

Do readiness potentials happen all the time?

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ABSTRACT

The Readiness Potential (RP) is a slow negative EEG potential found in the seconds preceding voluntary actions. Here, we explore whether the RP is found only at this time, or if it also occurs when no action is produced. Recent theories suggest the RP reflects the average of accumulated stochastic fluctuations in neural activity, rather than a specific signal related to self-initiated action: RP-like events should then be widely present, even in the absence of actions. We investigated this hypothesis by searching for RP-like events in background EEG of an appropriate dataset for which the action-locked EEG had previously been analysed to test other hypotheses [Khalighinejad, N., Brann, E., Dorcham, A., Haggard, P. *Dissociating cognitive and motoric precursors of human self-initiated action*. *Journal of Cognitive Neuroscience*. 2019, 1-14]. We used the actual mean RP as a template, and searched the entire epoch for similar neural signals, using similarity metrics that capture the temporal or spatial properties of the RP. Most EEG epochs contained a number of events that were similar to the true RP, but did not lead directly to any voluntary action. However, these RP-like events were equally common in epochs that eventually terminated in voluntary actions as in those where voluntary actions were not permitted. Events matching the temporal profile of the RP were also a poor match for the spatial profile, and vice versa. We conclude that these events are false positives, and do not reflect the same mechanism as the RP itself. Finally, applying the same template-search algorithm to simulated EEG data synthesized from different noise distributions showed that RP-like events will occur in any dataset containing the 1/f noise ubiquitous in EEG recordings. To summarise, we found no evidence of genuinely RP-like events at any time other than immediately prior to self-initiated actions. Our findings do not support a purely stochastic model of RP generation, and suggest that the RP may be a specific precursor of self-initiated voluntary actions.

1. Introduction

Voluntary actions – those caused by internal processes within the agent themselves and not an external stimulus – have a neural signature distinct from that of actions in response to the environment (Fried et al., 2017; Haggard, 2008). A prominent feature of voluntary actions is that they are preceded by a *Bereitschaftspotential*, or *Readiness Potential* (RP): a slow, negative EEG potential over central midline neurons in the last second or so before the action (Kornhuber and Deecke, 1965; Libet, 1985; Haggard and Eimer, 1999). The RP has been the topic of intense interest, notably since Libet's (Libet, 1985; Libet et al., 1983) report that it begins before individuals consciously experience themselves coming to a decision to act.

What does the RP represent? The conventional view (Kornhuber and Deecke, 1965; Libet, 1985; Passingham, 1993) is that the RP primarily reflects action preparation in supplementary motor area or/and pre-supplementary motor area (Shibasaki and Hallett, 2006; Lang et al., 1991; Yazawa et al., 2000), that begins when the agent unconsciously

decides to act (Libet, 1985) and culminates in the motor command being transmitted via the primary motor cortex (Brass et al., 2013). This account implies first that the RP is specific to voluntary actions: it should occur just prior to voluntary actions, but not prior to non-voluntary actions. Second, and crucially, the RP should not occur when the agent might in principle produce voluntary actions, but in fact does not. The first prediction has been supported (Shibasaki and Hallett, 2006; Brass et al., 2013). The second prediction is harder to test because of the way that the RP is measured. The RP prior to voluntary actions cannot be easily discerned on individual trials due to its small amplitude compared to the noise inherent in EEG recordings (Shibasaki and Hallett, 2006). As a result, RP studies typically average together a large number of trials, time-locked to the time of the action. Any single-trial EEG events that are similar to the RP but do not lead to actions (hereafter “RP-like events”) would be missed as they provide no overt action to which they can be aligned. Thus, the conventional interpretation of the RP as specifically linked to voluntary action relies on biased sampling: it is quite possible that RP-like events happen all the time, or at least at times unrelated to

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voluntary action. The claim that the RP is specific to voluntary actions seems premature without unbiased knowledge of when RP-like events occur.

Recently, Schurger and colleagues (Schurger et al., 2012; Schurger, 2018) proposed an alternative interpretation of the RP, which makes this question particularly interesting. They demonstrated that the RP could reflect evidence accumulation to an internal threshold for action (Usher and McClelland, 2001). In the absence of external perceptual evidence, the accumulator integrates stochastic neural fluctuations, producing a random walk which would cause the accumulator to reach threshold. When traces from multiple trials produced by this model are time-locked to the time at which threshold is crossed – that is, the time of action – and averaged, they reproduce the shape of the averaged RP. This indicates that the RP signal could reflect the ongoing state of this accumulator. As a result, the characteristic shape of the RP may represent an artefact of the biased, action-locked sampling of accumulating stochastic signals. More recently, Schurger (2018) showed that the RP could reflect the stochastically fluctuating inputs to the accumulator, rather than the accumulator's output, if these inputs themselves are autocorrelated and follow a random walk trajectory. An important consequence of the stochastic account is that RP-like events, particularly RP-like events with amplitude just short of the threshold required to trigger an action, should be found throughout the EEG, and not only just prior to voluntary actions. A somewhat similar possibility was raised by John C. Eccles, (1982, 1985), who suggested that RP-like potentials may not be a causal consequence of the decision to act, but instead might occur spontaneously, and that their peaks may provide an opportunity at which weak volitional signals are sufficient to trigger actions. Eccles' dualism in fact lead him to suggest that these volitional signals might be non-physical.

1.1. Our approach

In this work, we use a data-mining approach to test whether RP-like events can be found throughout the EEG, or only prior to voluntary actions. The mean RP observed just prior to voluntary actions represents our best estimate of what RP-like events that do not lead immediately to actions would look like, if they exist. We use the mean RP as a matched template filter, and compare it to a rolling window of the raw EEG from individual trials to identify the windows that most resemble the RP – the *RP-like events* present on each trial (see Woody, 1967, for a similar approach in another domain).

Of course, applying this filter to noisy data is bound to reveal some events that resemble the RP, simply by chance. We must therefore verify that any events we find are really due to the same mechanism as the RP. One way to do this is to analyse epochs from a control condition. In the *voluntary action* condition, participants were allowed to perform an action at a time of their own choosing. In the *instructed action* condition, participants performed the same action, but only after being instructed to do so by a visual prompt. The timing of this instruction was yoked to the time of a voluntary action in a previous block, ensuring that the timing of these actions was matched.

We sketch the predictions of the classical (Kornhuber and Deecke, 1965; Libet, 1985; Passingham, 1993) and stochastic (Schurger et al., 2012) accounts of the RP in Fig. 1. According to the classical account (Fig. 1B), the RP occurs just prior to voluntary actions, and at no other time. This means that any RP-like events we find in the resting EEG would be false positives: signals resemble the RP, but are produced by a different mechanism. Two predictions follow from this. First, the degree to which these events match the RP should not differ between conditions. Second, events that happen to match the temporal profile of the RP may

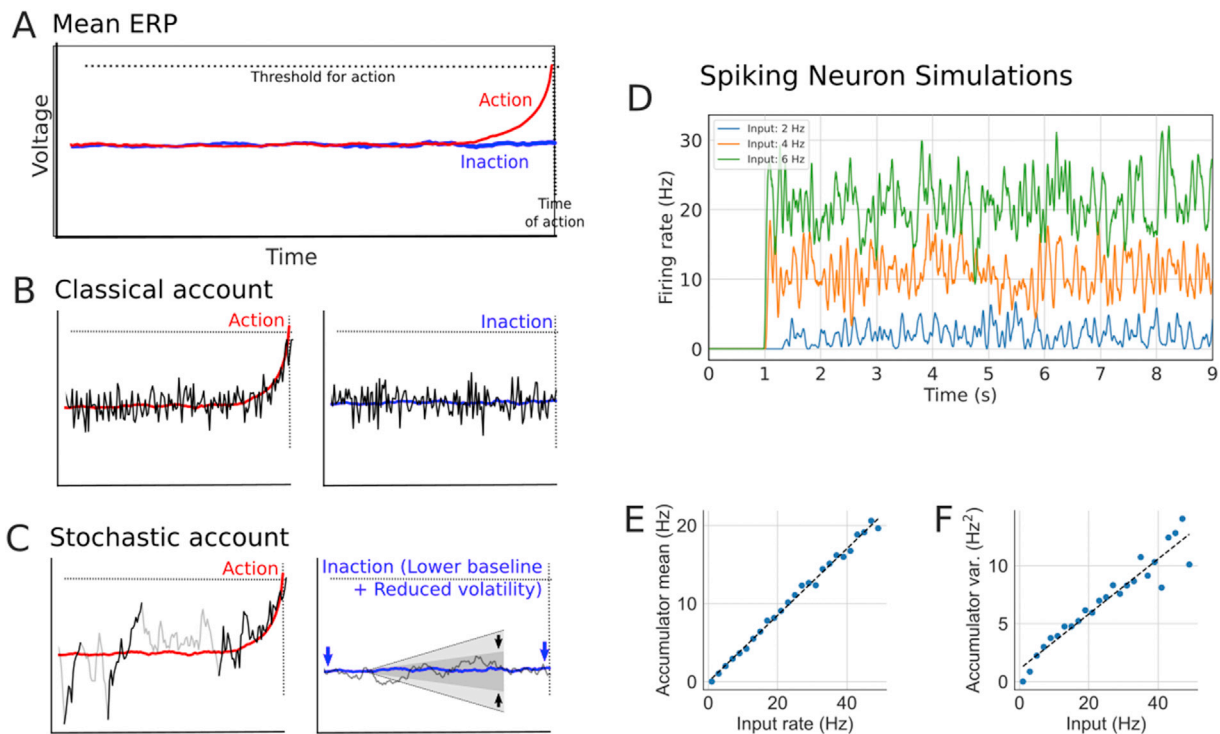


Fig. 1. A. The characteristic shape of the Readiness Potential (RP) in the moments prior to voluntary actions (red) is absent in average EEG epochs where no action is performed (blue). B. According to the classic account, the EEG signal on a single trial is a noisy read-off of the underlying RP, and ramps up as action preparation begins. In the absence of action the single trial EEG is a noisy read-off from a flat signal. C. According to the stochastic account, the RP is found when random walks that trigger actions on crossing threshold are averaged together locked to the time they do so. The negative EEG drifts that cross threshold are therefore generated by the same process as other, earlier drifts which do not, and so do not lead to voluntary actions (black). When actions cannot be planned, the mean activation of the accumulator is reduced. Due to the relationship between firing rates and spontaneous variability, this will reduce the volatility of the accumulator, and so produce poorer matches to the RP. D. Single trial neural firing rates for a simple simulated evidence accumulation circuit. As input firing rate increases, so do both the mean (E.) and the variance (F.) of the firing rate of putative accumulator neurons, due to the Poisson firing statistics of both populations.

not necessarily match the spatial profile, and vice versa.

The predictions for the stochastic account require some derivation. According to the model proposed by Schurger (Schurger et al., 2012), in a task like Libet's, the moment of action onset is influenced by a stochastic leaky accumulator process. In contexts where a voluntary action is likely, this accumulator receives a weak input, reflecting the will to act in the near future. The accumulator is 'leaky' (it includes a decay parameter), and so its activation does not increase indefinitely, but reaches a stable point where the input and the decay cancel out. In other words, in contexts where voluntary actions are likely, the baseline level of the accumulator is raised closer to threshold. Because the accumulator is stochastic, its state will follow a random walk with this stable point as its mean – formally, it is an Ornstein-Uhlenbeck process. Eventually, this random walk will cross the threshold for action, and the movement will be executed. Crucially, it is random fluctuations, rather than any specific volitional "signal", that are the proximal cause of the accumulator crossing threshold. Therefore, the RP should be only one of many peaks in the EEG signal, albeit the only peak high enough to reach the threshold. For this reason, the stochastic account predicts that RP-like events should be found not only immediately prior to action, but also at random times in the background EEG, as long as the appropriate inputs are provided to the accumulator.

In contexts where voluntary actions are not intended, the baseline input to the accumulator will be low, and so the accumulator will be far below threshold. This means that any random fluctuations will generally not be sufficient to trigger actions. But will such random fluctuations still occur in this context? The original work only explicitly considered the case where voluntary actions are rendered likely by a baseline shift, and where noise in the accumulation process is constant over time – as is typically the case in models that do not simulate the activity of individual neurons (Bogacz et al., 2006). However, perceptual accumulation has been shown to be noisier when the input to the accumulator is stronger (Scott et al., 2015). The relationship between the mean strength of a signal and its variability is ubiquitous in human cognition, and is known as scalar variability, or Weber's law (e.g. Gallistel and Gelman, 2000). This phenomenon also emerges in neural circuits. Rather than firing at evenly-spaced intervals, individual neurons show variable inter-spike intervals with an approximately Poisson distribution, with variance between 1 and 1.5 times the mean rate of firing (Shadlen and Newsome, 1998). Random fluctuations in evidence accumulation are partly due to this inherent noisiness of neural firing rates (Bogacz et al., 2006). It therefore follows that a stronger input to the accumulator should not only increase the baseline level of activation – and so the firing rates – but also increase the variability of the input neurons' firing rates. Furthermore, because the input to the accumulator is integrated over time, increasing the variance of the input produces an increase in low-frequency fluctuations, rather than an increase in noise at all frequencies. This leads to more prominent slow fluctuations in the EEG signal, producing events that better resemble the RP. As a result, in contexts where voluntary actions are allowed, and are enabled by an increase in mean input to the accumulator, such as a baseline shift, one would expect more RP-like events to occur than in contexts that disfavour voluntary action, and where the mean firing rate is therefore lower and the accumulator less variable (Fig. 1C, right). Fig. 1D and E show the behaviour of a simple simulated neural circuit under different levels of input, and illustrate the relationship between input firing rate, accumulator firing rate, and accumulator volatility.

We used two different measures to quantify the incidence of false-positive RP-like peaks in resting EEG in each condition. One captures the temporal properties of the RP: a negative ramp-like trend peaking at the time of action. The other captures its spatial distribution: negative voltages over supplementary motor cortex relative to the rest of the scalp, centred around electrode FCz. If the events identified are due to the same mechanism as the RP, we would expect these approaches to be consistent: windows that match the temporal profile of the RP should also match the spatial profile, and vice versa. If these matching events are due to chance,

however, we would expect little consistency between the temporal and spatial patterns of RP-like events.

Of course, there are many ways we could measure the similarity of the raw data to the RP. For both our temporal and spatial analysis, we use inverse Euclidean distance metrics to quantify the similarity of the raw EEG to the template. Euclidean distance identifies windows that match both the shape and the amplitude of the template. In contrast, angle measures such as correlation coefficients consider only the shape of the signal, but not its amplitude (Bobadilla-Suarez et al., 2018). Our preliminary explorations found that correlation coefficient measures tended to identify many RP-like matching events that were orders of magnitude larger than the RP itself – leading us to prefer distance metrics. It is also possible to combine spatial and temporal information, with a given weighting, to produce a spatio-temporal template that can be compared to the raw data across all channels. Machine learning classifiers can also be trained to differentiate RPs from baseline data, and used to estimate the probability that a window of raw data contains an RP. In this manuscript, we restrict our discussion to classical temporal and spatial measures of similarity to the RP, based on Euclidean distance. However, we have obtained consistent results using a number of other approaches to estimate similarity (results not reported).

2. Methods

2.1. Data collection

We analysed EEG recordings from a task in which participants were sometimes allowed to act (press a button) at a time of their own choosing, and sometimes required to wait for a visual cue before acting. The RP data from this task has been published elsewhere (Khalighinejad et al., 2019). The present analysis focusses on the background EEG component, and is independent of the specific data epochs, research questions and results of the previous paper. The design was similar to that reported by our group previously (Khalighinejad et al., 2018), with some modifications. To elicit voluntary actions, participants completed what was ostensibly a simple visual discrimination task, while EEG was recorded. Participants were required to watch a random dot kinematogram, and indicate, as soon as the dots began to move coherently in the same direction, whether they moved left or right of the vertical. The interval between the start of the trial and the onset of coherent motion was long and highly variable, and was drawn from a shifted, truncated exponential distribution ($\lambda = 1/14$ per s, $\text{offset} = 2$ s, $\text{truncated at } 60$ s).

In the *voluntary action* condition participants could skip to the next trial at will, obtaining a small reward and avoiding a potentially long wait, by making a bimanual action (pressing both response keys at the same time). In the instructed action condition, participants performed this same skip action when and only when the on-screen fixation dot turned red, which occurred at a time yoked to a voluntary skip on the previous block. Thus, the skip actions were endogenous in the voluntary action condition, but exogenous in the instructed condition. In contrast, if participants did not skip, they would always make an exogenous action in response to the dot motion stimuli, when these eventually appeared.

Twenty participants completed two 60 minute sessions. All participants gave informed consent prior to taking part in the study, and the experiment was approved by the departmental ethics committee. In the first session, participants were allowed to skip on as many trials as they liked. In the second session, one week later, participants were only allowed to skip 50% as many times as they chose to in the previous session. The experiment was designed to investigate how this restriction altered the consistency of volitional processes, but those research questions are not relevant here. Importantly, the second session resulted in long EEG epochs during which the participant might or might not initiate an endogenous action. These long epochs gave us unusually long portions of EEG in which people might have made voluntary actions, but in fact did not. These epochs were an ideal dataset for searching for RP-like events. We analysed epochs where actions came at least 11 s after the

beginning of the trial, and took the final 10 s of these epochs. Due to the small and variable number of eligible trials per participant – mean number of voluntary skip actions >11 s = 23.5, SD = 7.9, range = [8, 33] – we pooled data across all participants.

2.2. EEG processing

EEG was recorded from 20 scalp electrodes (F3, Fz, F4, FC1, FCz, FC2, C3, C1, Cz, C2, C4, CP1, CPz, CP2, P3, Pz, P4, O1, Oz, and O2) using a BioSemi ActiveTwo system (BioSemi, 2011). Horizontal and vertical electro-oculogram (EOG) recordings were made using external bipolar channels positioned on the outer canthi of each eye as well as superior and inferior to the right eye. Reference electrodes were positioned on the mastoid bone behind the right and left ears. EEG signals were recorded at a sampling rate of 2048 Hz. A trigger channel was used to mark the time of important events on the signal. Data were preprocessed using the MNE package for python (Gramfort et al., 2013) and custom python and R

scripts. Signals were recorded at 2048 Hz, re-referenced to the average of the mastoid electrodes, subjected to low-pass (30 Hz), high-pass (0.1 Hz), and notch (50 Hz; line noise) filtering, and resampled to 256 Hz.

Epochs were extracted spanning from 11 s before to 0.5 s after voluntary and instructed skip actions on trials where these actions occurred after at least 11 s. Epochs containing extremely large artefacts (changes in voltage greater than 500 μ V) were discarded, before ICA was used to subtract ocular artefacts from the data. Following ICA, we excluded trials with peak-to-peak amplitudes greater than 150 μ V. Pooling across all participants, this pipeline produced 363 voluntary action epochs, and 398 instructed action epochs.

3. Results

3.1. EEG analysis

Fig. 2A shows the ERP for the 2 s prior to voluntary actions across all

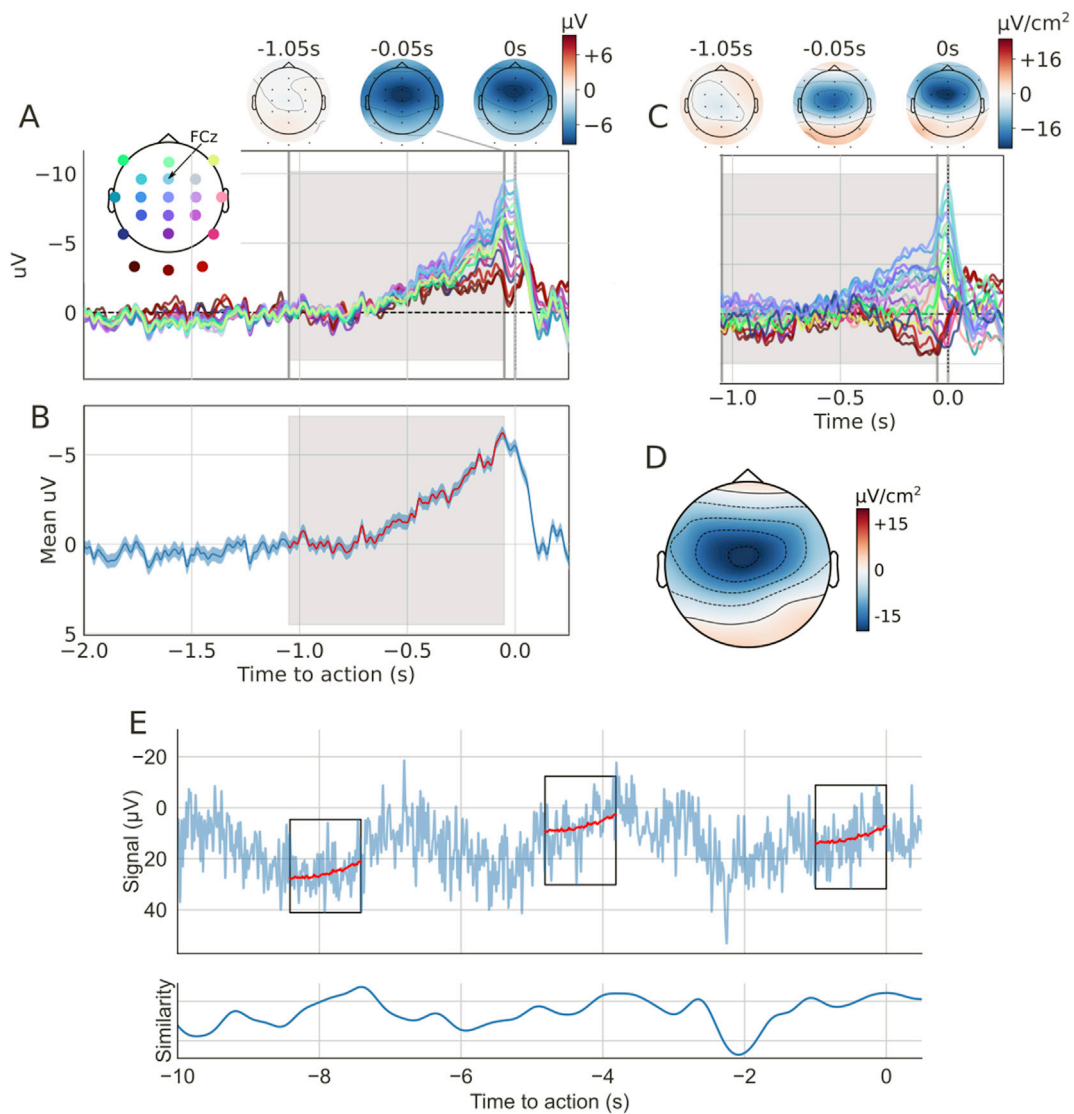


Fig. 2. **A.** EEG prior to voluntary actions, across 20 electrodes. We defined the shaded region [-1.05 s, -0.05 s] as the Readiness Potential (RP) window. **B.** Mean EEG signal across all 20 electrodes. We use this data as a prototype for the time course of the RP. **C.** Current source density transformation of the EEG, with volume conduction artefacts attenuated. The RP is confined to a smaller area of the scalp close to supplementary motor area. **D.** Voltage across the scalp at -0.05 s, the peak of the RP, after current source density transformation. We use this data as a prototype for the spatial properties of the RP. **E.** Procedure for matching temporal template to single-trial EEG. Inverse Euclidean distance between the template and the EEG was calculated over a 1-s sliding window. Top: raw EEG from a single trial. The template (red) is shown overlaid on windows where the match is strong. Bottom: similarity over time on this single trial in arbitrary units, where similarity at time t is calculated over the interval $(t - 1, t)$.

20 electrodes, referenced to the average of the mastoids. The negative ramp of the RP can be seen in the second prior to action across a broad range of electrodes centred on Fcz, a conventional site for RP recording. We defined the period from -1.05 to -0.05 s prior to action as the RP window, avoiding the final 50 ms prior to action which could contain components generated by the movement itself. This window was selected based on visual inspection of the data. The apparent onset of the RP is known to vary considerably between studies (Shibasaki and Hallett, 2006).

EEG from a single electrode, on a single trial, is noisy. For this reason, to capture the temporal profile of the RP we analyse the mean signal across all 20 electrodes over time. The unweighted mean signal was strongly correlated with both the raw signal from FCz, $r = 0.94$, and with a weighted mean based on the spatial pattern at the end of the RP window, $r = 0.99$. Importantly, the unweighted mean signal is a pure temporal measure, and does not encode any spatial properties of the RP. Almost identical results were obtained using the signal from FCz or the weighted mean based on the spatial pattern. Fig. 2B show the ERP derived from this mean signal. This provides an estimate of the RP's temporal profile. We used the 256 samples of this time series over the RP window (-1.05 to -0.05 s), mean-centred, as our temporal RP template. To estimate the temporal similarity of the single-trial EEG over time to

the RP, we calculated the Euclidean distance between the template and the mean signal on each trial in a sliding window, mean centred at each time-step. Similarity was defined as the inverse of the Euclidean distance. Each similarity metric was z-transformed to have a mean of 0 and a standard deviation of 1 across the whole dataset. We also low-pass filtered the similarity metric at 8 Hz for analysis. Fig. 2E illustrates how this metric is calculated for a single trial.

Fig. 2C–D shows the current source density (CSD) transformation of the same data, estimated by applying a surface Laplacian filter. This transformation attenuates the effect of volume conductance on the EEG signal. As a result, the RP component is more narrowly restricted to electrodes around Fcz. This captures our best estimate of the RP's spatial profile: a negative potential centred around FCz, giving way to positive voltages at more posterior sites. We used this pattern, over 20 electrodes, as our spatial template. To estimate the spatial similarity of the single-trial EEG over time to the RP we calculated the Euclidean distance between this template and the single-trial raw EEG at each time point.

Note that our two metrics capture distinct properties of the RP. The temporal metric uses the signal over time, averaging across channels. The spatial metric uses the CSD-transformed pattern over the scalp at a single moment in time. In other words, the temporal metric captures deflections across the scalp, regardless of their spatial distribution. The spatial metric

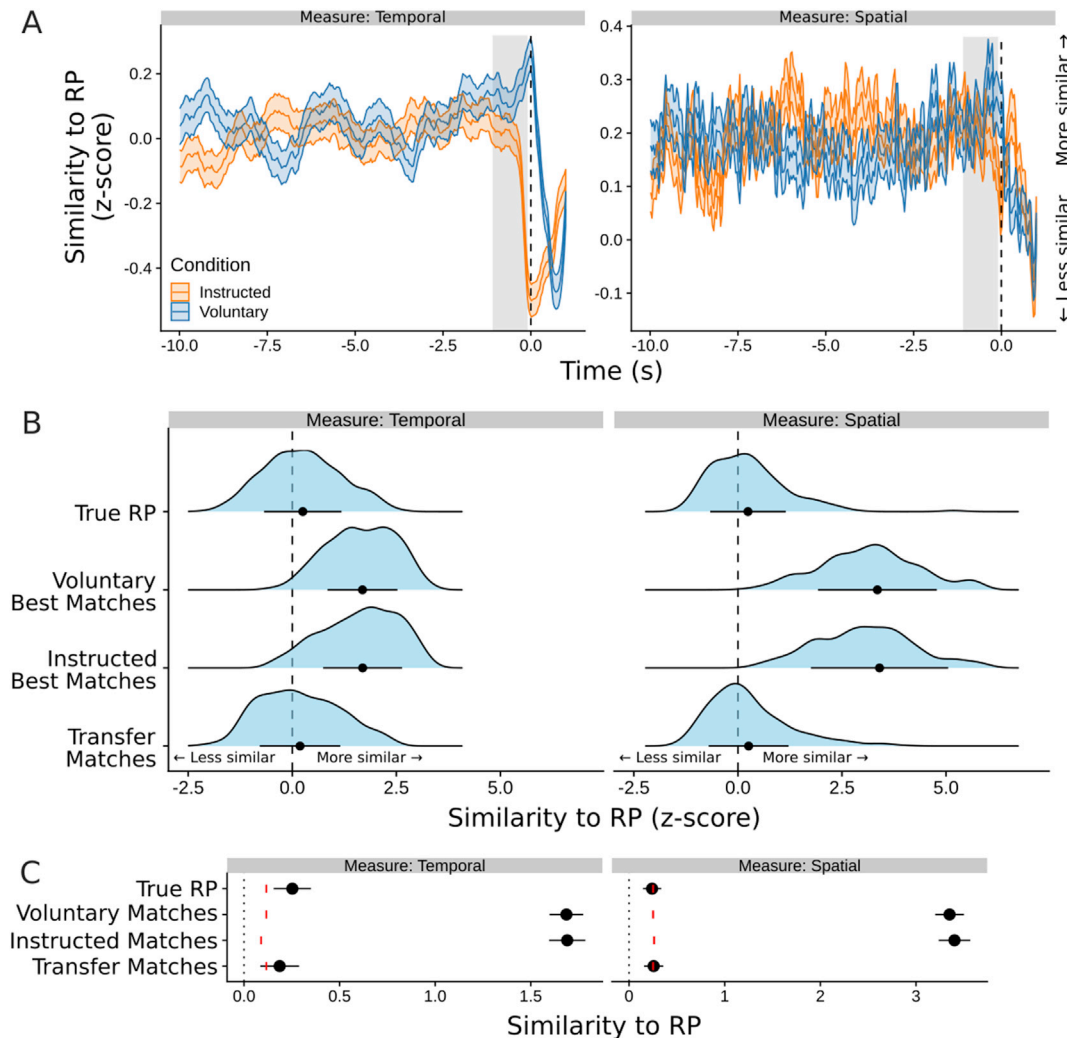


Fig. 3. Similarity of data to the RP template. **A.** Average similarity over time. Temporal similarity is calculated over a 1 s sliding window, and so is temporally smoother than spatial similarity. **B.** Distribution of similarity scores across epochs for the actual RP prior to actions – that is, the similarity of the template to the data used to generate it (top), best-matching windows from epochs in the voluntary and instructed conditions (middle), and similarity for each metric calculated at the maximal time windows for the other metric (bottom). Error bars show standard deviations. **C.** Mean and standard error for similarity scores, across trials. Red bars show 97.5 percentiles from the permutation distributions. Means greater than these values are significant at $p < .05$.

captures the spatial pattern at the end of a window, but is insensitive to how these patterns change over time. It is also worth noting that the temporal and spatial signatures of the RP do not emerge at the same time. The negative deflection across channels begins at approximately -0.8 s prior to action (Fig. 2B). However, signals from prefrontal (FCz) and occipital (Oz) sites begin to diverge later, from approximately -0.4 s (Fig. 2C).

Fig. 3 shows the average temporal (left) and spatial (right) similarity over time in each condition. For most time windows, we find no difference in average similarity to the RP between conditions. At the time of the RP itself, unsurprisingly, we find that epochs in the voluntary action condition – those used to produce the RP template – become more similar to this template, while those in the instructed action condition do not. This is particularly true of the temporal similarity measure. The decrease in similarity prior to instructed actions is due to the P300 response evoked by the onset of the cue to skip.

Next, for both metrics we selected the most RP-like window on each trial, excluding windows that overlap with the actual RP (Fig. 3B–C). We exclude this window in order to find only RP-like events that do not end with the initiation of an action. Note that by doing so we also avoid testing the template against the data that was used to generate it. These RP-like events were significantly more similar to the template than even the single-trial RPs themselves, in both the voluntary condition – temporal similarity $t(724) = 21.81$, $p < .001$, $BF_{10} > 4 \times 10^{77}$, spatial similarity $t(724) = 35.01$, $p < .001$, $BF_{10} > 5 \times 10^{153}$ – and the instructed condition – temporal similarity $t(759) = 21.10$, $p < .001$, $BF_{10} > 1 \times 10^{74}$, spatial similarity $t(759) = 35.32$, $p < .001$, $BF_{10} > 5 \times 10^{140}$. In the voluntary action condition, the most RP-like event was a better fit than the RP itself on that particular trial on 97.2% (temporal template) and 98.9% (spatial template) of trials.

According to the stochastic view of the RP, we should find events that are more similar to the RP in the voluntary action condition than in the instructed action condition. We quantify this by comparing the similarity score for the most similar window on each trial in the voluntary and instructed action epochs. Importantly, we found that these peak similarity scores did not differ between conditions; temporal: $t(759) = 0.06$, $p = .949$, $BF_{01} = 12.31$; spatial: $t(759) = 0.49$, $p = .647$, $BF_{01} = 11.13$.

Given that we find the same RP-like events in the instructed condition as in the voluntary action condition, we sought to better understand what these events represent. From each trial, we extracted the most RP-like event according to either the temporal or spatial similarity score, and

averaged across trials to produce *pseudo-Readiness Potentials*, maximally comparable to the event-related potential of the original RP. We repeated this procedure using a randomly-chosen window from each trial to create a baseline pseudo-RP.

Fig. 4A shows the time course of the RP and the generated pseudo-RPs. The pseudo-RP constructed from the best temporal matches successfully reproduces the time course of the true RP, and has lower variance across trials. The pseudo-RP constructed from the best spatial matches did not show a negative slope, and was indistinguishable from the baseline pseudo-RP. Fig. 4B shows the spatial distribution of the RP and pseudo-RPs. The pseudo-RP constructed from the best spatial matches qualitatively matches the true RP. However, the magnitude of the negative peak is more pronounced for the RP, $-19.8 \mu\text{V}/\text{cm}^2$ at FCz, than the pseudo-RP, $-9.5 \mu\text{V}/\text{cm}^2$ at Cz. The pseudo-RP constructed from the best temporal matches showed no clear components, and was also indistinguishable from the baseline pseudo-RP.

These findings indicate that the RP-like temporal and spatial events we find in our data are unrelated. Segments of the EEG that match the temporal pattern of the RP do not match its spatial profile. Similarly, segments that match the spatial profile do not match the temporal profile. We confirmed this by estimating the correlation between our metrics, and found that the two measures were extremely weakly correlated, $\rho = .07$ across the whole dataset, or mean $\rho = 0.01$ within trials. This makes it unlikely that the RP-like events retrieved by our data search are actually produced by the same mechanism as the true RP. This in turn is consistent with the classical view that RP like events happen only prior to voluntary actions, but not at other times.

3.2. Modelling

Given the presence of apparently RP-like temporal events in our EEG epochs independent of voluntary action, we next sought to test whether these results would be expected if our data consisted of only physiological noise. An affirmative result would indicate that the RP-like events we found may be a natural artefact of the background biological noise in EEG recordings, rather than the hallmark of any action-related neural process. Biological time series are characterised by $1/f^\alpha$ spectral scaling (Wagenmakers et al., 2004): the spectral power at each frequency band is inversely proportional to the frequency itself, $\text{Power} \propto 1/\text{Freq}^\alpha$, with the exponent ranging from $\alpha = 0$ (uncorrelated white noise), to $0 < \alpha < 2$ (pink noise), to $\alpha = 2$ (red or Brownian noise, reflecting a random walk or

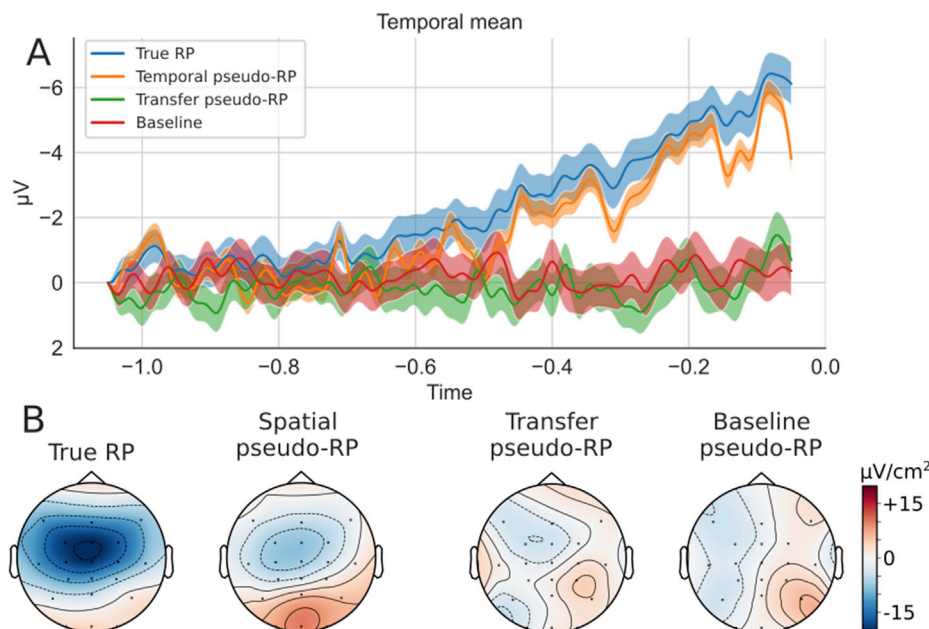


Fig. 4. Pseudo-Readiness Potentials, produced by averaging together putatively RP-like events. **A.** The true temporal RP, and temporal pseudo-RPs produced from the windows that best match the temporal template in the raw data, windows that best match the spatial template, and a baseline constructed by taking random windows on each trial. **B.** The true spatial RP, and spatial pseudo-RPs from the best spatial match, the best temporal match, and random baseline windows. Note **A.** shows raw voltages measured in μV , while **B.** shows CSD estimates measured in $\mu\text{V}/\text{cm}^2$.

diffusion process). α is therefore also proportional to the correlation between consecutive samples of the underlying process. The RP itself is a slow negative ramp, or a low-frequency oscillation in the frequency domain. As a result, RP-like events should be more easily found in signals with greater power at lower frequencies, i.e. $1/f^\alpha$ with a higher value of α (see Fig. 5A).

In our data, we found no differences between voluntary and instructed condition epochs at any frequency range. This provides further evidence that the EEG did not differ between conditions apart from in the moments just prior to action. In both conditions, the data showed $1/f^\alpha$ scaling with $\alpha \approx 1.17$ (Fig. 5B). As is typical of resting-state EEG, alpha-band power (8–12 Hz) was greater than would be expected in pure $1/f^\alpha$ noise. Note that this spectral profile is also ‘whiter’ (closer to $\alpha = 0$) than what would be produced by the accumulator model proposed by Schurger and colleagues. This is due to the presence of additional sources of physiological and electrical noise in the EEG, and to the application of an extremely mild high-pass filter to the data which reduces power at frequencies below 0.1 Hz.

To explore how $1/f^\alpha$ scaling relates to the presence of RP-like events in the EEG data, we simulated a series of datasets of $1/f^\alpha$ scaled noise, for values of α between 0 and 1.5, scaled the amplitude of the simulated data to match that of the EEG, and repeated our analysis on each of these artificial datasets using the same RP template as before. This confirmed that there is a positive monotonic relationship between α and the similarity of events in the data to the temporal RP. That is, as the power law exponent increases, and as the signal becomes dominated by low frequency components, finding a 1-s window displaying a negative drift becomes more probable (Fig. 5C). Importantly, at $\alpha = 1.17$, the scaling seen in our EEG data, the similarity of the RP-like events found in the simulated data matches that seen in the EEG. We conclude from these simulations that the RP-like events we find in our EEG data are completely consistent with what one would find when searching for matches to a template in sufficiently long series of autocorrelated $1/f^\alpha$ noise, and the strength of these events in our data is what would be expected in spectrally-matched noise.

4. Discussion

We found temporal and spatial events in raw EEG signals that resembled the average Readiness Potential, occurring long before any overt voluntary actions. However, these events do not support the hypothesis that Readiness Potentials happen in the absence of action, for two reasons. First, RP-like events were found to no greater extent in epochs leading up to voluntary actions than in epochs where voluntary responses were not permitted. Second, our two measures of similarity to the RP – temporal and spatial – were unrelated to each other. Indeed, the prevalence of temporal RP-like events in our data was no different from what would be expected in a dataset containing only physiologically-plausible noise with a similar spectral profile. We therefore conclude that these RP-like events are indeed false positives: sections of EEG that resemble aspects of the RP by chance, but are not produced by the same process.

The conventional view of the RP is that it represents a specific, causal precursor to voluntary actions that is produced after the unconscious decision to act has been made (Kornhuber and Deecke, 1965; Libet, 1985). Our results are entirely consistent with this view. The alternative is that RPs are stochastic fluctuations that happen to carry a neural signal across the action threshold (Schurger et al., 2012; Schurger, 2018). We noted above that in order for this to occur, the neural signal must be increased to a level close to the threshold. This in turn should make the signal more volatile, and so more likely to also produce RP-like events that do not cross threshold, at least according to a Poisson neural spiking model. We did not find evidence to support this prediction.

It could still be the case that the stochastic hypothesis is true, but that RP-like fluctuations occur equally in voluntary action contexts and in other contexts. For instance, we assumed that as the mean firing rate increases in the SMA neurons responsible for the RP, so does the variance over time. This is the case in individual neurons (Shadlen and Newsome, 1998), in many cortical circuits (Shadlen and Newsome, 1998; Churchland et al., 2011), and in psychophysics (Weber’s law). However, this property can be suppressed in more complex circuits, where recurrent feedback loops lead to non-linear attractor dynamics (Wang, 2008).

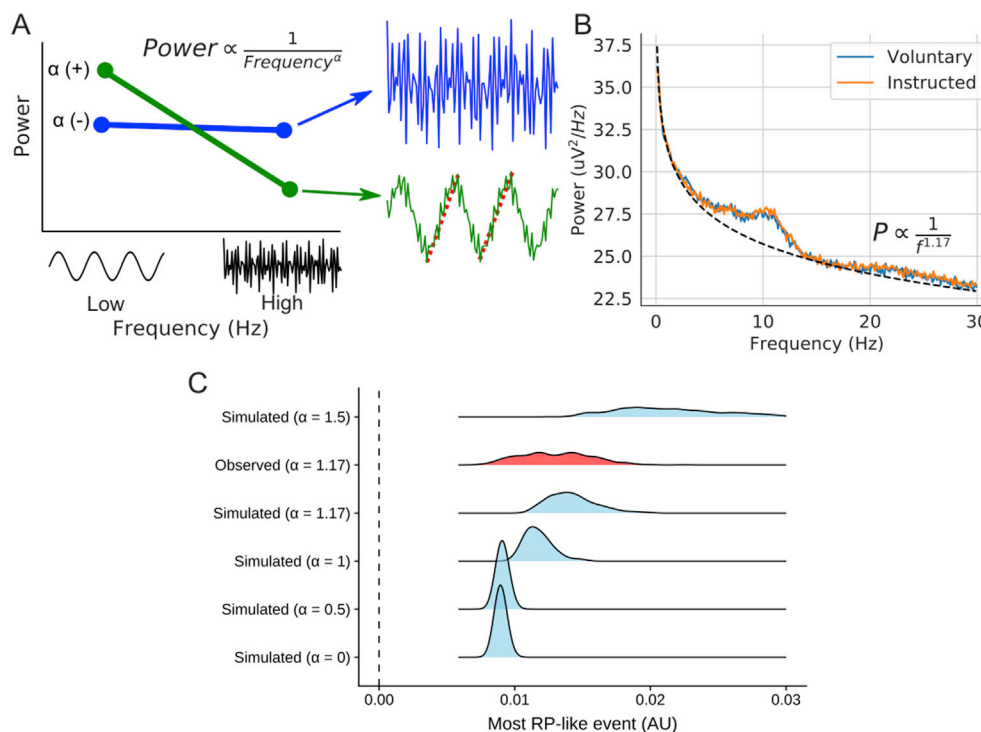


Fig. 5. A. RP-like events (red dashed lines) should be more pronounced when the EEG is dominated by low frequencies ($1/f^\alpha$ scaling with a high value of α , green) than when there is similar power in low and high frequencies (a low value of α , blue). B. Spectral profiles of EEG data in each condition. The EEG data show $1/f^\alpha$ scaling, with $\alpha \approx 1.17$ (dashed line) in both conditions. C. Similarity to the temporal RP template for the best-matching windows per trial, for simulated $1/f^\alpha$ noise (blue) and the observed EEG (red). Simulated noise with higher values of α produced RP-like events that better matched the RP template. The similarity of the RP-like events found in the EEG data matched that of those found in simulated noise with a matched spectral profile.

Further work is needed to resolve whether this is the case for the circuit that produces the RP.

Similarly, we assumed that the baseline level of the accumulator was greater in the voluntary action condition, where participants intended to act spontaneously, than in the instructed action condition, where they did not. This baseline shift explains how a stochastic accumulator model can successfully trigger actions when there is a general intention to act, but yet does not also produce occasional random actions at times when they would be inappropriate (Schurger et al., 2012). Another possibility, however, is that the mean level of the accumulator remains constant but the threshold for action is reduced in the voluntary action condition (see Bogacz et al., 2010; Forstmann et al., 2008). Many models of evidence accumulation struggle to distinguish baseline shifts from threshold shifts.

A third possibility is that stochastic fluctuations occur independent of context, and that they are necessary but not sufficient for voluntary actions to be produced. In cases where action is intended, there may be a functional link between these fluctuations and activity in the primary motor cortex and spinal cord. Otherwise, the fluctuations may occur but not trigger any downstream activity. In other words, volition creates the conditions under which ongoing neural fluctuations can trigger actions, or, equivalently, neural fluctuations provide occasional windows during which volition can trigger actions. This proposal is similar to the suggestion by Eccles, 1982, 1985: ubiquitous RP-like potentials are necessary but not sufficient to produce action at specific time points. Accumulator models (Schurger et al., 2012; Usher and McClelland, 2001; Bogacz et al., 2006) provide a way to formalise this idea. This model of course faces the same difficulty as classical models of RP, namely to provide a convincing account of what causes the volitional signal that makes action possible.

In a previous study, Schultze-Kraft and colleagues (Schultze-Kraft et al., 2016) trained real-time EEG classifiers to predict upcoming voluntary actions, based in part on the RP. If these classifiers can successfully use the RP to predict actions, without producing an excessive number of false alarms, it follows that the RP does not occur in the absence of action, consistent with our conclusions here. However, the appropriate evaluation measures (e.g. Weiss and Hirsh, 1998) are not reported in this work, making it difficult to draw such a conclusion.

Our task differs from typical RP studies in a number of ways (Khalighinejad et al., 2018, 2019). The RP was initially recorded in a task where participants are asked to press a button at a time of their own choosing, without any external stimulation (Kornhuber and Deecke, 1965). We instead elicited self-initiated actions during a task where there was a long and unpredictable waiting period at the start of each trial, during which participants saw dots moving randomly with 0% coherence. Each trial began once these dots began to move coherently in the same direction. Participants here produced self-initiated actions in order to skip the current trial, and begin the waiting period for the next trial, on the basis that they may not have to wait as long in the next trial. However, we have demonstrated on a number of occasions (Khalighinejad et al., 2018, 2019) that this task does produce the RP, and participants do not initiate actions inappropriately in the instructed action condition. It may be worthwhile to apply our analyses to EEG recorded during other voluntary action paradigms, bearing in mind that a sufficiently long epoch is required.

Finally, our conclusions are based on a null result: RP-like events were found to the same extent in epochs leading up to voluntary actions and in epochs where voluntary actions were not permitted. Bayesian analyses provided strong statistical evidence that the two conditions did not differ in this regard. However, we cannot rule out the possibility that there are naturally-occurring RP-like events that our EEG recordings failed to capture, or our analyses failed to detect. We might have failed to detect such RP-like events due to having an inappropriate template. For example, our template is based on the pooled true RP, which is necessarily followed by a voluntary action. We then used this template to search for RP-like events which were not related to voluntary actions. Thus, the presence of EEG activity linked strictly to action execution in

the template, but not in the sample, might potentially be relevant to our failure to find any RP-like events. However, we mitigated this risk by using a search template that excluded the final 50 ms prior to action, so action execution effects are unlikely to be responsible for any failed detections. Nevertheless, we cannot exclude the possibility that our methods failed, for some other reason, to detect RP-like events that were indeed present. We hope that the current results might stimulate further developments in this area.

Note

Data and analysis scripts associated with this manuscript can be found at in the accompanying Open Science Framework repository, at <https://osf.io/t2rv3/>.

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