

# **The Readiness Potential reflects internal source of actions, not decision uncertainty**

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## Abstract

Voluntary actions are preceded by the Readiness Potential (RP), a slow EEG component generated in supplementary motor area. The RP is usually thought to be specific to internally-driven decisions to act, and reflect post-decision motor preparation. Recent work suggests instead that it may reflect noise or conflict during the decision itself, with internally-driven decisions tending to be more random, more conflictual and thus more uncertain than externally-driven actions. To contrast accounts based on endogenicity with accounts based on uncertainty, we recorded EEG in a task where participants decided to act or withhold action to accept or reject gambles. We found no difference in an RP-related motor component when comparing actions driven by strong versus weak evidence, indicating that the RP does not reflect uncertainty. In contrast, the same RP-related component showed higher amplitudes actions performed without external evidence (*guesses*) than for those performed in response to equivocal, conflicting evidence. This supports the view that the RP reflects the internal generation of action, rather than decision uncertainty.

Key words: Voluntary action; Readiness Potential; Supplementary motor area.

# Introduction

Actions are voluntary if they are produced spontaneously, and not in response to an external trigger. Voluntary actions are preceded by the *Readiness Potential* (RP): a slow negative EEG component recorded over midline electrodes in the second or so prior to action, generated primarily by the Supplementary Motor Area (SMA; Kornhuber & Deecke, 1965; Shibasaki & Hallett, 2006). The RP can be seen prior to the time at which participants report being aware of a decision to move, raising questions about the role of conscious intentions in action (Libet, 1985). However, it is not yet clear what the RP reflects. One view, informed by neuroanatomical and neurophysiological accounts of the frontal cortex, is that there are two distinct neural pathways for action. The lateral pathway, for exogenous stimulus-driven actions, connects sensory regions to the primary motor cortex (M1) via the lateral premotor cortex. The medial pathway, for internally-generated endogenous actions, connects the prefrontal cortex to M1 via the medially-located SMA (Passingham, 1993; Passingham, Bengtsson, & Lau, 2010). This proposal is supported by functional neuroimaging results comparing simple self-initiated movements to externally-triggered movements, or to baseline (Frith, Friston, Liddle, & Frackowiak, 1991; Jahanshahi et al., 1995), and source localisation of the RP (Shibasaki & Hallett, 2006). There is also evidence from non-human primates that lesions to medial premotor pathways impair self-initiated actions while leaving responses to stimuli intact (Passingham, 1993; Thaler, Chen, Nixon, Stern, & Passingham, 1995). However, direct recordings from rodent motor regions suggest self-initiated actions require the same computations as externally-triggered actions, but at a slower timescale (Elsayed, Lara, Kaufman, Churchland, & Cunningham, 2016; Lara, Elsayed, Zimnik, Cunningham, & Churchland, 2018).

The alternative view is that the RP reflects uncertainty in the decision that leads to actions. Schurger, Sitt and Dehaene, (2012) showed that the RP could be produced by a noisy signal integration process when the input signal is weak. In such cases, random noise in the process eventually passes the threshold for action. When signals are averaged together, time locked to when the threshold is crossed, this model reproduces the slow ramping shape of the RP. Importantly, this model assumes decisions that are based on accumulation of *internal* noise, in the absence of external evidence.

Alternatively, Nachev and colleagues (Nachev, Rees, Parton, Kennard, & Husain, 2005; Nachev, Kennard, and Husain, 2008) propose that SMA plays a role in detecting conflict in decision-making, along with the neighbouring anterior cingulate cortex. They suggest that the SMA activity (and hence the RP) during voluntary action tasks is not due to the self-initiated nature of the movements, but can also occur for *external* stimuli. Instead, SMA is activated because the decision to act is under-determined by external stimuli in these tasks, leading to competition and conflict (Botvinick, Cohen, & Carter, 2004). Thus, the current literature suggests at least two possible explanations of the RP: the RP either reflects that an action is produced endogenously, or it reflects uncertainty and noise in the decision leading to action.

To test these competing theories, we recorded EEG as human participants decided to act or withhold action as part of a gambling task. We manipulated both the source of the information driving participants' decisions (endogenous or exogenous) and, for trials where exogenous information was presented, manipulated the strength of the evidence in favour of action (strong or weak), to produce decisions that were either certain or uncertain.

This approach differs from many previous voluntary action studies, where participants are merely asked to make an action at a time they themselves choose (Kornhuber & Deecke, 1965; Libet, 1985; but see Khalighinejad, Schurger, Desantis, Zmigrod, & Haggard, 2018). By embedding self-initiated actions in an economic decision-making paradigm, we provide a bridge between the study of voluntary action and that of decision-making and action more broadly.

## Materials and Methods

We presented participants with a gambling task, where they must either act or refrain from acting, in order to accept or decline a gamble (see Figure 1). On some trials, the gamble had clearly positive or negative expected value. In these cases, the decision to act or not act is driven by strong exogenous cues, and can be made with certainty. We will call these trials *easy decisions*. In other trials, the gamble had an expected value close to 0. In these cases, the decision whether or not to act is still based on exogenous cues, but these cues provide only weak evidence, and the decision is made under high uncertainty. We will call these trials *difficult decisions*.

On a further subset of trials, participants did not see the gamble until after they had made a decision. Participants were instead told that half of these trials would be ‘good’ and half ‘bad’. They were further instructed that the average expected value across these hidden gambles was 0, so that on average one would break even from accepting these gambles. We will call these *guesses*. These trials are similar to standard non-guess trials with expected values close to 0. However, in the former case, participants must still weigh up the on-screen evidence in order to decide whether to act. In the current case, no such evidence is present, and participants know from the offset that they must decide endogenously whether to act.

Easy and difficult decisions here correspond to what philosophical terminology refers to as ‘choosing’ (deciding by considering reasons and evidence) and ‘picking’ (deciding even though the evidence is equivocal, e.g. between two identical options) respectively (Ullmann-Margalit & Morgenbesser, 1977). Our guess trials are also a case of picking, but decisions in this condition are based on an explicit instruction to generate action/non-action decisions internally, rather than equivocal external stimuli.

Our three conditions – easy decisions, difficult decisions, and guesses, thus differ along two dimensions (Table 1). First, they differ in the source, exogenous or endogenous, of the evidence that goes into the decision. If the RP reflects the activation of the medial endogenous action pathway (Passingham, 1993), we should see a stronger RP signal on guessing trials than for either easy or difficult decisions. Second, our conditions differ in the strength of evidence, and thus the certainty of the decision. If the RP reflects decision uncertainty, we should see a stronger RP for the difficult decisions (expected value close to 0) than the easy decisions (expected value far from 0).

Evidence source	Evidence strength	
	Weak	Strong
Exogenous	Easy decision	Difficult decisions
Endogenous	Guesses	-

Table 1. Different types of action classified in terms of evidence source, and evidence strength.

## Participants

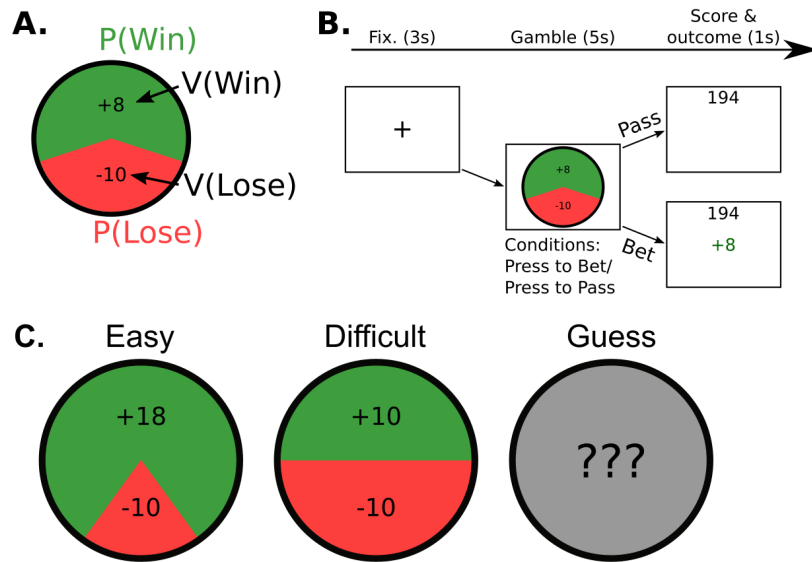
Twenty participants (7 males, mean age = 25.5, SD = 4.7) completed the experiment, and were compensated £7.50 per hour for participation. The experiment lasted approximately 40 minutes. All procedures were approved by the UCL ICN ethics committee. This sample size was selected to match previous RP studies (Khalighinejad, Brann, Dorgham, & Haggard, 2019; Khalighinejad et al., 2018).

## Stimuli and Procedure

Participants were presented with 300 gambles, comprised of certain decisions, uncertain decisions, and guesses. For standard trials, the probability of winning or losing,  $P(\text{Win})$  and  $P(\text{Loss})$ , and the amount (value) that could be won or lost,  $V(\text{Win})$  and  $V(\text{Loss})$ , were represented by a roulette-style wheel (Figure 1).  $P(\text{Win})$  and  $P(\text{Loss})$  were indicated by the size of the segments filled in green or red, respectively, while the amount that could be won or lost was shown numerically in each segment. The probability of winning varied from 20% to 80%, in 10% increments. The winning amount varied from +2 to +18 points in 2 point increments, while the losing amount was fixed at -10 points. The full set of probability/value combinations are shown in Figure S1, along with the expected value of each, calculated as  $P(\text{Win}) \times V(\text{Win}) - P(\text{Loss}) \times V(\text{Loss})$ . The average expected value across all bets was  $\pm 0$ . Gambles with an expected value of close to 0 were presented more often than those with extreme high or low values (see Figure S1).

Eighty-eight gambles out of the 300 were designated as guess trials. The gamble wheel on these trials was replaced by a grey circle, with text reading “???” inside (Figure 1). Participants were told that on these trials they would not see what the gamble was, but should guess ‘at random’ whether or not they wanted to take it. They were additionally told “On average, half of the guess gambles will be good, and half will be bad, so it’s totally up to you whether or not you want to take the risk on each one”.

After viewing each gamble, participants indicated whether they wanted to accept or reject it. In an *act-to-bet* condition, they pressed the spacebar within 5 seconds to accept the gamble, or withheld any action to reject it – thus, rejection was the default. In an *act-to-pass* condition, they pressed the spacebar to reject the gamble and withheld action to accept it – acceptance was the default. Thus, across conditions, we could dissociate making a motor action from the expected value of gambles. After accepted gambles, participants saw outcome feedback showing the number of points that had been won or lost, in green or red font respectively, along with their cumulative points total, for 1 s. After rejected gambles, participants saw only their cumulative total for 1 s before proceeding to the next gamble.



*Figure 1. Stimuli and procedure. A. Gambles were presented visually in the form of a roulette wheel. The green and red areas indicate the probability of winning and losing respectively. Digits indicate the points that could be won or lost. B. Each gamble was presented for 5 s. Participants either pressed the spacebar in this time to accept the gamble or to reject it, depending on the condition. C. Three types of gamble. Easy decisions had clearly positive or negative expected values. Difficult decisions had expected values close to 0. For Guesses, the expected value on each particular trial was unknown.*

Participants completed two practice blocks of 10 gambles each, one in each condition. In the experiment itself, participants completed four blocks of 75 gambles each. Response conditions alternated between blocks, and the first block (act-to-bet or act-to-pass was counterbalanced). For each participant, the same set of gambles were presented in blocks 1 and 2 and, again in blocks 3 and 4, in random order.

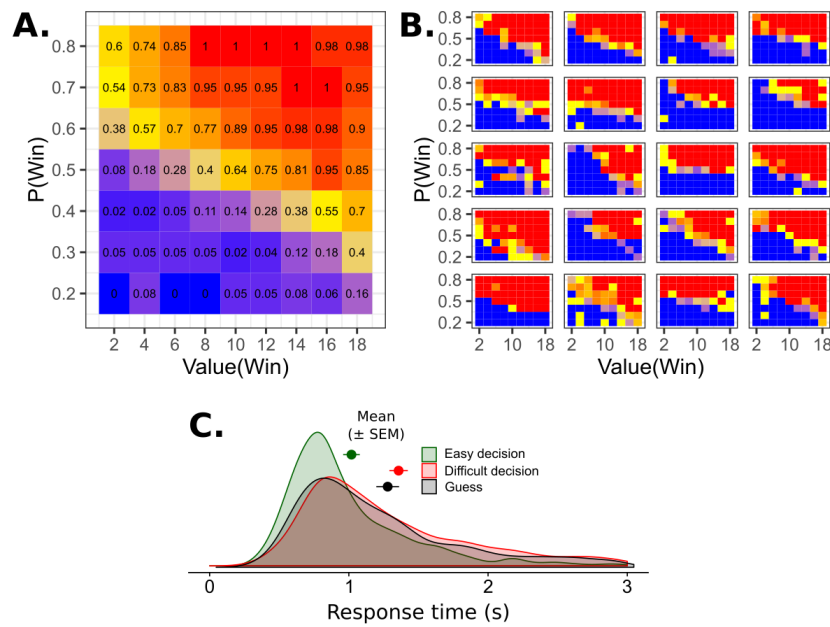
## Results

### Behavioural Results

We first examined participants' responses by fitting multilevel logistic regression models, with all parameters allowed to vary by participant. On standard trials, participants were unsurprisingly more likely to accept gambles with higher  $P(\text{Win})$ ,  $b = 4.03$ ,  $SE = 0.31$ ,  $z = 12.933$ ,  $p < .001$ , and higher  $V(\text{Win})$ ,  $b = 1.80$ ,  $SE = 0.16$ ,  $z = 11.400$ ,  $p < .001$  (Figure 2A). The influence of  $V(\text{Win})$  was greater for higher values of  $P(\text{Win})$ , interaction  $b = 0.61$ ,  $SE = 0.08$ ,  $z = 7.630$ ,  $p < .001$ . We found that participants' responses were better fit by a four-parameter model, [ $P(\text{Win})$ ,  $V(\text{Win})$ , their interaction, and an intercept term;  $AIC = 2797$ ,  $BIC = 2860$ ] than by two- (intercept and expected value;  $AIC = 3089$ ,  $BIC = 3121$ ) or one-parameter (expected value only;  $AIC = 3092$ ,  $BIC = 3117$ ) models. This indicates that participants relied on a heuristic weighted combination of each gambles attributes, and not the optimal decision-theoretic combination (see Supplementary Results for full model comparison; see also Rouault, Drugowitsch, & Koechlin, 2019). Participants were slightly more likely to gamble in the act-to-bet condition (51.8%) than the act-to-pass condition (47.4%),  $b = 0.50$ ,  $SE = 0.10$ ,  $z = 5.060$ ,  $p < .001$ .

For each participant, we sought to identify the standard, non-guess trials that were sometimes accepted, and sometimes rejected (Figure 2B). We fit logistic regression models to each participant's responses in order to estimate the probability,  $P(\text{Bet})$  of each gamble being accepted by that participant, and transformed this quantity to obtain the probability of the participant acting on each particular trial,  $P(\text{Act}) = P(\text{Bet})$  in the act-to-bet condition, and  $1 - P(\text{Bet})$  in the act-to-pass condition. We use this variable as a predictor in our EEG analyses, below. We identified the 50% of gambles closest to the point of indifference, where  $P(\text{Bet}) = .5$ , for each participant, and coded these as difficult decisions for that participant. We coded the remainder as easy decisions. This method takes into account how each participant weighted  $P(\text{Win})$  and  $V(\text{Win})$ . Finally, in guessing trials, participants chose to bet on 49% of act-to-bet trials,  $SD = 30\%$ , and on 46% of act-to-pass trials,  $SD = 26\%$ ,  $t(19) = 0.702$ ,  $p = .491$ .

Response times (RTs) followed a shifted log-normal distribution, consistent with an accumulation-to-threshold decision process (Figure 2C). There were very few RTs close to the 5 s limit, indicating that participants decided relatively early after stimulus presentation whether or not to act. Response times for certain decisions (1.02 s,  $SD = 0.27$  s) were significantly faster than those for uncertain decisions (1.35 s,  $SD = 0.30$  s),  $t(19) = 8.991$ ,  $p < .001$ , or guesses (1.28 s,  $SD = 0.37$  s),  $t(19) = 4.307$ ,  $p < .001$ . Importantly, response times for uncertain decisions and guesses did not differ significantly,  $t(19) = 1.418$ ,  $p = .172$ .

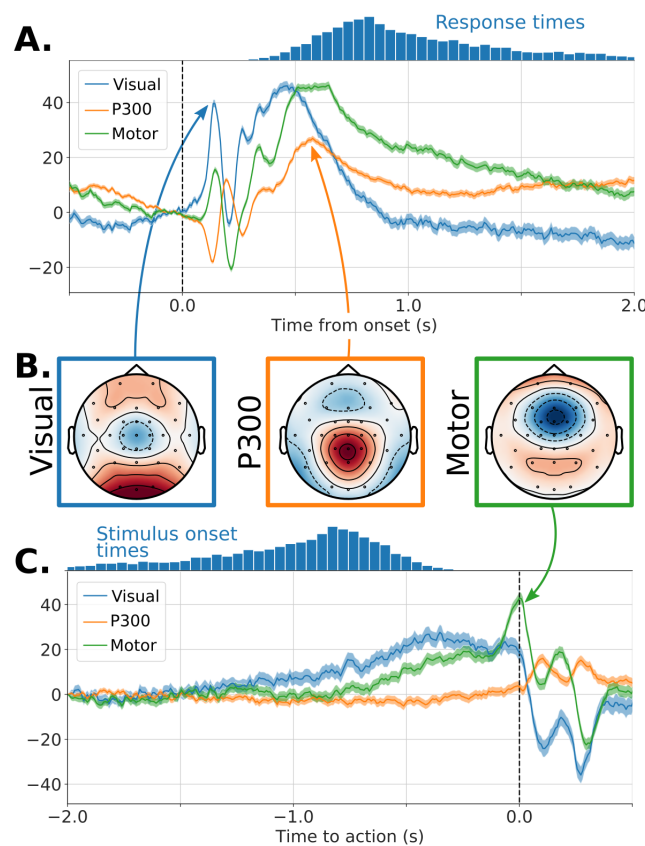


*Figure 2. Participants' decisions and response times. A. The probability of participants accepting each gamble,  $P(\text{Bet})$ , as a function of the number of points that could be won,  $V(\text{Win})$ , and the probability of winning,  $P(\text{Win})$ . B. Choices for individual participants. Each participant was influenced by both  $V(\text{Win})$  and  $P(\text{Win})$ . C. Response times for easy decisions, difficult decisions, and guesses. Participants were significantly faster to produce actions for easy decisions than difficult decisions or guesses. Response times for difficult decisions and guesses did not differ.*

## EEG Acquisition

EEG was recorded using 32 + 6 channel BioSemi ActiveTwo system. We placed two reference electrodes on the mastoids, and monitored eye movements and blinks using electrodes placed on the outer canthi of each eye and above and below the right eye. During recording, EEG data were referenced to CMS-DRL, and offsets were maintained  $<30 \mu\text{V}$ . Data were recorded at 1024 Hz.

Data were processed and analysed offline using custom python scripts and the MNE package (Gramfort et al., 2013). All channels were re-referenced to the average of the two mastoids. EEG segments with clear movement artefacts were removed prior to processing. We applied high pass (cut-off 0.05 Hz, width 0.1Hz) and low pass (cut-off 50 Hz, width 12.5 Hz) FIR filters, and a notch filter at 50 Hz to the raw data, and resampled to 125 Hz. ICA was used to identify and remove artefacts due to eye movements and blinks (Makeig, Bell, Jung, & Sejnowski, 1996).



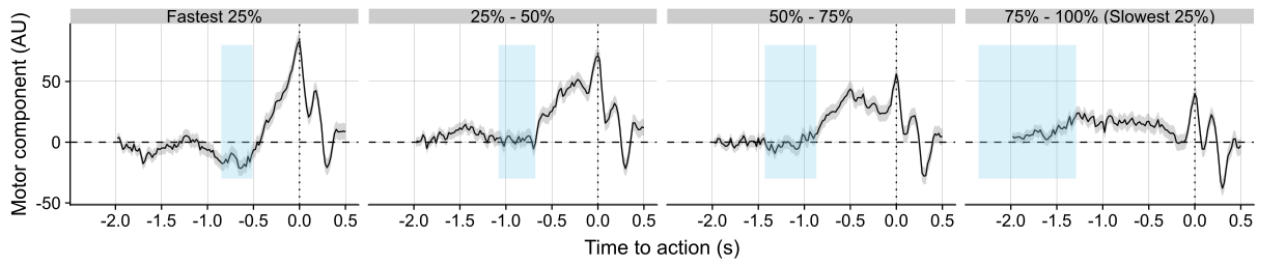
*Figure 3. Time course and topography of the visual, CPP, and motor components extracted by varimax PCA. A. Time course locked to stimulus onset. B. Spatial topography. C. Time course locked to the time of action.*

On 96.4% of trials where responses occurred, they took place within 3 s of stimulus onset. Trials with slower response times than this were excluded from the analysis. Stimulus-locked epochs were extracted from -0.5 s to +2 s relative to the onset of the gamble stimulus, and baselined between -0.1 and 0 s. Response-locked epochs were extracted from -2 s to +0.5 s relative to the response time on trials where participants pressed the response button, and baselined between -2.1 s and -2 s prior to action. We excluded all epochs where voltages from any electrode exceeded  $\pm 120 \mu\text{V}$  from baseline. 7.7% of stimulus-locked epochs and 5.0% of response-locked were excluded in total.

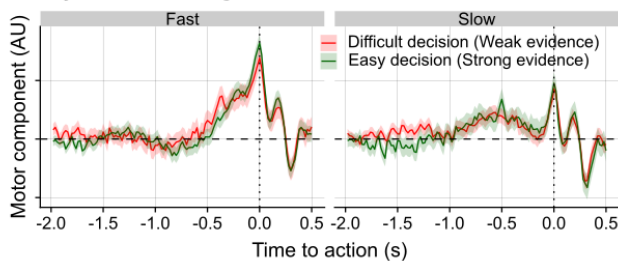
To isolate EEG components corresponding to motor preparation and execution, we followed the procedure proposed by Kayser and Tenke (2006). We first estimated current source density (CSD) from the EEG using the surface Laplacian algorithm provided by Cohen (2014). We set the Laplacian smoothing parameter to  $m = 5$ . We conducted Principal Components Analysis on the CSD data, pooling across participants, using the data between -1 s and 0 s prior to action on trials where an action was produced. We retained 9 components for varimax rotation with eigenvalues greater than 1 (Figure S2). Consistent rotations were obtained by retaining as few as three components.

After rotation, the three components shown in Figure 3 satisfied both a criterion of importance (i.e., variance explained) and interpretability (i.e., spatiotemporal pattern consistent with established neurophysiological studies). These capture early visual processing, the centro-parietal positivity response (CPP, also known as the P300, see O'Connell, Dockree, & Kelly, 2012), and a negative motor component centred around electrode FCz. These components explained 18%, 14%, and 14% respectively of the variance in the response-locked EEG between -2 s and 0 s prior to action. Plots of the time course of all components with eigenvalues greater than 1, as well as the corresponding rotated components, can be found in Supplementary Materials. In our analysis we focus on the negative motor preparation component, which we take to be analogous to the RP recorded prior to purely self-initiated actions.

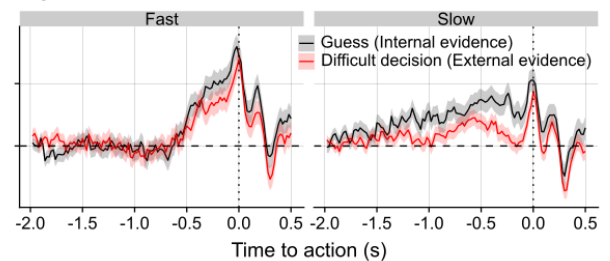
#### A. By RT quartile



#### B. By RT x Strength of Evidence



#### C. By RT x Source of evidence



**Figure 4. Action-locked event-related potentials.** **A.** The shape of the action-locked motor component varied with response times. In trials with rapid responses, the ERP overlaps with stimulus-evoked activity, and produces a sharper ramp prior to action. Blue regions show mean  $\pm 1$  SD stimulus onset times within each quartile. **B.** Decision evidence strength did not affect the shape of the action-locked ERP after controlling for differences in response speed. **C.** Endogenously-produced actions on guess trials produced greater RP-like motor potentials than exogenously-produced actions on hard decision trials. This was particularly the case for slower responses.



## EEG Results

First, we observed that the shape of the response-locked motor preparation component depends on the response time on each trial (Figure 4A). This is caused by the initial stimulus-evoked activity which peaks approximately 500-600 ms after stimulus onset (Figure 4A), shortly after the peak of the P300 response. This peak is present even on trials where no action was executed, and occurs well before the average RT on trials where action did take place (see Figure S4). This indicates that this activity is not due to actual motor execution. To explore the influence of this activity on our response-locked analyses, we plotted the motor component, locked to the time of action, separately across quartiles of the RT distribution. The signal over the 100 ms prior to action is consistent across RT quartiles. Prior to this time, the shape of the motor preparation component depends on RT. On trials with rapid responses, the motor component ramps up from stimulus onset to the time of action (Figure 4A). On trials with slower responses, early motor component activity peaks and begins to decline before the moment-related activity begins.

Based on this strong relation between response speed and neural activity, we included RT as a covariate in analyses of the motor component. To do this, we modelled the activation of the motor component over time in the window from 2 s to 0.1 s prior to action using a hierarchical generalised additive model. We used a cubic splines basis matrix to capture the non-linear shape of the ERP over time (Hastie, Tibshirani, & Friedman, 2001). Based on BIC model comparison, we used regression splines with 5 knots. Interactions between all predictors and the basis matrix were included to capture the change in the ERP over time due to each predictor. For each predictor, the null hypothesis is that the shape of the ERP over time is unaffected by changes in the predictor. We test these null hypotheses using type II Wald  $\chi^2$  tests, comparing the fit of models with and without these time  $\times$  predictor interactions. This test is analogous to classical ANOVA.

Our first goal was to test whether the motor preparation component is greater for uncertain decisions than certain decisions (Nachev et al., 2008; Schurger et al., 2012). We tested this by fitting a model to actions from certain and uncertain decisions, including  $P(\text{Act})$ , varying from around 0.5 (high uncertainty) to 1.0 (low uncertainty) as a predictor. We also included response speed (inverse response times) and trial number as covariates. All predictors were z-transformed to obtain standardised regression weights. Mean ERPs for this test are shown in Figure 4B, with trials split into weak or strong evidence conditions for visualisation. We found statistically significant effects of response speed,  $\chi^2(5) = 188.8$ ,  $p < .001$ , and trial number,  $\chi^2(5) = 18.2$ ,  $p = .003$ . However, we found no significant effect of  $P(\text{Act})$ ,  $\chi^2(5) = 6.5$ ,  $p = .263$ . There was a significant  $P(\text{Act}) \times$  response speed interaction,  $\chi^2(5) = 42.6$ ,  $p < .001$ . This reflected the slightly higher activation approximately 1.4 s prior to action on trials with slower RTs. This effect is only transient, and is eliminated by -1 s prior to action, indicating that it is unrelated to motor preparation. Therefore, we conclude that evidence strength does appreciably not affect the shape of the motor preparation component once differences in RT between trials have been controlled for.

Our second goal was to test whether the motor preparation component is greater for actions based on endogenous evidence (guess trials) than actions based on uncertain exogenous evidence (uncertain decisions). Recall that in both contexts participants' sometimes decided to act, and sometimes to withhold action. In addition, response times did not differ significantly between the two conditions. However, participants must consider external evidence for uncertain decisions, but

not when guessing. If the RP reflects decisions that are due to endogenous rather than exogenous evidence, we would expect to see a greater motor component activity in guessing than in picking. Mean ERPs for this test are shown in Figure 4C. We again found a statistically significant effect of response speed,  $\chi^2(5) = 161.40$ ,  $p < .001$ . The effect of trial number was not significant,  $\chi^2(5) = 5.26$ ,  $p = .385$ . Crucially, we also found a significant main effect of context,  $\chi^2(5) = 21.13$ ,  $p < .001$ . In line with our predictions, the amplitude of motor preparation component was greater for guesses than for uncertain decisions. There was also a context  $\times$  response speed interaction,  $\chi^2(6) = 41.2$ ,  $p < .001$ . This reflects that the difference between contexts can be seen throughout the ERP on trials with slow RTs, but only at times closer to the action for trials with faster RTs (e.g. only after the onset of the stimuli). Therefore, we conclude that the shape of the motor preparation component is affected by the source of decision evidence, even when controlling for RT.

## Discussion

We sought to test whether the RP typically seen prior to voluntary actions reflects the fact that these actions are endogenously generated (Passingham, 1993; Passingham et al., 2010) or the fact that they are driven by noisy decision processes with high uncertainty (Nachev et al, 2005; 2008; Schurger et al., 2012). Behavioural paradigms used to study the RP typically have no external triggering stimuli, and instead rely on a contextual instruction to “move when you feel like it”. This has made it difficult to manipulate under experimental control the conditions under which voluntary action decisions are made. Here we use a novel combination of external stimuli from the established value-based decision-making field, and EEG filtering to extract RP-related signals under well-controlled conditions design to test contrast theoretical explanations of the causes of RP. Using a go/no-go gambling task and EEG filtering, we were indeed able to isolate a negative motor preparation component that resembled the classical RP. We found that this component was more prominent prior to internally-generated actions than prior to actions driven by external evidence. This is consistent with the proposal that the RP reflects internal generation of action. We found no clear difference between actions driven by strong and weak external evidence once differences in RT were controlled for. This is inconsistent with the idea that the RP reflects noise or uncertainty in decision-making.

The RP is often thought to be specific to ‘voluntary’ actions. However, it is often unclear just what is meant by a ‘voluntary action’ Fried, Haggard, He, and Schurger (2017) set out a number of key features of volition, which are useful in making sense of our results. One feature of voluntary actions is that they occur without an external trigger. In our task, every trial includes some external stimulus as participants must respond to the gamble presented. On standard trials, the stimulus both indicates that a decision must be taken (act or don’t act, bet or don’t bet) and provides the information to drive that decision: P(Win) and V(Win). On guess trials, the stimulus only indicates a decision must be taken. The information that drives the decision must be recalled from memory. On this account, actions on guess trials are more voluntary than those on standard trials, although less voluntary than completely self-paced actions (e.g. Libet, 1985). Since the RP-like motor component occurred more clearly on guess trials than on trials with external evidence, we conclude that the RP is a feature of internally triggered actions.

Some theories of volition emphasise the spontaneous or innovative character of voluntary actions: a voluntary action is often not predictable from the current context. This feature is consistent with the idea that voluntary actions are triggered by random fluctuations in the brain (Schurger et al., 2012),

and the proposal that voluntary actions preferentially involve medial frontal cortex and produce the RP, because they involve cognitive conflict (Nachev et al., 2008). In our design, both guess trials and difficult standard trials were voluntary in this sense. In both cases, when presented with a single stimulus participants sometimes chose to bet, and sometimes chose to pass; they were somewhat random or unpredictable. Response times were also slower than for easy standard trials, indicating cognitive conflict. Following this logic, actions based on difficult decisions are more voluntary – less predictable, involve more conflict – than those based on easy decisions. This is consistent with another proposed feature of volition: an action is voluntary if the actor “could have done otherwise” (e.g. Frankfurt, 1969). Importantly, we found that the more spontaneous actions in our difficult condition did not show a stronger RP-related motor component than the less spontaneous actions in our easy condition, once response times were controlled for. In contrast, we found strong differences between difficult decisions and guess trials, despite these actions being relatively spontaneous. On these grounds, we conclude that the RP is not a reliable marker of spontaneity or unpredictability of action decisions. A possible concern is that participants may not make an independent decision on each trial. Instead, participants might establish a simple decision rule, for instance to bet on all trials where  $P(\text{Win}) > 0.5$ . There are a number of reasons why this seems unlikely. First, participants are slower to respond difficult trials than easy trials. This would not be the case if participants followed a simple perceptual decision rule. Second, all participants responded inconsistently to at least some range of the probability/value space (i.e., the yellow regions in Figure 3B). Third, the responses of participants using a simple decision rule would be predicted by  $P(\text{Win})$  or  $V(\text{Win})$  only. We instead found that participants’ responses were influenced by  $P(\text{Win})$ ,  $V(\text{Win})$ , and their interaction, and were broadly consistent with the expected value of the gambles shown. We conclude from these that participants made up their mind about each standard gamble on a trial-by-trial basis.

Similarly, participants might decide in advance whether to bet or not on the guess trials. We found that participants on average bet on roughly half of these trials, and 18/20 participants bet on between 15% and 85% of the 88 guess trials. The remaining four participants, who bet on 3, 4, 11, and 86 of the 88 guess trials, may have decided in advance how to respond when the guess prompt was presented, and so would not be producing internally-generated actions on these trials. However, our results were unchanged when these participants were excluded. In fact, we would expect that including these participants should make us less likely to find a difference between guess trials and difficult decisions.

In this work, we report a number of methodological improvements which are likely to be of use in future studies of voluntary action. To isolate EEG signals related to motor preparation from those elicited by the visual stimuli, we used a combination of surface Laplacian filtering and principle components analysis. While similar methods have been used in previous work (Kayser & Tenke, 2006) to our knowledge this is the first application of these methods to extract a Readiness Potential from trials where external stimuli are also presented. Deconstruction of EEG to extract a response-related component when stimulus-related components are also present is consistent with the recent finding that preparatory signals are essentially in form for internally-generated and externally-triggered situations, though differing in accumulation rate (Elsayed et al, 2016; Lara et al, 2018). Further details are provided in the Supplementary Materials, and in the analysis code provided with this manuscript.

To model the shape of the motor component over time, we used hierarchical generalised additive models. These models are widely used to analyse non-linear time series in other domains, particularly in ecology (Pedersen, Miller, Simpson, & Ross, 2019), but to date have rarely been applied to neural time series. This technique is particularly useful for modelling slow, smooth components such as the RP and contingent negative variation. It is somewhat less suited to modelling fast, non-linear components such as N1-P2, where a large number of basis functions are needed to capture the shape of the waveform. We plan to expand on this method in future work.

These models allowed us to control for response times in our analyses of the motor component. Differences in action latencies are a crucial but often overlooked confound in RP studies. It is well documented that the amplitude of the RP increases as participants wait longer before acting (Khalighinejad, Brann, Dorgham, & Haggard, 2019; Schurger, 2018; Verleger, Haake, Baur, & Śmigasiewicz, 2016). As a result, differences in RP amplitude between conditions are not interpretable unless differences in action latencies are controlled for, statistically or experimentally. This is a particular issue when trials begin with the presentation of a visual stimulus, as in this study, and others (Maoz, Yaffe, Koch, & Mudrik, 2017). Unless perceptual and motor EEG components can be perfectly dissociated, apparent differences in the shape of the motor component may be artefacts caused by the onset or offset of visual components.

Finally, there is an important distinction between the RP and the lateralised readiness potential (LRP; Haggard & Eimer, 1999). The LRP is generated by the primary motor cortex contralateral to the hand used to act. While the RP reflects readiness to act in general, the LRP reflects preparation of a specific action. In the current experiment participants responded only with the right hand. As a result, it is not possible to isolate the LRP from the motor preparation in general. It is likely that the later stages of our motor preparation component actually capture the LRP (Shibasaki & Hallett, 2006). Future work might test how our findings generalise to cases where participants must decide between two actions, or between inaction and two possible actions. Such a design would make it possible to disentangle readiness to act, conflict between competing actions, and internal and external sources of information.

## References

- Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, 8(12), 539–546. <https://doi.org/10.1016/j.tics.2004.10.003>
- Brass, M., & Haggard, P. (2008). The What, When, Whether Model of Intentional Action. *The Neuroscientist*, 14(4), 319–325. <https://doi.org/10.1177/1073858408317417>
- Cohen, M. X. (2014). *Analyzing neural time series data: Theory and practice*. MIT press.
- Elsayed, G. F., Lara, A. H., Kaufman, M. T., Churchland, M. M., & Cunningham, J. P. (2016). Reorganization between preparatory and movement population responses in motor cortex. *Nature Communications*, 7, 13239. <https://doi.org/10.1038/ncomms13239>
- Frankfurt, H. G. (1969). Alternate Possibilities and Moral Responsibility. *The Journal of Philosophy*, 66(23), 829–839. <https://doi.org/10.2307/2023833>
- Frith, C. D., Friston, K., Liddle, P. F., & Frackowiak, R. S. (1991). Willed action and the prefrontal cortex in man: A study with PET. *Proceedings. Biological Sciences*, 244(1311), 241–246. <https://doi.org/10.1098/rspb.1991.0077>
- Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., ... Hämäläinen, M. (2013). MEG and EEG data analysis with MNE-Python. *Frontiers in Neuroscience*, 7. <https://doi.org/10.3389/fnins.2013.00267>
- Haggard, P., & Eimer, M. (1999). On the relation between brain potentials and the awareness of voluntary movements. *Experimental Brain Research*, 126(1), 128–133. <https://doi.org/10.1007/s002210050722>
- Haggard, Patrick. (2019). The Neurocognitive Bases of Human Volition. *Annual Review of Psychology*, 70(1), 9–28. <https://doi.org/10.1146/annurev-psych-010418-103348>
- Hastie, T., Tibshirani, R., & Friedman, J. H. (2001). *The Elements of Statistical Learning: Data Mining, Inference, and Prediction*. Springer Science & Business Media.
- Jahanshahi, M., Jenkins, I. H., Brown, R. G., Marsden, C. D., Passingham, R. E., & Brooks, D. J. (1995). Self-initiated versus externally triggered movements. I. An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. *Brain: A Journal of Neurology*, 118 ( Pt 4), 913–933.
- Kayser, J., & Tenke, C. E. (2006). Principal components analysis of Laplacian waveforms as a generic method for identifying ERP generator patterns: I. Evaluation with auditory oddball tasks. *Clinical Neurophysiology*, 117(2), 348–368. <https://doi.org/10.1016/j.clinph.2005.08.034>
- Khalighinejad, N., Brann, E., Dorgham, A., & Haggard, P. (2019). Dissociating Cognitive and Motoric Precursors of Human Self-Initiated Action. *Journal of Cognitive Neuroscience*, 1–14. [https://doi.org/10.1162/jocn\\_a\\_01380](https://doi.org/10.1162/jocn_a_01380)
- Khalighinejad, N., Schurger, A., Desantis, A., Zmigrod, L., & Haggard, P. (2018). Precursor processes of human self-initiated action. *NeuroImage*, 165, 35–47. <https://doi.org/10.1016/j.neuroimage.2017.09.057>
- Kornhuber, H. H., & Deecke, L. (1965). Hirnpotentialänderungen bei Willkürbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und reafferente Potentiale. *Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere*, 284(1), 1–17. <https://doi.org/10.1007/BF00412364>
- Lara, A. H., Elsayed, G. F., Zimnik, A. J., Cunningham, J. P., & Churchland, M. M. (2018). Conservation of preparatory neural events in monkey motor cortex regardless of how movement is initiated. *ELife*, 7, e31826. <https://doi.org/10.7554/eLife.31826>

- Libet, B. (1985). Unconscious cerebral initiative and the role of conscious will in voluntary action. *Behavioral and Brain Sciences*, 8(4), 529–539. <https://doi.org/10.1017/S0140525X00044903>
- Makeig, S., Bell, A. J., Jung, T.-P., & Sejnowski, T. J. (1996). Independent component analysis of electroencephalographic data. *Advances in Neural Information Processing Systems*, 145–151.
- Maoz, U., Yaffe, G., Koch, C., & Mudrik, L. (2017). Neural precursors of decisions that matter—An ERP study of deliberate and arbitrary choice. *BioRxiv*, 097626. <https://doi.org/10.1101/097626>
- Nachev, P., & Hacker, P. (2014). The neural antecedents to voluntary action: A conceptual analysis. *Cognitive Neuroscience*, 5(3–4), 193–208. <https://doi.org/10.1080/17588928.2014.934215>
- Nachev, P., Kennard, C., & Husain, M. (2008). Functional role of the supplementary and pre-supplementary motor areas. *Nature Reviews Neuroscience*, 9(11), 856–869. <https://doi.org/10.1038/nrn2478>
- O’Connell, R. G., Dockree, P. M., & Kelly, S. P. (2012). A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. *Nature Neuroscience*, 15(12), 1729–1735. <https://doi.org/10.1038/nn.3248>
- Passingham, R. E. (1993). *The frontal lobes and voluntary action*. Oxford, England: Oxford University Press.
- Passingham, R. E., Bengtsson, S. L., & Lau, H. C. (2010). Medial frontal cortex: From self-generated action to reflection on one’s own performance. *Trends in Cognitive Sciences*, 14(1), 16–21. <https://doi.org/10.1016/j.tics.2009.11.001>
- Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ*, 7, e6876. <https://doi.org/10.7717/peerj.6876>
- Rouault, M., Drugowitsch, J., & Koechlin, E. (2019). Prefrontal mechanisms combining rewards and beliefs in human decision-making. *Nature Communications*, 10(1), 301. <https://doi.org/10.1038/s41467-018-08121-w>
- Schurger, A. (2018). Specific Relationship between the Shape of the Readiness Potential, Subjective Decision Time, and Waiting Time Predicted by an Accumulator Model with Temporally Autocorrelated Input Noise. *Eneuro*, ENEURO.0302-17.2018. <https://doi.org/10.1523/ENEURO.0302-17.2018>
- Schurger, A., Sitt, J. D., & Dehaene, S. (2012). An accumulator model for spontaneous neural activity prior to self-initiated movement. *Proceedings of the National Academy of Sciences*, 109(42), E2904–E2913. <https://doi.org/10.1073/pnas.1210467109>
- Shibasaki, H., & Hallett, M. (2006). What is the Bereitschaftspotential? *Clinical Neurophysiology*, 117(11), 2341–2356. <https://doi.org/10.1016/j.clinph.2006.04.025>
- Thaler, D., Chen, Y.-C., Nixon, P. D., Stern, C. E., & Passingham, R. E. (1995). The functions of the medial premotor cortex. *Experimental Brain Research*, 102(3), 445–460. <https://doi.org/10.1007/BF00230649>
- Ullmann-Margalit, E., & Morgenbesser, S. (1977). Picking and choosing. *Social Research*, 757–785.
- Verleger, R., Haake, M., Baur, A., & Śmigajewicz, K. (2016). Time to Move Again: Does the Bereitschaftspotential Covary with Demands on Internal Timing? *Frontiers in Human Neuroscience*, 10. <https://doi.org/10.3389/fnhum.2016.00642>