randomly from a uniform distribution ranging between 3 and 20 s. The duration of each uninterrupted letter stream was variable and dependent on pseudo-randomized constraints. In particular, the letter stream stopped with a 20% probability after any self-paced action and with a 75% probability after any awareness report. After the letter stream was interrupted, participants were asked to report which letter was on the screen at the time they became aware of their intention to move. They reported it by pressing the corresponding key on the keyboard (note: the results of this analysis are reported in [Supplementary Note S1](#)). The interruption probabilities follow the original study ([Parés-Pujolràs et al. 2019](#)) and were designed to obtain a similar number of reports for both conditions. The task lasted around

an hour and a half on average, including breaks ($M = 84.64$ min, $SD = 17.50$ min; range: 60–107 min).

In Experiment 2, the task was divided into 8 blocks of 36 letter streams each, and each stream ended with one single orange letter which appeared at a random time between 3 and 20 s from trial onset. The letter stream terminated after each orange letter presentation, and participants were then shown a rating scale to report how ready to move they felt at the time of the orange probe. Participants provided their reports by pressing one of eight numeric keyboard keys ranging from 0 ('not ready at all') to 7 ('about to move'). The task lasted around an hour and a half on average, including breaks ($M = 84.40$ min, $SD = 4.24$ min; range: 78–95 min).

EEG recording

EEG was recorded from 26 scalp sites (FZ, FCZ, CZ, CPZ, PZ, POZ, FC1, FC2, C1, C2, CP1, CP2, F3, F4, F7, F8, C3, C4, CP5, CP6, FC5, FC6, P3, P4, O1 and O2) using active electrodes (g.LADYbird) fixed to an EEG cap (g.GAMMAcap) according to the extended international 10/20 system. EEG data were acquired using a g.GAMMAbox and g.USBamp with a sampling frequency of 256 Hz. The signal was recorded using g.Recorder (g.tec, medical engineering GmbH, Austria). All electrodes were online referenced to the right ear lobe. Vertical and horizontal electroocular activity was recorded from electrodes above and below the right eye and on the outer canthi of both eyes.

Behavioural analysis

In Experiment 1, participants performed 6 blocks of 20-letter streams each. We excluded all trials in which participants made double-presses during the 2-s response interval after an orange letter probe (i.e. both made a self-paced movement and reported awareness of an intention; percentage of excluded trials: $M = 2.28\%$, $SD = 2.48\%$). Skewness in the individual reaction-time distributions was estimated using the 'e1071' package in R ([Meyer](#)

et al. 2021). We further analysed the subjective times of awareness by subtracting the time of action from the time of presentation of the reported letter (see [Supplementary Note S1](#)).

In Experiment 2, all participants provided 288 readiness ratings (8 blocks of 36 trials each). For each rating, we calculated the time elapsed since the last self-paced keypress and the orange letter probe. Participants were not given any instructions regarding whether to move or not after the orange letter was presented and before the rating. In some trials where people moved, it may have been the case that movements were mere reactions to the orange letter or that the orange letter happened to appear on the screen at the time when they were about to execute a self-paced movement. Regardless of the drivers of post-probe actions, trials where participants moved differ substantially from those where they did not move. Thus, we excluded the trials in which there was a self-paced movement after the probe to remove the possibility that retrospective reconstruction and reaction time influenced the judgement of intention in those trials (percentage of excluded trials: $M = 14.84\%$, $SD = 16.63\%$).

EEG preprocessing

EEG data were processed using Matlab R2014b (MathWorks), Matlab R2017b (MathWorks) and the EEGLAB plugin version 13.5.4b ([Delorme and Makeig 2004](#)).

First, scalp and eye electrodes were re-referenced to the average of two mastoid electrodes. Continuous EEG and electrooculogram data were filtered with a 0.01-Hz high-pass filter. Then, data were downsampled to 200 Hz and filtered with a 30-Hz low-pass filter. These filters were applied offline using an eighth-order Butterworth filter with zero phase shift.

Second, an independent component analysis was computed on the continuous data using the EEGLAB 'runica' algorithm. Vertical eye movement components were visually identified and removed from the signal.

Next, EEG signals were locked to either orange letters or self-paced actions. In Experiment 1, epochs started 2.5 s before the event (i.e. orange letter or action) and finished 0.5 s after it ([Parés-Pujolràs et al. 2019](#)). In Experiment 2, epochs started 1.5 s or 2.5 s before the orange letter or self-paced action, respectively, and finished 1 s after it. Shorter epochs were chosen to maximize the number of available trials for orange letter analysis. Baseline correction was performed using the 500-ms interval at the beginning of the epoch (for orange letters, $[-2.5$ to -2 s] relative to the event in Experiment 1 and $[-1.5$ to -1 s] in Experiment 2). Finally, artefact rejection was performed by removing all epochs with $>120 \mu\text{V}$ fluctuations from the baseline in the preselected channel (Cz). Epochs in which there was a key press in the interval preceding the event of interest were rejected to prevent overlapping evoked potentials in both experiments. The rejection interval prior to orange letters was $[-3$ to 0 s] in Experiment 1 and $[-2$ to 0 s] in Experiment 2.

Time-frequency decomposition

To investigate whether beta activity preceding intention probes influenced subjective reports, we performed time-frequency decompositions of the EEG activity in all epochs. The EEG power spectra were obtained by computing a seven-cycle continuous Morlet wavelet transform in the frequency range of 13–30 Hz, corresponding to the beta band ([Little et al. 2019](#)). The beta-band amplitude was obtained by calculating the square root of the average power across these frequencies over time.

Beta burst quantification

It has been recently proposed that rapid bursts of activity in the beta range may have a prominent functional role yet may get obscured in the traditional trial-averaged analyses. We have therefore quantified the beta burst rate following the approach of [Little et al. \(2019\)](#). Beta bursts were defined by periods at which the beta amplitude exceeded our empirically defined threshold. To calculate the threshold, the median beta amplitude was calculated for each single trial of the orange letter epochs. A range of threshold values around the median (median + 5 SD, in steps of 0.25) were tested. For each threshold, we correlated the trial-wise beta amplitude with the beta burst count for that given epoch. The threshold was chosen in order to maximize this correlation. The purpose of this empirical cut-off setting method is to identify the threshold that best captures how variability in individual trial beta events can account for the average mean beta amplitude ([Shin et al. 2017](#)). In our data, the empirically defined threshold was 1.5 (Experiment 1) and 1.25 (Experiment 2) standard deviations above the median amplitude. This threshold was then used for each subject so that their relative thresholds were matched at the empirically defined SDs above the subject-specific median of the beta amplitude. See [Supplementary Fig. S1](#) for sample single-trial time-frequency decompositions with visible beta bursts. The so-identified bursts were then used to quantify the burst rate and to obtain the timing at which the last beta burst occurred prior to an intention probe. The burst rate indexes the number of bursts observed per second on any given trial. We calculated the burst rate in each trial by dividing the number of bursts observed in each epoch by the duration of the time analysed (1.75 s in Experiment 1 $[-2$ to -0.250 s], 1 s in Experiment 2 $[-1.25$ s to -0.250 s], where 0 is the time of the orange probe). Note that the last 250 ms prior to the probe was excluded from analysis to avoid post-probe data leaking into the pre-event signal. Burst timing was measured as the time at which the last burst prior to the intention probe ended. The dynamics of the time-resolved beta burst probability closely matched those of the average beta amplitude during self-paced actions, as expected from previous studies ([Little et al. 2019](#)), proving the validity of our burst quantification method (see [Supplementary Fig. S1](#)).

Statistical analysis

In Experiment 1, we compared the participant-averaged EEG signal preceding awareness probes using a cluster-based permutation analysis ([Maris and Oostenveld, 2007](#)) in the FieldTrip toolbox ([Oostenveld et al., 2011](#)). The main contrast of interest involved a stimulus-locked analysis, comparing potentials preceding orange letters that were followed either by a movement by which participants reported their awareness of being about to act ('Aware' trials) or by a different movement that corresponded to participant's self-paced action and that was not associated with awareness of ongoing preparation at the time of probing ('Unaware' trials). The cluster-based tests were performed on the individual participant averages using the following parameters: two-tailed dependent samples t-test, time interval $[-2$ to 0 s relative to the orange letter presentation] and number of draws from the permutation distribution = 100 000. This comparison was pre-registered. We further ran exploratory analyses to test whether our three frequency-based features of interest—the mean beta amplitude, the beta burst rate and the timing of the last beta burst preceding awareness probes—differed across our conditions. To do so, we fitted three multilevel linear regressions with the 'lme4' package in R ([Bates et al. 2015](#)). Significance testing was performed using the Wald chi-squared test as implemented in the 'car' package for R

(Fox 2019). A random intercept was included to account for the between-subject variability, and all *P*-values were FDR-corrected to account for the fact that three related measures were investigated. *Post hoc* contrasts were run using the 'lsmeans' function from the 'emmeans' package (Lenth et al. 2021), and all *P*-values in these *post hoc* tests were corrected for multiple comparisons using the Tukey method.

In Experiment 2, we analysed the relationship between the beta-band dynamics over a central electrode (Cz) and subjective readiness ratings by fitting three separate linear mixed-effects ordinal regressions with the 'ordinal' R package (Christensen 2018), since the reports were given on an eight-item ordinal scale. Each regression included one of our three frequency-based features—the z-scored mean beta amplitude, the beta burst rate and the timing of the last beta burst preceding awareness probes—as predictors of subjective ratings. We repeated the regressions including the time elapsed between the probe and their previous keypress as a predictor to control for the possibility that participants were basing their ratings on time rather than on an internal brain signal. A random intercept was included to account for the between-subject variability, and all *P*-values were FDR-corrected to account for the fact that three related measures were investigated. For the RP analysis, we extracted the mean EEG amplitude at Cz in the last 100 ms before the probe and ran a fourth linear regression to test its relationship to subjective readiness.

In contrast to the lateralized RP (LRP), which is contralateral to the movement and can normally only be observed around 0.5 s before movement, the initial slow RP ramp can be measured as early as 2 s in advance of a movement (e.g. Haggard and Eimer 1999). Since our experiments are based on an interruption paradigm, and such interruption may occur at various times before a potential movement onset, we chose to investigate the earlier, bilateral aspect of the RP rather than the more short-lived LRP.

Results

Experiment 1

In Experiment 1, we first investigated whether the presence of an RP-like central negativity preceding an intention probe correlated specifically with awareness reports or whether it simply correlated with motor preparation. For this analysis, we grouped trials according to participants' behaviour after an awareness probe. In our task, during the 2-s response interval following an orange letter, participants might do any of the following: (i) ignore the orange letter and not press any key ('No movement'), (ii) press a key with their other hand to indicate that they were aware of an intention to move when the orange letter appeared ('Aware') or (iii) perform a self-paced movement with the designated hand if they were unaware of any intention to move at the time of the orange cue ('Unaware').

On average, participants did not move after 42.59% (SD = 14.92%; 'No movement') of orange probes, reported awareness on 25.38% (SD = 14.02%; 'Aware') and performed a self-paced movement following 32.04% (SD = 15.94%; 'Unaware') of the orange letters. Reaction times in unaware vs. aware movements varied across participants (see Supplementary Fig. S2), although a majority ($N = 13$) showed a left-skewed distribution with most keypresses shortly following the orange letter (see Fig. 1 and Supplementary Fig. S2). At short latencies (<200 ms) after the orange letter, only self-paced actions occurred. These were presumably movements that would have occurred whether the orange letter had appeared or not, because the 'point of no

return' had by then been passed (Schultze-Kraft et al. 2016). Importantly, in this subset of actions, participants might have been aware of their intention to move when the orange letter was presented but were unable to inhibit their ongoing movement preparation. However, participants performed their movements with the hand designated for self-paced actions rather than awareness reports. Since movements were not executed to indicate awareness of an impending movement, these trials are still labelled 'Unaware'. Furthermore, self-paced actions outnumbered awareness reports at longer latencies. On average, keypresses indicating awareness occurred significantly closer to the orange letter probe than self-paced movements ($t_{(18)} = 3.83$, $P = 0.001$).

In a previous study (Parés-Pujolràs et al. 2019), we showed that movements following an intention probe were preceded by a central EEG negativity resembling a truncated RP. Since awareness reports in that study were executed with the same hand as self-paced actions, the concern remained that some of the keypresses executed after an orange letter was presented might not reflect genuine intention awareness, but rather be spontaneous movements that might have occurred irrespective of the intention probe. In the present study, we addressed this confound by instructing participants to use one hand for self-paced movements and the other hand for reporting awareness. The temporal overlap between these two responses (Fig. 2a) demonstrates how this confound could affect studies using a single response. By overcoming this limitation, with the current design, we could directly distinguish whether neural signals preceding a probe were related specifically to intention awareness or to unconscious movement preparation associated with self-paced actions. To test this, we compared the Cz amplitude preceding an intention probe in the 'Aware' condition to 'Unaware' trials, in which participants performed self-paced button presses shortly after an orange letter (up to 2 s), thus indicating that they were not conscious of any intention to move at the time of the cue presentation. Electrode Cz was the location around which the RP component was centred at the time of self-paced movements occurring in the absence of orange letters (Supplementary Fig. S6a).

We initially predicted that, if the RP tracks a motor preparation process that reaches awareness once a certain threshold is crossed, greater negativities should be observed in 'Aware' compared to 'Unaware' actions. However, a cluster-based permutation analysis identified two significant clusters with greater negativities in the self-paced actions compared to the awareness reports ($P = 0.022$, $P = 0.043$; Fig. 2b). Thus, contrary to our prediction, when participants were not aware of an intention to move at the time of the probe, but nevertheless executed a self-paced action shortly thereafter, the RP amplitudes over the central electrode Cz were significantly higher than the potentials observed in trials where participants reported being aware of an intention to move.

We next investigated whether the beta-band activity at the single-trial level was linked to participants' awareness reports. Reflecting recent advances in understanding the relation between beta-band EEG features and motor function, we tested whether our three conditions of interest differed in the beta-band features: the mean beta amplitude, the average burst rate and the time of the last beta burst before probing. We found a significant effect of condition on the mean beta amplitude ($X_{(2)}^2 = 14.02$, $P = 0.003$) and beta burst rate ($X_{(2)}^2 = 8.25$, $P = 0.024$). Trials in which participants did not move after an orange probe ('No response') showed the highest beta amplitudes and burst rates, while 'Aware' trials showed the lowest ones ('No response' vs. 'Aware' mean beta amplitude: $t_{(3063)} = 3.74$, $P < 0.001$, burst rates:

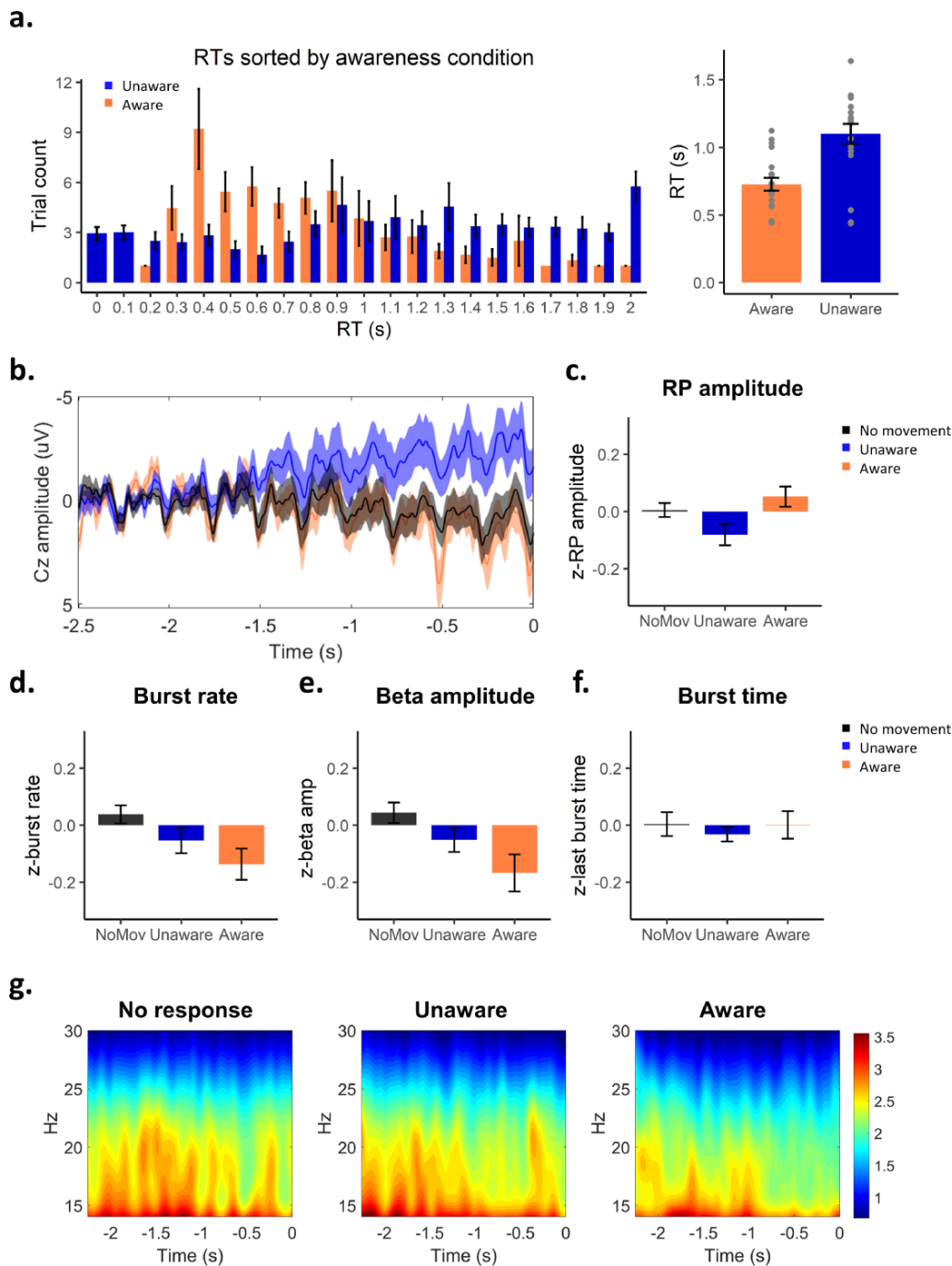


Figure 2. Experiment 1. (a) Grand-averaged (\pm SE) response time (RT) distribution, locked to the presentation of an orange letter (time = 0, x-axis) and sorted by awareness condition. On average, participants moved significantly faster following an orange letter in awareness reports compared to self-paced actions. See [Supplementary Fig. S1](#) for individual participant reaction-time distributions. (b) Grand-averaged EEG amplitude over Cz locked to orange letters (time 0) and sorted by response to the orange letter. (c) Grand-averaged amplitude (\pm SEM) over the last 100 ms before the orange letter presentation. The Cz amplitude significantly correlated with whether participants would perform the self-paced movement: the more negative the EEG amplitude, the more likely participants were to move in a self-paced manner. (d, e). When intention probes were preceded by low beta burst rates (d) and low mean beta amplitudes (e), participants were more likely to report being aware of an impending movement (Aware) than they were to move in a self-paced manner (Unaware) or not move at all (No Movement). (f) There was no significant effect of the precise timing of the last beta burst preceding intention probe on the probability of reporting awareness. Bar graphs illustrate the mean (\pm SE) z-scored beta burst rate (d); beta amplitude mean (e); and time from the last beta burst (f), grand-averaged across participants and sorted according to the raw rating values. Note: data were z-scored for illustration purposes only, inferential testing is based on raw values. (g) Grand-averaged beta power before intention probes, sorted according to participants' response to the orange letters.

$t_{(3057)} = 2.83, P = 0.013$). The 'Unaware' trials, in which participants were not conscious of an intention at the time of the orange probe but nonetheless moved within 2 s, showed intermediate

beta amplitudes (mean beta amplitude: 'Unaware' vs. 'Aware': $t_{(3063)} = 2.31, P = 0.054$; 'Unaware' vs. 'No Response': $t_{(3063)} = 1.23, P = 0.432$; beta burst rates: 'Unaware' vs. 'Aware': $t_{(3007)} = 1.32,$

$P=0.381$; 'Unaware' vs. 'No Response': $t_{(3029)}=1.44$, $P=0.322$; Fig. 2d). The time of the last beta burst ($X^2_{(2)}=0.86$, $P=0.650$) before the probe did not differ between conditions. These results suggest that the level of motor preparation as indexed by the beta-band amplitude was the lowest in 'No Response' trials, in which no movement was executed after an orange probe, and the highest in 'Aware' trials. The fact that most self-paced actions occurred significantly later than awareness reports following an orange probe (Fig. 2a) further supports the idea that the neural activity before the probe in self-paced trials in our task represents an intermediate stage of preparation, perhaps inaccessible to consciousness. We observed no correlation between the mean beta amplitude and the RP amplitude on a trial-by-trial basis ($r=-0.006$, $t_{(17)}=0.250$, $P=0.806$).

Thus, contrary to our initial, pre-registered hypothesis, these results suggest that the RP may not be related to prospective conscious access to motor preparation states. However, we found some evidence that participants' subjective reports of readiness rely on a different internal motor preparation signal: the beta-band power. In a second experiment, we further investigated this hypothesis.

Experiment 2

In Experiment 2, we obtained graded rather than dichotomous reports of intention awareness. As in Experiment 1, participants watched a stream of black letters and executed self-paced actions whenever they felt like it. Occasionally, an orange letter would be presented on the screen. The letter stream then stopped, and participants were asked to report how ready they felt for their next movement at the time of the interruption.

We first ran an ordinal regression analysis on a single-trial level to test whether RP amplitudes at Cz significantly predicted participants' readiness ratings. Electrode Cz was, as in Experiment 1, the location around which the RP component was centred at the time of self-paced movements occurring in the absence of orange letters (Supplementary Fig. S6b). We found no significant relationship between the EEG amplitude at Cz preceding the orange probe on the subsequent rating of readiness ($X^2_{(1)}=0.655$, $P=0.418$; see Fig. 3a and b). We observed that one participant ($n=1$) did not show any discernible RP preceding normal self-paced actions (see Supplementary Fig. S5). However, a control analysis excluding this participant from the analysis did not significantly change the results ($X^2_{(1)}=1.430$, $P=0.232$).

We next ran three mixed ordinal regressions using the z-scored burst rate, the z-scored mean beta amplitude, and the time of the last beta burst before probing as predictors in three separate mixed ordinal regressions. We found that the lower the burst rate ($X^2_{(1)}=15.31$, $P<0.001$) and the mean beta amplitude ($X^2_{(1)}=13.90$, $P<0.001$), the higher the readiness ratings participants provided (Fig. 3). The timing ($X^2_{(1)}=0.98$, $P=0.322$) of the last beta burst did not significantly predict the subjective readiness ratings. These single-trial effects were also visible in the grand-averaged beta power preceding intention probes (Fig. 3f).

We ran additional analyses to investigate whether these relations between beta-band and awareness ratings could be due to a correlation with some other confounding factors. For example, participants may have used the time elapsed between their last movement and the orange letter to infer their readiness level. That is, they could have based their reports on an overt marker (elapsed time) rather than an internal signal. To control for this possibility, we included the time elapsed since the

last self-paced keypress as a covariate in all of our analyses. The effects of the mean beta amplitude ($X^2_{(1)}=10.44$, $P=0.006$) and beta burst rate ($X^2_{(1)}=9.56$, $P=0.006$) remained significant. All reported effects were also significant at an electrode location contralateral to the movement, C3 (see Supplementary Note S2 and Fig. S8). Perhaps unsurprisingly, in all models, the time of the last keypress also had a significant effect on the readiness ratings (all $P<0.05$). The longer the interval elapsed between the last keypress and the probe, the greater the readiness rating. This suggests that both the time elapsed from the last self-paced action and the beta-band power informed participants' readiness judgements.

As in Experiment 1, we observed no correlation between the mean beta amplitude and the RP amplitude in this dataset ($R=0.029$, $t_{(16)}=1.32$, $P=0.204$).

Discussion

Conscious insight into motor preparation states is often thought to be important for voluntary control: only if someone can consciously access what they are about to do could they do otherwise. Many voluntary actions in our daily lives are performed with a sense of 'tacit consent' and are not necessarily preceded by an explicit conscious intention or a 'fiat' command (Ach 2006). However, some actions are sometimes preceded by such a feeling. This is particularly the case in actions that are not mere reactions to an environmental stimulus, but rather self-paced. The build-up leading to bungee jumping, throwing a dart or starting a musical performance, for example, is often accompanied by a conscious feeling of readiness. Here, we used spontaneous, self-paced movements as a proxy for these kinds of actions. Importantly, our interruption paradigms capitalize on the 'conscious accessibility' to motor preparedness as opposed to 'spontaneous conscious access' to an intention to move. By prompting participants to introspect and report how ready to move they were, our paradigms are designed to help people to consciously access motor readiness states that may have gone unnoticed in other circumstances.

In this study, we tested whether EEG signals related to motor preparation could be used to predict the prospective subjective feeling of readiness on a trial-by-trial basis. Previous research has suggested that both the RP (Parés-Pujolràs et al. 2019; Schultze-Kraft et al. 2020) and the EEG power in the beta band (Verbaarschot et al. 2016) may constitute neural bases of the experience of 'being about to move'. Yet, the relationship of these motor preparation signals to the prospective subjective experience of readiness remains elusive. Here, we combined a self-paced action task with random intention probing to investigate whether participants' subjective feelings of being about to act—while not yet having actually acted—were associated with signals linked to movement preparation.

In our first experiment, participants performed a self-paced task with one hand and responded to an intention probe by pressing a key with another hand if they felt like they were about to execute their next self-paced movement at the time of probing. During the response interval, participants sometimes reported awareness of an intention to move ('Aware' trials), while on other occasions they were not conscious of any ongoing preparation and either moved in a self-paced manner nonetheless ('Unaware' trials) or did not move at all ('No movement' trials). We found RP-like signals preceding the intention probe on trials where participants made a self-paced action within the response interval,

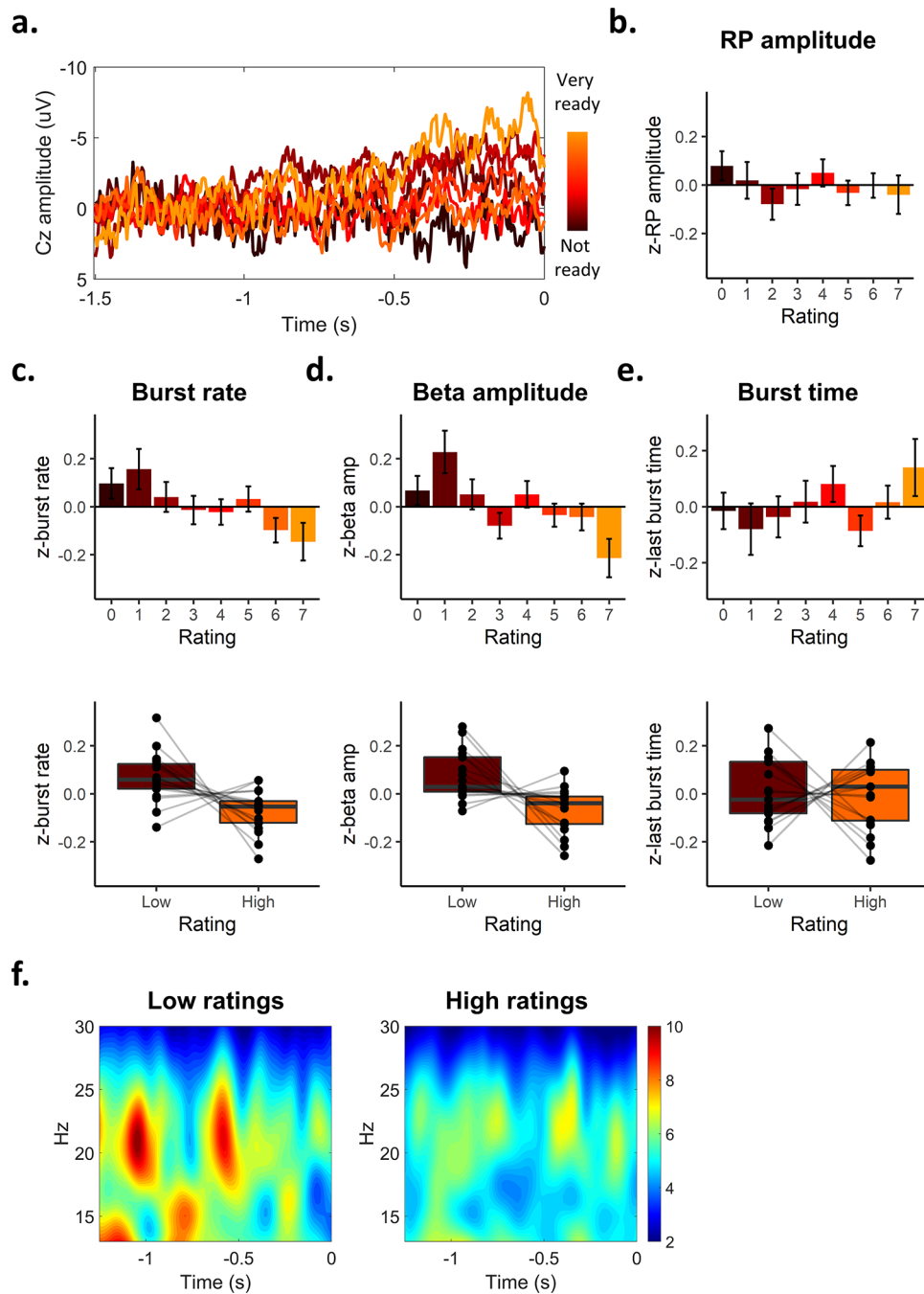


Figure 3. Experiment 2. (a) Grand-averaged EEG amplitude over Cz locked to orange letters (time 0) and sorted by readiness rating (0–7). See [Supplementary Fig. S3](#) for individual participant readiness rating distributions. (b) Grand-averaged amplitude (\pm SEM) over the last 100 ms before the orange letter presentation. No significant correlation was found between the average amplitudes of the EEG signal preceding the probe and the readiness rating given by participants. (c–e) Bar graphs (top) illustrate the mean (\pm SE) z-scored beta burst rate (c); mean beta amplitude (d); and time from the last beta burst (e), pooled across participants and sorted according to the raw rating values. For illustration purposes in the boxplots (bottom), we averaged all trials within each participant and grouped them according to whether participants gave a low (<participant mean) or a high (>participant mean) readiness rating after the intention probe. Overlaid dots indicate single-participant averages. When intention probes were preceded by high beta burst rates, participants tended to give lower readiness ratings. (d) Lower average beta amplitudes preceding intention probes predicted high readiness ratings. (e) There was no significant effect of the timing of the last beta burst preceding intention probe on readiness ratings. (f) Grand-averaged beta power before intention probes, sorted according to participants' readiness ratings

but not on trials when they reported being aware of a motor intention (Fig. 2b). This suggests that the RP-like signal found before the probe in our unaware condition was not related to awareness of intention, but rather to unconscious preparation of an impending self-paced movement.

We further investigated single-trial beta-band dynamics to test whether neural features in the frequency domain might explain the subjective experience reports better than the RP. We found that neural activity preceding intention probes showed the lowest beta-band amplitude and the lowest beta burst rate in 'Aware'

trials and the highest rates in 'No movement' trials (Fig. 2). The neural activity preceding intention probes in 'Unaware' trials (i.e. trials where participants were not aware of an intention at the time of probing but moved in a self-paced manner shortly afterwards) showed intermediate beta burst rates and average amplitudes. Given that the beta-band amplitude is related to the strength of motor preparation, this suggests that, on average, participants were more ready to move (i.e. their motor cortex was more excitable prior to the probe) in trials where they reported awareness of an intention compared to those where they were unaware of motor preparation, but still moved in a self-paced manner within the 2-s post-probe response interval.

This interpretation is further supported by the analysis of reaction times. A minority of post-orange 'Unaware' actions occurred very shortly after the probe (<200 ms), suggesting that these were self-paced actions that had already been initiated and were beyond the point of no return (Schultze-Kraft et al. 2016) at the time the orange cue appeared. However, most actions in 'Unaware' trials occurred significantly later than awareness reports ('Aware' trials; Fig. 2a). This suggests that the neural activity preceding trials where participants did not report being conscious of any ongoing motor preparation but executed a self-paced action shortly after the probe may represent an intermediate stage of readiness, seemingly inaccessible to consciousness. The finding that these actions were nonetheless preceded by an RP-like deflection, while the awareness reports were not, further suggests that the beta-band activity and the RP may play distinctive roles in action triggering—we elaborate on this possibility later.

In our second experiment, we replicated and extended these results. Most previous studies on motor intention awareness have used dichotomous report methods of various kinds (Matsushashi and Hallett 2008; Kühn and Brass 2009; Parés-Pujolràs et al. 2019; Schultze-Kraft et al. 2020). However, it has been proposed in different experimental contexts that subjective awareness is a gradual, rather than dichotomous phenomenon (Overgaard et al. 2006; Nieuwenhuis and de Kleijn 2011). Here, we obtained for the first time such graded reports in the context of motor readiness—we refer to those as 'readiness reports'. Besides being more in line with the continuous nature of both motor preparation and subjective awareness, graded readiness reports also allowed us to maximize the variability in the subjective reports and hence investigate the more sensitive link between continuous variations in the EEG activity and the subjective experience of readiness.

As in Experiment 1, we found no link between the negativity over motor sites and subjective ratings (Fig. 3). In particular, it was not the case that higher 'readiness' ratings were preceded by stronger negativities, as one might expect if there were a positive relationship between the RP amplitude and conscious feeling of intention. However, we further validated the finding that beta-band activity is related to the subjective feeling of readiness. Both the rate of beta bursts and the average beta band were significant predictors of participants' readiness reports. The rate of beta bursts and the average beta amplitude preceding intention probes were inversely related to readiness ratings: the lower the rate of beta bursts and mean beta amplitudes, the higher the ratings participants provided (Fig. 3d).

Together, our results provide evidence that the prospective 'readiness' reports correspond to a well-known motor preparation signal: the single-trial dynamics in the beta band. Low beta burst rates and average amplitudes are known to precede movement initiation and be related to the objective level of motor readiness (Little et al. 2019). Our study shows that these signals are consciously accessible to participants before movement execution

and that they inform the prospective awareness reports. Crucially, in this experiment, we excluded all trials in which participants pressed a key after the intention probe to remove the possibility that their readiness reports were retrospectively influenced by an overt movement event and *post hoc* confabulation (Aarts et al. 2005; Kühn and Brass 2009; Schultze-Kraft et al. 2020; Rebouillat et al. 2021).

Furthermore, our findings suggest that, while the RP is a reliable precursor of self-paced actions, it may not in itself be the key marker of a consciously accessible motor process. This represents a revision of the interpretation of our own previous study (Parés-Pujolràs et al. 2019). In this study, we suggested that RPs were associated with a prospective awareness of intention to act. However, we acknowledged that since participants performed self-paced actions and awareness reports with the same hand, this study could not completely distinguish between unaware preparation for self-paced actions that may have occurred irrespectively of the orange probe and the genuine awareness reports. Here, in contrast, awareness reports were made with one hand, while self-paced actions that were not interrupted during the awareness period were made with the other hand, allowing a clear disambiguation. Since here we did not find any reliable association between RP and awareness reports, it seems likely that the association reported previously (Parés-Pujolràs et al. 2019) was in fact confounded by some trials where self-paced action preparation was interrupted prior to awareness. By avoiding this confound, the present study offers a clearer view of possible neural precursors of action awareness. While the RP was not associated with prospective action awareness, the beta-band EEG power was. Thus, the conclusion remains that neural activity associated with action preparation may form the neural substrate of subjective prospective motor awareness, with the present study providing a more rigorous analysis of the specific biomarkers involved.

More broadly, our results highlight a potential interaction and distinctive role for the beta-band activity and the RP at the level of motor initiation and voluntary control. Humans and non-human primates are able to voluntarily control the synchronization of neural firing at different frequencies, including beta (Khanna and Carmena 2017; He et al. 2020) and low-gamma bands (Engelhard et al. 2013). Furthermore, recent evidence suggests that no such type of voluntary control is possible over the amplitude of the RP (Schultze-Kraft et al. 2021). Thus, one possibility is that the voluntarily controllable and consciously accessible beta-band power may effectively act as a threshold-setting mechanism for action, indexing the excitability of the motor cortex. In turn, the RP may result from the (involuntary) accumulation of stochastic noise in these motor areas (Schurger et al. 2012) and act as a trigger determining 'when' exactly endogenously triggered movements occur—namely, we hypothesize, when the threshold set by the beta band activity is crossed.

Conclusions

In sum, the present study provides support to the idea that people have prospective access to their spontaneous motor preparation processes, as previously suggested, but shows that the subjective feeling of intention correlates with single-trial beta-band dynamics rather than with the negative-going deflections over the motor cortex that characterize the RP, against previous suggestions (Parés-Pujolràs et al. 2019). Further studies are required to explore how these two signals interact during voluntary motor initiation and how they relate to the feeling of readiness preceding spontaneous action initiation.

Supplementary data

Supplementary data are available at NCONSC online.

Data availability

All data and analysis code are available at Open Science Framework (<https://osf.io/dh8j9/>).

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Significance statement

In this study, we investigated the neural bases of subjective readiness to act. In two EEG experiments, we probed participants to report their motor readiness at random times during a self-paced action task. These judgements were made in the absence of action execution, crucially preventing any influence by *post hoc* action-related confabulation. The converging findings of both experiments show that the subjective feeling of readiness in the absence of action has an identifiable neural correlate in beta-band EEG oscillations, but not in the RP. Our novel methodological approach avoids confounds often present in previous work and provides a significant advance in our understanding of the neural bases of motor awareness.

Conflict of interest statement

None declared.

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