Human self-initiated action is preceded by a reliable process of noise reduction

Short title: Neural precursors of self-initiated action

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Abstract

A gradual buildup of electrical potential over motor areas precedes self-initiated movements. These "readiness potentials" (RPs) could simply reflect stochastic fluctuations in neural activity. We operationalised self-initiated actions as endogenous 'skip' responses while waiting for target stimuli in a perceptual decision task. Across-trial variability of EEG decreased more markedly prior to self-initiated compared to externally-triggered skip actions. This convergence towards a fixed pattern suggests a consistent preparatory process prior to self-initiated action. A leaky stochastic accumulator model could reproduce these features of the data, given the additional assumption of a decrease in noise level at the input to the accumulator prior to self-initiated, but not externally-triggered actions. The assumed reduction in neural noise was supported by analyses of both within-trial EEG variability and of spectral power. We suggest that a process of noise reduction is consistently recruited prior to self-initiated action. This precursor event may underlie the emergence of RP.

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Keywords: self-initiated action; externally-triggered action; readiness potential; stochastic

fluctuations; human

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1   **Introduction**

2   Functional and neuroanatomical evidence has been used to distinguish between two broad

3   classes of human actions: self-initiated actions that happen endogenously, in the absence of

4   any specific stimulus (Haggard, 2008; Passingham, Bengtsson, & Lau, 2010), and reactions

5   to external cues. Endogenous actions are distinctive in several ways. First, they depend on

6   an internal decision to act and are not triggered by external stimuli. In other words, the agent

7   decides internally what to do, or when to do it, without any external cue specifying the action

8   (Passingham et al., 2010). Second, we often deliberate and consider reasons before

9   choosing and performing one course of action rather than an alternative. Thus, endogenous

10   actions should be responsive to reasons (Anscombe, 2000). These features of endogenous

11   action capture many key attributes of human volition. While there has been extensive

12   research on action selection and initiation in response to external cues, the brain

13   mechanisms for endogenous, self-initiated actions have been less studied.

14   Many studies of human voluntary action involve the paradoxical instruction to 'act *freely*' e.g.,

15   "press a key when you feel the urge to do so" (Cunnington, Windischberger, Deecke, &

16   Moser, 2002; Jahanshahi et al., 1995; Libet, Gleason, Wright, & Pearl, 1983; Wiese et al.,

17   2004). However, the situation and task demands of such experiments are complex, and

18   have been justly criticised (Nachev & Hacker, 2014). We adapted for humans a paradigm

19   previously used in animal research (Murakami, Vicente, Costa, & Mainen, 2014), which

20   embeds endogenous actions within the broader framework of reward-guided perceptual

21   decision-making. Participants responded to the direction of unpredictably-occurring dot

22   motion stimuli by pressing left or right arrow keys (Gold & Shadlen, 2007). Importantly, they

23   could also choose to skip waiting for the stimuli to appear, by pressing both keys

24   simultaneously whenever they wished. The skip response thus reflects a purely endogenous

25   decision to act, without any direct external stimulus, and provides an operational definition of

26   a self-initiated action. Self-initiated 'skip' responses were compared to a block where

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27   participants made the same bilateral 'skip' actions in response to an unpredictable change in

28   the fixation point (Figure. 1).

29   Controversies regarding precursor processes have been central to neuroscientific debates

30   about volition (Dennett, 2015; Libet et al., 1983). The classical neural marker of precursor

31   processes for endogenous action is the readiness potential (RP: Kornhuber & Deecke,

32   1965). The RP is taken to be "the electro-physiological sign of planning, preparation, and

33   initiation of volitional acts" (Kornhuber & Deecke, 1990) and was considered a pre-requisite

34   of the conscious intention to act (Libet et al., 1983; Sinnott-Armstrong & Nadel, 2010).

35   Classical studies explicitly or implicitly assume that the RP reflects a putative 'internal

36   volitional signal', with a constant, characteristic ramp-like form, necessarily preceding action

37   initiation - although this signal is heavily masked by noise in any individual trial (Dirnberger,

38   Lang, & Lindinger, 2008). However, the very idea that the RP reflects a specific precursor

39   process leading to endogenous action has been recently challenged. Alternative models

40   suggest that the rising ramp pattern of the mean RP does not reflect a goal-directed process

41   but rather reflects subthreshold stochastic fluctuations that influence the precise time of

42   crossing the threshold for movement (Murakami et al., 2014; Schurger, Sitt, & Dehaene,

43   2012). Crucially, averaging these random fluctuations time-locked to action initiation results

44   in the rising ramp pattern of the mean RP, with its appearance of a stable ERP component.

45   According to the stochastic account, the RP reflects cross-trial averaging of data epochs

46   time locked to crests in autocorrelated neural noise, rather than a specific, goal-directed

47   process that causes action. This view, which can be formally expressed in a quantitative

48   model, and tested against neural data (Murakami et al., 2014; Schurger et al., 2012), has

49   radically revised neuroscientific theories of voluntary action.

50   Both classical and stochastic models can reproduce the existence of mean RP, treating it as

51   signal or as averaged noise, respectively. However, the two models make different

52   predictions about EEG variability prior to action. On the stochastic model, neural activity

53   eventually and necessarily converges because stochastic fluctuations must always approach

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54   the motor threshold from below. The time of convergence depends only on the temporal

55   autocorrelation of the EEG signal. On the classical model, the distribution of single trial RPs

56   *additionally* converges because the RP marks a consistent precursor process that reliably

57   precedes self-initiated action. While variability of RP activity has rarely been studied

58   previously (but see Dirnberger et al., 2008), several studies of externally-triggered

59   processing have used variability of neural responses to identify neural codes. For example,

60   variability goes down in the interval between a go cue and movement onset (Churchland,

61   Yu, Ryu, Santhanam, & Shenoy, 2006), and during perceptual processing (He, 2013;

62   Schurger, Sarigiannidis, Naccache, Sitt, & Dehaene, 2015). We thus hypothesised that

63   variability of neural activity should decrease more markedly prior to self-initiated skip actions.

64   The *additional* decrease in variability would be a marker of a consistent preparatory process,

65   or precursor for self-initiated action.

66   We found an additional drop in inter-trial variability beginning 1.5 s before self-initiated skips,

67   compared to externally-driven skip actions. This differential convergence suggests a

68   consistent precursor process that reliably precedes self-initiated action. The gradual onset of

69   differential convergence suggests that the precursor process has a variable duration, rather

70   than a fixed duration (Dirnberger et al., 2008), although we could not formally compare these

71   alternative models using our methods. We showed that a modified version of an established

72   computational model based on stochastic fluctuations on neural activity (Schurger et al.,

73   2012; Usher & McClelland, 2001) could capture the patterns of EEG variability found in our

74   data. Crucially, the model required a specific modification to explain the data, namely a

75   neurocognitive process of noise reduction, time-locked to the moment of action. Our model

76   further predicts that decreases in within-trial EEG fluctuation and spectral power should be

77   observed prior to self-initiated action. These predictions were confirmed. Importantly, these

78   differences between conditions began well before the stimulus onset in our externally-

79   triggered condition (Figures 2 & 7), so presumably reflects changes in ongoing EEG prior to

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80   self-initiated action. Thus, impending self-initiated voluntary action appears to be associated

81   with a distinctive, time-specific stabilisation of premovement EEG patterns.

82   **Results**

83   *Behavioural data.*

84   Participants (n=22) waited for a display of random dots to move coherently (step change

85   from 0% to 100% coherence) towards the left or right. They responded with the left or right

86   hand by pressing a left or right arrow key on a keyboard, accordingly. They received a

87   reward for correct responses. However, the time of movement onset was drawn

88   unpredictably from an exponential distribution, so waiting was sometimes extremely long. In

89   the '*self-initiated*' condition blocks (Figure 1A), participants could skip waiting if they chose

90   to, by pressing the left and right response keys simultaneously. The skip response saved

91   time, but produced a smaller reward than a response to dot motion. The experiment was

92   limited to one hour, so using the skip response implied a general understanding of the trade-

93   off between time and money. A skip response thus reflects a purely endogenous decision to

94   act, in the absence of any external instruction to act, and based on the tradeoff between

95   later, larger, and smaller, earlier rewards. This provides an operational definition of volition

96   within our experimental design, which captures some of the important features of

97   endogenous voluntary control, as well as the linkage of self-initiated action to other aspects

98   of cognition, such as decision-making and judgement (Schüür & Haggard, 2011). In the

99   '*externally-triggered*' condition blocks, participants could not choose for themselves when to

100   skip. Instead, they were instructed to make skip responses by an external signal (Figure 1B)

101   (see materials and methods).
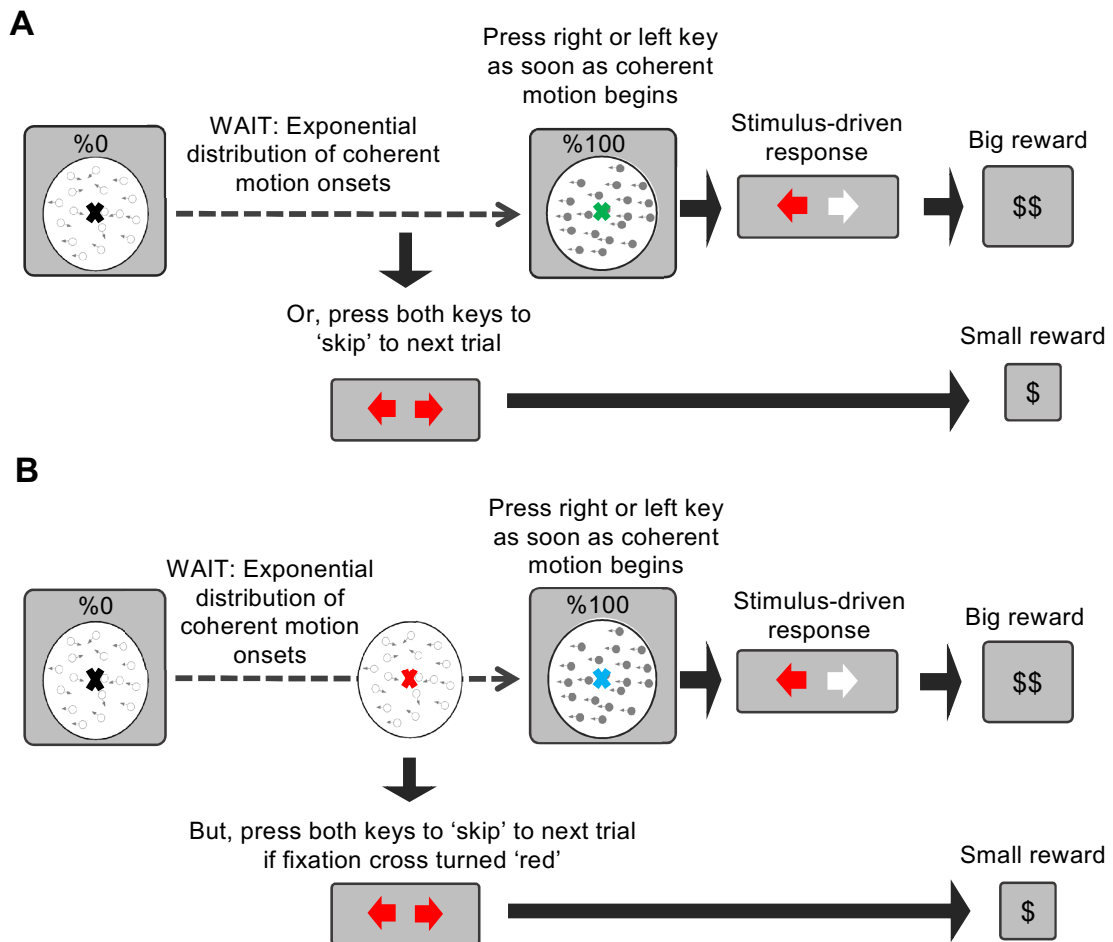
X Fixation cross changes colour during the trial

Figure 1. Timeline of an experimental trial. Participants responded to the direction of dot-motion with left and right keypresses. Dot-motion could begin unpredictably, after a delay drawn from an exponential distribution. A. In the 'self-initiated' blocks participants waited for an unpredictably occurring dot-motion stimulus, and were rewarded for correct left-right responses to motion direction. They could decide to skip long waits for the motion stimulus, by making a bilateral keypress. They thus decided between waiting, which lost time but brought a large reward, and 'skipping', which saved time but brought smaller rewards. The colour of the fixation cross changed continuously during the trial, but was irrelevant to the decision task. B. In the 'externally-triggered' blocks, participants were instructed to make bilateral skip keypresses when the fixation cross became red, and not otherwise.


On average participants skipped 108 (SD = 16) and 106 (SD = 17) times in the self-initiated and externally-triggered conditions, respectively. They responded to coherent dot motion in

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116   the remaining trials (N = 177, SD = 61), with a reaction time of 767 ms (SD = 111 ms).

117   Those responses were correct on 86% (SD = 4%) of trials. The average waiting time before

118   skipping in the self-initiated condition (7.3 s, SD = 1.6) was similar to that in the externally-

119   triggered condition (7.6 s, SD = 1.6), confirming the success of our yoking procedure (see

120   materials and methods). The waiting time varied more across trials within each individual,

121   than across individuals, suggesting that self-initiated skip responses represented an on-line

122   decision to act, rather than a pre-decided stereotyped response. Thus, the SD across trials

123   had a mean of 3.17 s (SD across participants = 1.42 s) for self-initiated skips. Our yoking

124   procedure ensured similar values for externally-triggered skips (mean of SD across trials

125   3.15 s, SD = 1.43 s). In the externally-triggered condition, the average reaction time to the

126   fixation cross change was 699 ms (SD = 67 ms). On average participants earned £2.14 (SD

127   = £0.33) from skipping and £2.78 (SD = £0.99) from correctly responding to dot motion

128   stimuli. This reward supplemented a fixed fee for participation. The mean and distribution of

129   waiting time before skip action of each participant are presented in Table S1 and Figure S1.

130   *EEG variability decreases disproportionately prior to action in self-initiated and externally-*

131   *triggered conditions.*

132   EEG data were pre-processed and averaged separately for self-initiated and externally-

133   triggered conditions. Figure 2A shows the grand average RP amplitude in both conditions.

134   The mean RP for self-initiated actions showed the familiar negative-going ramp. Note that

135   our choice to baseline-correct at the time of the action itself (see materials and methods)

136   means that the RP never in fact reaches negative voltage values. This negative-going

137   potential is absent from externally-triggered skip actions (Jahanshahi et al., 1995; Papa,

138   Artieda, & Obeso, 1991). The morphology of the mean RP might simply reflect the average

139   of stochastic fluctuations, rather than a goal-directed build-up. However, these theories offer

140   differing interpretations of the variability of individual EEG trajectories across trials (see

141   intro).

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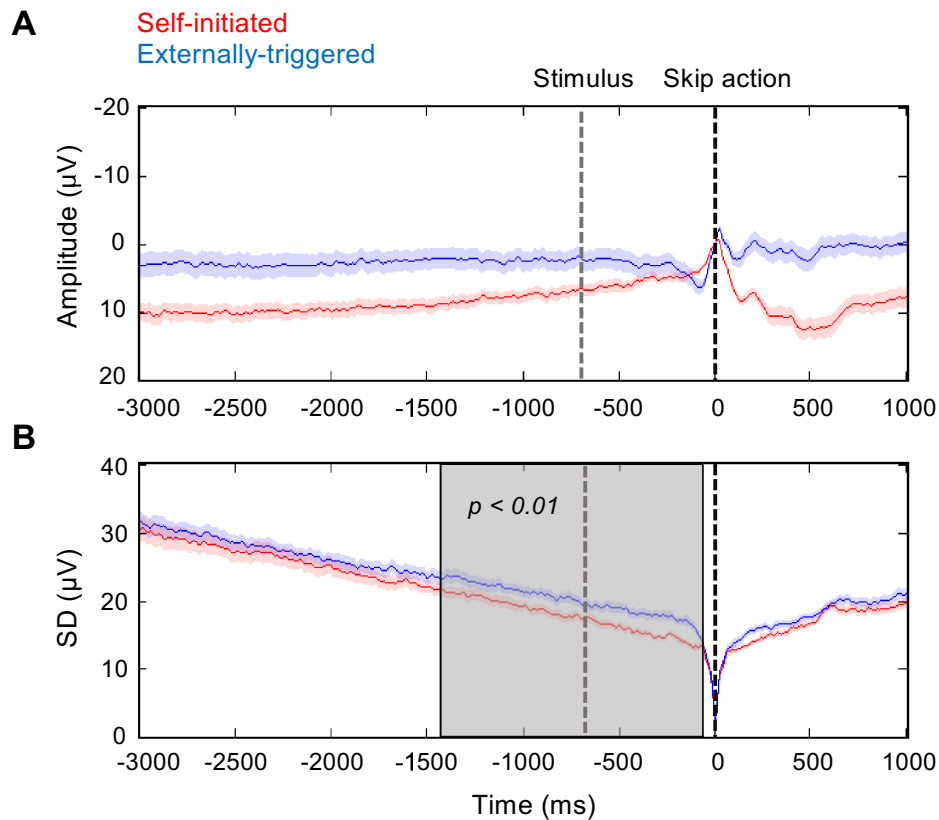
Figure 2. EEG activity prior to skip actions. The red and blue lines represent self-initiated and externally-triggered skip conditions, respectively. Data is time-locked to the skip action (black vertical line), baseline-corrected in a 10 ms window around the skip, and recorded from FCz electrode. The average time of the skip instruction (fixation cross changing to red) in the externally-triggered condition is shown as a grey vertical line. A. Grand average RP amplitude ± standard error of the mean across participants (SEM). B. Standard deviation across trials averaged across participants ± SEM. Shaded grey area shows a significant difference between standard deviation traces across central electrodes, detected by cluster-based permutation test.

To investigate this distribution we computed standard deviation of individual trial EEG, and found a marked decrease prior to self-initiated skip action. This decrease is partly an artefact of the analysis technique: individual EEG epochs were time-locked and baseline-corrected at action onset, making the across-trial standard deviation at the time of action necessarily zero (but see Figure S2). However, this premovement drop in EEG standard deviation was more marked for self-initiated than for externally-triggered skip actions, although the analysis techniques were identical. Paired-samples t-test on jack-knifed data showed that this difference in SD was significant in the last three of the four pre-movement time bins before

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159   skip actions (see materials and methods): that is from -1.5 to -1 s (t(21) = 4.32, p < 0.01 , d_z

160   = 0.92, p values are Bonferroni corrected for four comparisons), -1 to -0.5 s (t(21) = 5.97, p <

161   0.01 , d_z = 1.27), and -0.5 to 0 s (t(21) = 5.39, p < 0.01 ,d_z = 1.15).

162   To mitigate any effects of arbitrary selection of electrodes or time-bins, we also performed

163   cluster-based permutation tests (see materials and methods). For the comparison between

164   SDs prior to self-initiated vs externally-triggered skip actions, a significant cluster (p < 0.01)

165   was identified extending from 1488 to 80 ms premovement (Figure 2B, see also Figure S2

166   for a different baseline). This suggests that neural activity gradually converges towards an

167   increasingly reliable pattern prior to self-initiated actions. Importantly, this effect is not

168   specific to FCz but could be observed over a wide cluster above central electrodes (Figure

169   S3). However, the bilateral skip response used here makes the dataset suboptimal for

170   thoroughly exploring the fine spatial topography of these potentials, which we hope to

171   address in future research.

172   It has been shown that stimulus anticipation is preceded by a cortical negative wave, the

173   contingent negative variation (CNV) (Walter, Cooper, Aldridge, McCallum, & Winter, 1964).

174   The CNV has been associated with expectation and temporal processing (Casini & Vidal,

175   2011; Van Rijn, Kononowicz, Meck, Ng, & Penney, 2011). Hence, our measures in the self-

176   initiated condition could reflect both accumulating conditions that make a skip action

177   desirable (e.g., passage of time without dot motion onset), and the preparation of the skip

178   action itself. However, our externally-triggered skip condition controls for effects of mere

179   passage of time, and expectation of dot motion onset.

180   To ensure that the key cognitive factors in the task were balanced between self-initiated and

181   externally-triggered conditions, we also analysed mean and SD EEG amplitude prior to

182   stimulus-triggered responses to coherent dot motion (as opposed to skip responses). We did

183   not observe any negative-going potential prior to coherent dot motion (Figure 3A), again

184   suggesting that temporal expectation did not strongly contribute to our ERPs. More

185   importantly, the SD of EEG prior to coherent dot motion onset did not differ between

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186   conditions in any time window (p > 0.5, Bonferroni corrected for four comparisons) (Figure

187   3B). This suggests that the disproportionate drop in SD prior to skip actions cannot be

188   explained merely by a difference in expectation of dot stimuli or temporal processing.

189   Moreover, an explanation based on temporal processing would presumably predict stronger

190   EEG convergence when participants wait longer before skip action. In fact, we found a

191   negative correlation between EEG convergence and waiting time (Figure S4).
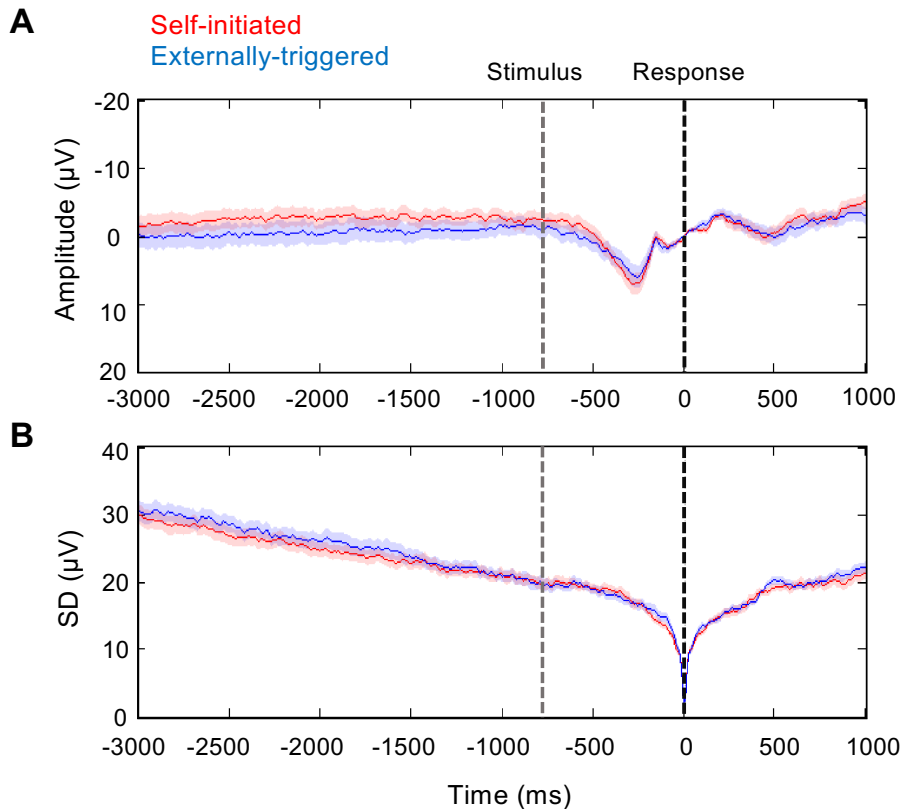
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193   Figure 3. EEG activity prior to response to coherent dot motion direction. The red and blue lines

194   represent activity in self-initiated and externally-triggered blocks, respectively. Data is time-locked to

195   the response to coherent dot motion direction (black vertical line), baseline-corrected in a 10 ms

196   window around the response, and recorded from FCz electrode. The average time of the coherent dot

197   motion onset is shown as a grey vertical line. A. Grand average ERPs ± SEM across participants. B.

198   Standard deviation across trials, averaged across participants ± SEM across participants.

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200   Finally, variability in the reaction time to respond to externally-triggered skip cues could

201   potentially smear out stimulus-driven preparation of skip actions. Such jitter in RT would

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202   have the artefactual effect of increasing EEG variability across trials. To rule out this

203   possibility we checked whether across-trial EEG convergence was correlated across

204   participants with variability in behavioural reaction time to the skip response cue, but found

205   no significant correlation between the two variables. This suggests that the difference in

206   EEG convergence between self-initiated and externally-triggered skip conditions could not

207   be explained by mere variability in RT to skip cues (Figure S5).

208   *Modelling the converging EEG distribution of self-initiated actions.*

209   Leaky stochastic accumulator models have been used previously to explain the neural

210   decision of 'when' to move in a self-initiated task (Schurger et al., 2012). A general

211   imperative to perform the task shifts the premotor activity up closer to threshold and then a

212   random threshold-crossing event provides the proximate cause of action. Hence, the precise

213   time of action is driven by accumulated internal physiological noise, and could therefore be

214   viewed as random, rather than decided (Schurger et al., 2012). However, the across-trial

215   variability of cortical potentials in our dataset suggests that neural activity converges on a

216   fixed pattern prior to self-initiated actions, to a greater extent than for externally-triggered

217   actions. This differential convergence could reflect a between-condition difference in the

218   autocorrelation function of the EEG. The early and sustained additional reduction in SD

219   before self-initiated actions motivated us to hypothesise an additional process of noise

220   control associated with self-initiated actions.

221   *Sensitivity analysis*

222   To investigate this hypothesis we first performed a sensitivity analysis by investigating how

223   changing key parameters of the model could influence across-trial variability of the output

224   *(for details see materials and methods)*. We modelled the hypothesised process of noise

225   control by allowing a gradual *change in noise (Δc)* prior to action. We also explored how

226   changes in the key *drift (I)* and *leak (k)* parameters would influence the trial-to-trial variability

227   of RP. We gradually changed each parameter while holding the others fixed, and simulated

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228   RP amplitude in 1000 trials time locked to a threshold-crossing event. SD was then

229   measured across these simulated trials. Simulated across-trial SDs showed that lower drift

230   rates and shorter leak constants were associated with a higher across-trial SD. Conversely,

231   reductions in noise were associated with a lower across-trial SD (Figure 4A-C). Thus, for the

232   model to reproduce the differential EEG convergence found in our EEG data, either the *drift*

233   or the *leak* should be higher, or the *change in noise* parameter should be lower, in self-

234   initiated compared to externally-triggered skip action conditions.

235   *Model fitting and optimal parameters*

236   We next fitted the model on the mean RP amplitude of each participant, separately for the

237   self-initiated and externally triggered conditions (Table S2, S3). The best fitting parameters

238   were then compared between the two conditions. The *drift* was significantly lower ($t(21) = $ -

239   4.47, $p < 0.001$, after Bonferroni correction for the three parameters tested) in the self-

240   initiated (mean across participants = 0.09, SD = 0.03) compared to the externally-triggered

241   condition (mean across participants = 0.13 , SD = 0.04) (Figure 4D). The *leak* was also

242   significantly lower ($t(21) = -4.20$, $p < 0.001$, Bonferroni corrected) in the self-initiated (mean

243   across participants = 0.40, SD = 0.21) compared to the externally-triggered condition (mean

244   across participants = 0.58, SD = 0.20) (Figure 4E). The *change in noise* was negative in the

245   self-initiated (mean across participants = -0.03, SD = 0.05) but positive in the externally-

246   triggered condition (mean across participants = 0.02, SD = 0.05). This difference was

247   significant between the conditions ($t(21) = -5.38$, $p < 0.001$, Bonferroni corrected) (Figure

248   4F). Finally, to investigate which parameters were most sensitive to the difference between

249   self-initiated and externally-triggered conditions, we expressed the effect of condition on

250   each parameter as an effect size (standardized mean difference, Cohen's dz). Importantly,

251   the effect size for the between-condition difference in the *change in noise* parameter (dz =

252   1.15, 95%CI = [0.60 1.68]) was larger than that for the *drift* (dz = 0.95, 95%CI = [0.44 1.45])

253   or the *leak* (dz = 0.89, 95%CI = [0.39 1.38]) parameters (Figure 4G).

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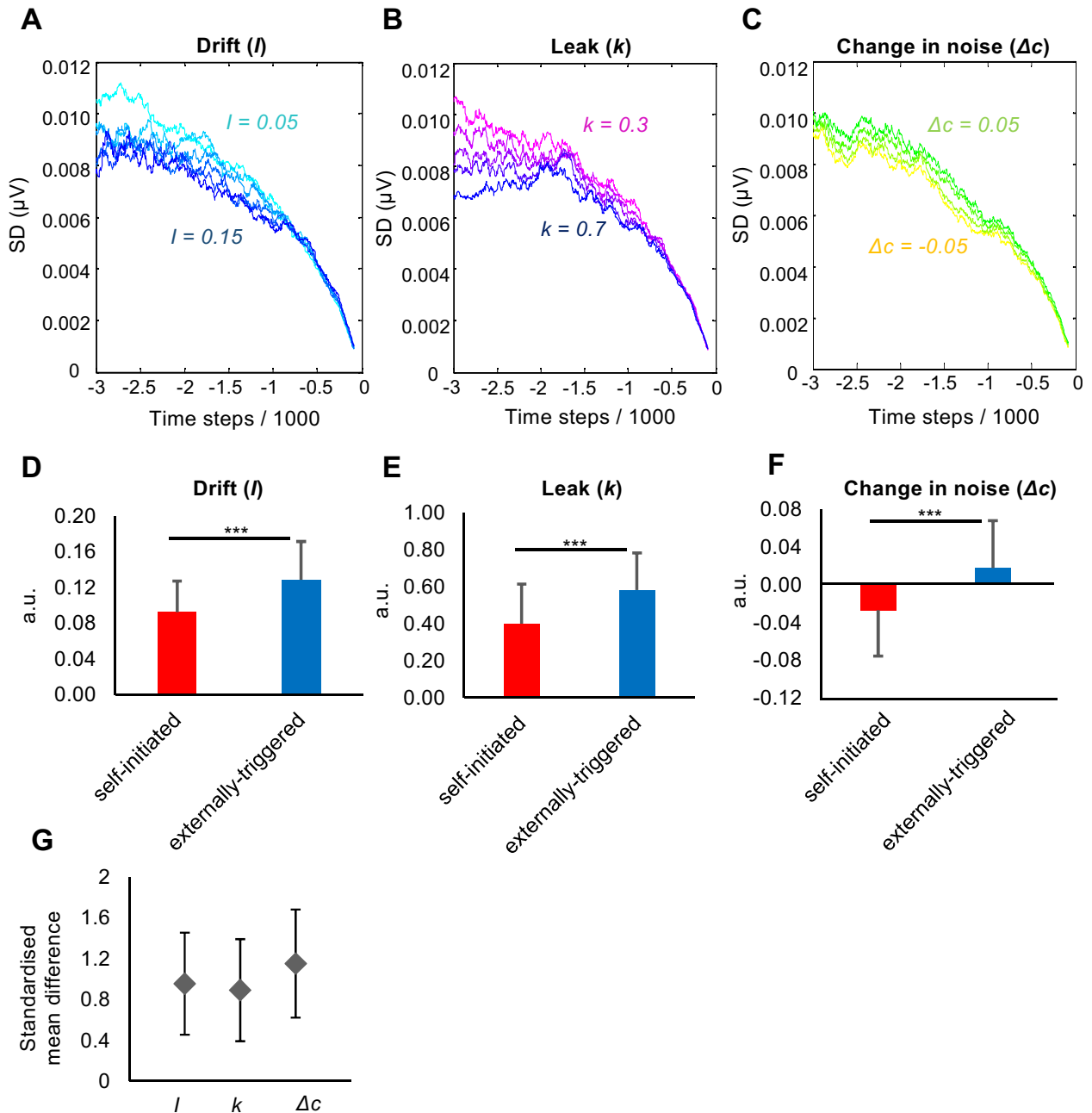
Figure 4 A-C. Results of sensitivity analysis. Effects of changing parameters of a stochastic

256 accumulator model on SD across 1000 model runs. (A) *Drift* gradually changed from 0.05 (cyan) to

257 0.15 (blue) in 0.02 steps, while other parameters were kept fixed. (B) *Leak* gradually changed from

258 0.3 (magenta) to 0.7 (blue) in 0.1 steps, while other parameters were kept fixed. (C) *Change in noise*

259 gradually changed from -0.05 (yellow) to 0.05 (green) in 0.02 steps, while other parameters were kept

260 fixed. D-F. The best fitting parameters to real mean RP amplitude in self-initiated (red) and externally-

261 triggered (blue) conditions. Asterisks show significant difference (p < 0.001). Error bars show SD

262 across participants. G. Effect sizes (d_z) for the between-condition difference in fitted *drift*, the *leak* and

263 the *change in noise* parameters. Error bars show 95% confidence interval.

264   So far, we fitted model parameters to the mean RP amplitude, and noted through separate

265   sensitivity analysis their implications for across-trial SD. Next, we directly predicted the drop

266   in across-trial SD of simulated RP data in self-initiated compared to externally-triggered

267   conditions, using the optimal model parameters for each participant in each condition. We

268   therefore simulated 22 RP data sets, using each participant's best fitting parameters in each

269   condition (see materials and methods), and computed the SD across the simulated trials. We

270   observed a marked additional drop in simulated across-trial SD in the self-initiated compared

271   to externally-triggered condition (Figure 5A, B). The differential convergence between

272   conditions in the simulated data closely tracked the differential convergence in our EEG data

273   (Correlation across participants, Pearson's r = 0.90, p < 0.001) (Figure 5C).


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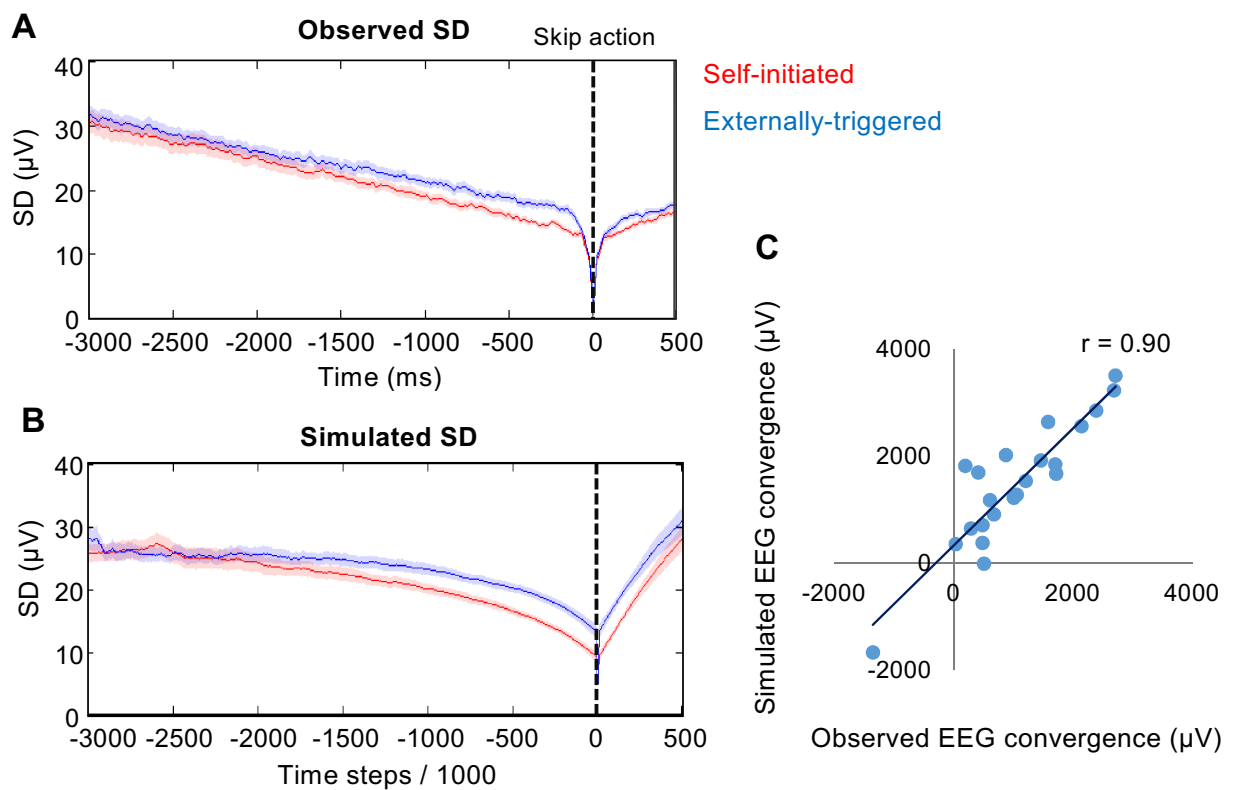
Figure 5. (A) Observed SD across trials averaged across participants ± SEM. Data are baselined to a 10 ms window around the skip and are recorded from FCz electrode. (B) Simulated SD across trials averaged across participants ± SEM. The red and blue lines represent activity in self-initiated and externally-triggered blocks, respectively. The black vertical line is the moment of skip action. (C) Correlation between observed and simulated EEG convergence. EEG convergence was measured by subtracting the area under the SD curve in self-initiated from the externally-triggered condition.

281 *Within-trial reduction in EEG variability*

282 Optimum parameter values from the model suggest that a consistent process of noise

283 reduction reliably occurs prior to self-initiated actions. This theory predicts that, compared to

284 externally-triggered actions, EEG variability should reduce more strongly not only across

285 trials but also within each single self-initiated action trial. To test this prediction we measured

286 SD within a 100 ms sliding window for each trial, and each condition (see materials and

287 methods) (Figure. 6A). We then used linear regression to calculate the slope of the within-

288 trial SD change for each trial, and compared slopes between the self-initiated and externally-

289 triggered conditions using a multilevel model with single trials as level 1 and participants as

290 level 2 variables. While EEG variability decreased within self-initiated skip trials (mean slope

291 = -0.01 µV/sample, SD across participants = 0.02 µV), it increased within externally-triggered

292 trials (mean slope = 0.01 µV/sample, SD across participants = 0.02 µV). The between-

293 condition difference in slopes was highly significant (t(4102) = 3.39, p < 0.001; Figure. 6B),

294 consistent with a progressive reduction of EEG variability prior to self-initiated actions.
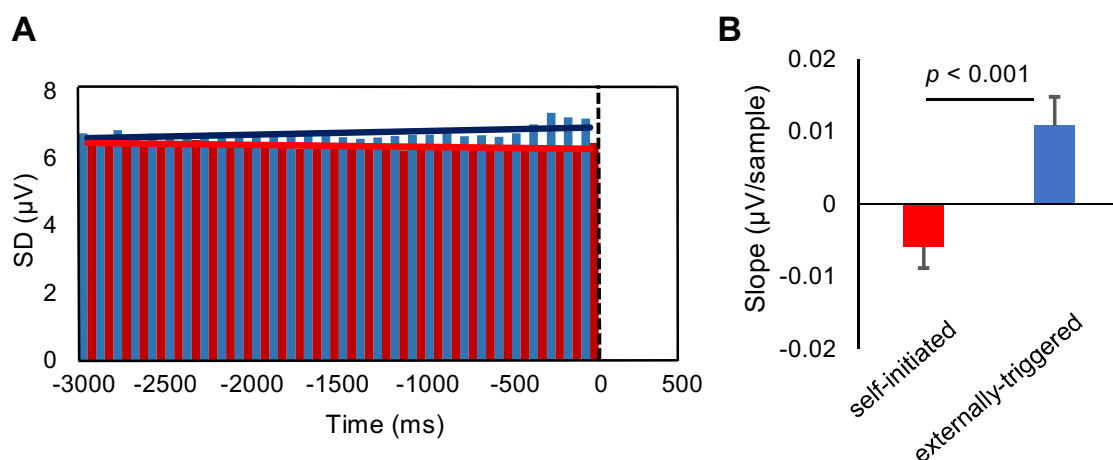
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296 Figure 6. Within-trial EEG variability. (A) SD was measured within 100ms windows for each trial and

297 each condition. Red and blue bars show within-trial SD in each time bin in self-initiated and externally-

298 triggered conditions, respectively. The solid red and blue lines show the linear fit to the time bins in

299 self-initiated and externally-triggered conditions, respectively. (B) The slope of the change in within-

300 trial variability was then compared between the self-initiated (red) and externally-triggered (blue) skip

301 conditions. Error bars show SEM across participants.

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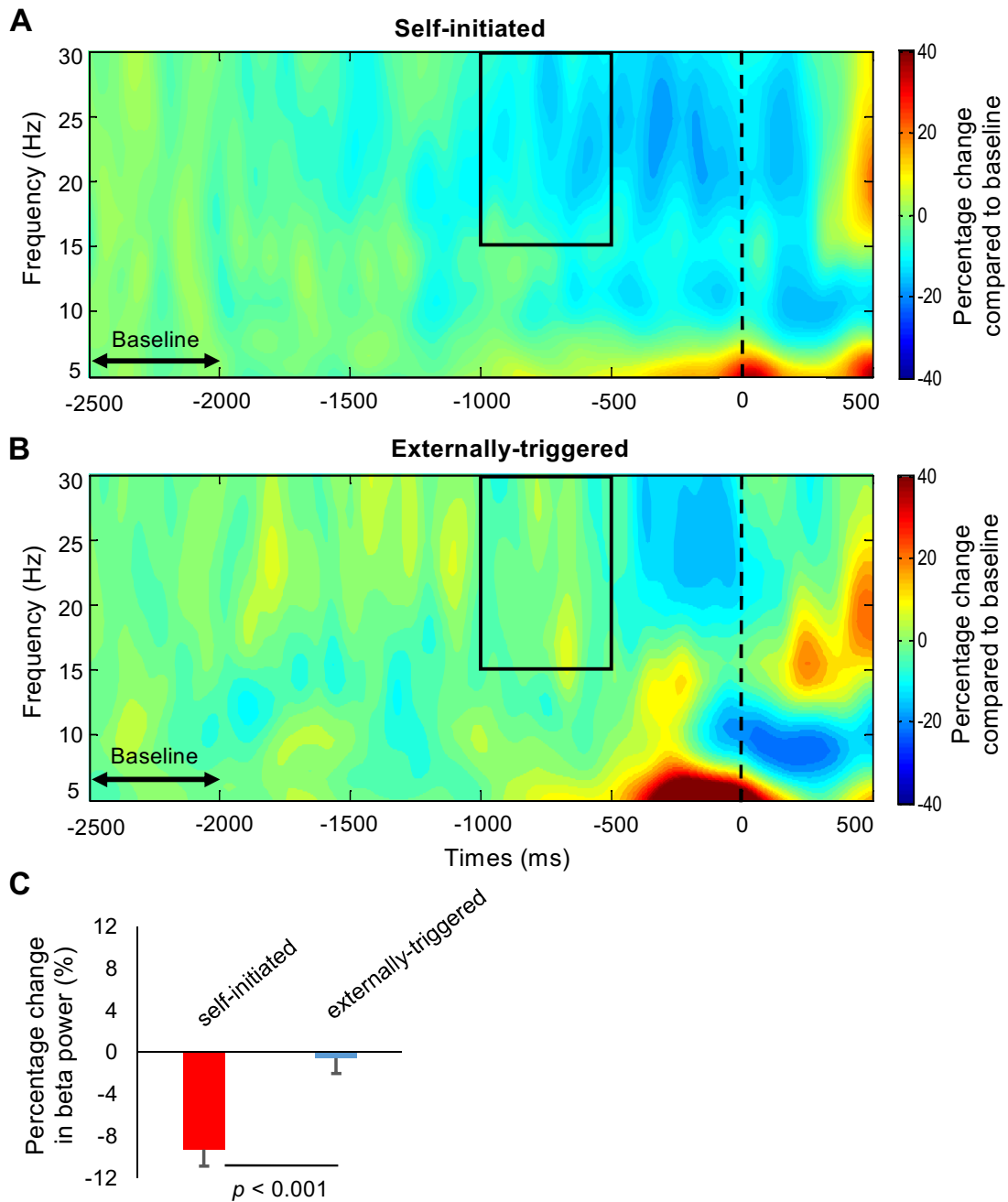
Figure 7. Percentage change in total EEG power compared to baseline (2.5 – 2 s prior to action) in self-initiated (A), and externally-triggered skip conditions (B). In each condition, the percentage change in power was computed 1 – 0.5 s prior to skip action, and from 15 – 30 Hz based on previous literature (region of interest shown by black box). (C) The percentage change from baseline was compared between the self-initiated (red bar) and externally-triggered (blue bar) conditions. Error bars show SEM across participants.

309   Previous discussions of amplitude variation in EEG focussed on synchronised activity within

310   specific spectral bands (Pfurtscheller & Neuper, 1994). Preparatory decrease in beta-band

311   power has been used as a reliable biomarker of voluntary action (Kristeva, Patino, & Omlor,

312   2007). While time-series methods identify activity that is phase-locked, spectral methods

313   identify EEG power that is both phase-locked and non-phase-locked, within each specific

314   frequency band (Cohen, 2014; Pfurtscheller & Lopes da Silva, 1999). Since motor threshold

315   models simply accumulate all neural activity, whether stochastic or synchronised, we

316   reasoned that reduction in the noise scaling factor within an accumulator model might be

317   associated with reduction in the synchronised activity. We therefore also investigated the

318   decreasing variability of neural activity prior to self-initiated action using spectral methods

319   (see materials and methods). Specifically, we focused on the event-related

320   desynchronization (ERD) of beta band activity (Bai et al., 2011; Calmels et al., 2006;

321   Stancák & Pfurtscheller, 1996). We compared ERD between the self-initiated and externally-

322   triggered conditions in a 500 ms window (1 – 0.5 s prior to action, based on previous reports

323   (Tzagarakis, Ince, Leuthold, & Pellizzer, 2010)). Beta power in this period decreased prior to

324   self-initiated skip (mean percentage change = -%9.3, SD = %7.4) (Figure. 7A), but not

325   before externally-triggered skip actions (mean percentage of change = -%0.6, SD = %6.9)

326   (Figure. 7B). Importantly, percentage change in beta power was significantly different

327   between the two conditions ($t(21) = -4.16$, $p < 0.001$) (Figure 7C).

328   **Discussion**

329   The capacity for endogenous voluntary action lies at the heart of human nature, but the brain

330   mechanisms that enable this capacity remain unclear. A key research bottleneck has been

331   the lack of convincing experimental paradigms for studying volition. Many existing paradigms

332   rely on paradoxical instructions equivalent to "be voluntary" or "act freely" (Haggard, 2005;

333   Libet et al., 1983). In a novel paradigm, we operationalized self-initiated actions as

334   endogenous 'skip' responses embedded in a perceptual decision task, with a long, random

335   foreperiod. Participants could decide to skip waiting for an imperative stimulus, by

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336   endogenously initiating a bilateral keypress. Although previous studies in animals also used

337   *'Giving up waiting'* to study spontaneous action decisions (Murakami et al., 2014), we

338   believe this is the first use of this approach to study self-initiated actions in humans.

339   Our experimental task provided a purely operational definition of self-initiated, endogenous

340   skip responses. Thus, the skip action can be understood from a strict behaviourist

341   perspective. However, skip responses have many of the hallmarks of volition traditionally

342   used in philosophy, including internal-generation (Passingham et al., 2010), reasons-

343   responsiveness (Anscombe, 2000), freedom from immediacy (Shadlen & Gold, 2004), and a

344   clear counterfactual alternative (Pereboom, 2011). Crucially, operationalising self-initiated

345   voluntary action in this way avoids explicit instructions to "act freely", and avoids subjective

346   reports about "volition". We compared such actions to an exogenous skip response triggered

347   by a visual cue in control blocks.

348   The neural activity that generates self-initiated voluntary actions remains controversial.

349   Several theories attribute a key role to medial frontal regions (Krieghoff, Waszak, Prinz, &

350   Brass, 2011; Nachev, Kennard, & Husain, 2008; Passingham, 1995). Averaged scalp EEG

351   in humans revealed a rising negativity beginning 1 s or more before the onset of

352   endogenous actions (Kornhuber & Deecke, 1965), and appearing to originate in medial

353   frontal cortex (Boschert, Hink, & Deecke, 1983; Deecke & Kornhuber, 1978). Since this

354   'readiness potential' does not occur before involuntary or externally-triggered movements, it

355   has been interpreted as the electro-physiological sign of planning, preparation, and initiation

356   of self-initiated actions (Keller & Heckhausen, 1990; Kornhuber & Deecke, 1990). RP-like

357   brain activities preceding self-initiated actions were also reported at the single-neuron level

358   (Fried, Mukamel, & Kreiman, 2011). However, the view of the RP as a causal signal for

359   voluntary action has been challenged, because simply averaging random neural fluctuations

360   that trigger a motor action also produces RP-like patterns (Schurger et al., 2012). Such

361   stochastic accumulator models were subsequently used to predict humans' (Schurger et al.,

362   2012) and rats' self-initiated actions in a task similar to ours (Murakami et al., 2014). Thus, it

20

363   remains highly controversial whether the RP results from a specific precursor process that

364   prepares self-initiated actions, or from random intrinsic fluctuations. We combined an

365   experimental design that provides a clear operational definition of volition, and an analysis of

366   *distribution across and within individual trials* of pre-movement EEG. Our results support a

367   novel combination of both the classical and the stochastic views. We report the novel finding

368   that self-initiated movements are reliably preceded by a process of noise reduction. This

369   process alters the pattern of stochastic fluctuations that accumulate towards the motor

370   threshold.

371   EEG showed decreased trial-to-trial variability prior to skip actions. This partly reflects the

372   time-locking and baseline-correction at the time of action: ERP methods necessarily imply

373   zero variability at the baseline (Luck, 2005). However, around 1.5 s prior to skip actions, the

374   decrease in variability became more marked for self-initiated compared to control externally-

375   triggered skip actions. Since the skip action in the externally-triggered control condition has

376   no endogenous volitional component, the decrease in variability prior to skip actions in the

377   control condition presumably reflects only the effects of time-locking, and the temporal

378   autocorrelation of the background EEG. However, the *additional* decrease in variability prior

379   to self-initiated action may reflect convergence of neural activity towards a steady trajectory

380   that precedes self-initiated actions. We hypothesised that this could indicate a consistent

381   preparatory process leading to self-initiated voluntary action.

382   Measurement of inter-trial variability has been extensively used in the analysis of neural data

383   (Averbeck & Lee, 2003; Churchland et al., 2011; Churchland et al., 2010, 2006; He, 2013;

384   Saberi-Moghadam, Ferrari-Toniolo, Ferraina, Caminiti, & Battaglia-Mayer, 2016; Schurger et

385   al., 2015). For example, presenting a target stimulus decreases inter-trial variability of neural

386   firing rate in premotor cortex (Churchland et al., 2006). Interestingly, RTs to external stimuli

387   are shortest when variability is lowest, suggesting that a decrease in neural variability is a

388   marker of motor preparation (Churchland et al., 2006). Moreover, reducing neural variability

389   is characteristic of cortical responses to any external stimulus (Churchland et al., 2010), and

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390   could be a reliable signature of conscious perception (Schurger et al., 2015). Importantly, in

391   previous studies, the decline in neural variability was *triggered* by a target stimulus, i.e.

392   decreasing neural variability was triggered exogenously (Churchland et al., 2010). Our

393   results show that inter-trial variability also decreases prior to a self-initiated action, in the

394   absence of any external target.

395   Integration to bound models have been recently used to account for the neural activity

396   preceding self-initiated actions in humans (Schurger et al., 2012) and rodents (Murakami et

397   al., 2014). In the absence of external evidence, these models are fed solely with internal

398   physiological noise. Importantly, when signal-to-noise ratio is low the timing of the decision

399   to move is mainly determined by random fluctuations. Schurger et al.'s model first shifts

400   premotor activity closer to a motor threshold. This is followed by a threshold-crossing event,

401   triggered by stochastic fluctuations (Schurger et al., 2012). By fitting a modified version of

402   the leaky stochastic accumulator model on each participant's mean RP amplitude, we

403   observed that integration of internal noise evolves differently prior to self-initiated and

404   externally-triggered skip actions. The rate of the *drift* and the *leak* was lower and the *change*

405   *in noise* was negative prior to self-initiated actions, compared to externally-triggered actions.

406   Importantly, analysis of across-trial variability of simulated data, using model parameters

407   optimised for each participant, implied that the marked drop in variability that we observed

408   prior to self-initiated action was mainly driven by a gradually reducing noise level. Previous

409   studies show that changes in noise level influences choice, RT and confidence in

410   accumulation-to-bound models of perceptual decision (Fetsch, Kiani, Newsome, & Shadlen,

411   2014; Furstenberg, Breska, Sompolinsky, & Deouell, 2015; Kiani, Hanks, & Shadlen, 2008;

412   Zylberberg, Fetsch, & Shadlen, 2016). Interestingly, the motivating effects of reward on

413   speed and accuracy of behaviour were recently shown to be attributable to active control of

414   internal noise (Manohar et al., 2015). In general, previous studies show an important role of

415   active noise control in tasks requiring responses to external stimuli (Kool & Botvinick, 2013;

416   Manohar et al., 2015). We have shown that similar processes may underlie self-initiated

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417   action, and that a consistent process of noise reduction may be a key precursor of self-

418   initiated voluntary action.

419   Finally, we showed that a decrease in premotor neural variability prior to self-initiated action

420   is not only observed across-trials, but is also realised within-trial and as a reduction in power

421   of beta frequency band. Clearly, any natural muscular action must have *some* precursors.

422   Sherrington's final common path concept proposed that descending neural commands from

423   primary motor cortex necessarily preceded voluntary action (Sherrington, 1906). However, it

424   remains unclear *how long* before action such precursor processes can be identified. Our

425   result provides a new method for addressing this question. The question is theoretically

426   important, because cognitive accounts of self-initiated action control divide into two broad

427   classes. In classical accounts, a fixed, and relatively long-lasting precursor process is

428   caused by a prior decision to act (Anscombe, 2000; Kornhuber & Deecke, 1990). In other

429   recent accounts, stochastic fluctuations dominate until a relatively late stage, and fixed

430   precursor processes would be confined to brief, motoric execution processes (Schurger et

431   al., 2012).

432   Our study cannot show whether self-initiated voluntary actions are caused by prior decisions,

433   or by randomness. However, our results do suggest that the contribution of stochastic

434   fluctuations is supplemented by a precursor process of noise reduction starting from around

435   1.5 s prior to action. Importantly, and by the same token, our results cannot show whether

436   the precursor process of noise reduction is initiated by some top-down decision, or is itself

437   triggered by some ongoing spontaneous fluctuations. Further, the precursor processes that

438   our method identifies may be necessary for self-initiated action, but may not be sufficient:

439   identifying a precursor process prior to self-initiated movement says nothing about whether

440   and how often such a process might also be present in the absence of movement. On one

441   view, the precursor process might occur quite frequently, but a last-minute decision might

442   influence whether the precursor process completes with a movement, or is vetoed. Our

443   movement-locked analyses cannot identify any putative vetoed precursor processes, or

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444 precursor-like processes that failed to result in a movement. However, our spectral analyses

445 (Figure 7) make this possibility unlikely. They show a gradual decline in total beta-band

446 power beginning around 1 s prior to self-initiated action. Any putative vetoed precursor

447 processes would produce partial versions of this effect at other time-points in the epoch, but

448 these are not readily apparent.

449 Inter-trial variability provides an additional dimension to information coding in the brain (He,

450 2013; Schurger et al., 2015; Stein, Gossen, & Jones, 2005). We showed that both inter- and

451 within-trial variability decreases prior to a self-initiated action, akin to a reliable preparatory

452 process. Our computational modelling further suggests that this preparatory stabilising

453 process may itself reflect some as yet unknown mechanism of noise reduction. Actively

454 regulating noise at optimal levels typically enhances system performance (Faisal, Selen, &

455 Wolpert, 2008; Fitts, 1954; Groen & Wenderoth, 2016; Shu, Hasenstaub, Badoual, Bal, &

456 McCormick, 2003). However, noise regulation can also arise incidentally, as a result of

457 attractor dynamics in the motor system, as in the "optimal subspace hypothesis" (Shenoy,

458 Sahani, & Churchland, 2013). Further, the noise reduction mechanism in our data could itself

459 be triggered either by a specific top-down signal or a stochastic event. Finally, we speculate

460 that the process of noise reduction not only explains the reduction in inter- and within-trial

461 EEG variability prior to self-initiated action, but also generates the slow rising negativity of

462 the RP, and the well-known beta ERD that precedes voluntary actions. ERD represents an

463 activation in cortical areas that produce motor behaviour (Pfurtscheller, 1992; Pfurtscheller &

464 Lopes da Silva, 1999). Factors such as effort and attention enhance the ERD (Defebvre,

465 Bourriez, Destée, & Guieu, 1996). However, the relation between ERD and RP remained

466 unclear. Our modelling results suggest that a reliable process of noise reduction could

467 explain both the ERD, and the RP.

468 Interestingly, our endogenous skip response resembles the decision to explore during

469 foraging behaviour (Constantino & Daw, 2015; Kolling, Behrens, Mars, & Rushworth, 2012).

470 That is, endogenous skip responses amounted to deciding to look out for dot-motion stimuli

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471   in forthcoming time-periods, rather than the present one. This prompts the speculation that

472   spontaneous transition from rest to foraging or vice-versa could be an early evolutionary

473   antecedent of human volition.

474   In conclusion, we show that self-initiated actions have a reliable precursor, namely a

475   consistent process of neural noise reduction prior to movement. We began this paper by

476   distinguishing between a classical model, in which a fixed preparation process consistently

477   preceded self-initiated action, and a fully stochastic model, in which the triggering of self-

478   initiated action is essentially random – though the artefact of working with movement-locked

479   epochs might give the appearance of a consistent precursor event such as the RP. We have

480   identified a reliable precursor process, but this precursor process can be accommodated as

481   a parameter change within the stochastic model framework. Future research might usefully

482   investigate whether the precursor process is the cause or the consequence of the subjective

483   'decision to act'.

484   **Materials and Methods**

485   *Participants.*

486   24 healthy volunteers, aged 18-35 years of age (9 male, mean age = 23 years), were

487   recruited from the Institute of Cognitive Neuroscience subject data pool. Two participants

488   were excluded before data analysis (they provided insufficient EEG data because of

489   excessive blinking). All participants were right handed, had normal or corrected to normal

490   vision, had no history or family history of seizure, epilepsy or any neurologic or psychiatric

491   disorder. Participants affirmed that they had not participated in any brain stimulation

492   experiment in the last 48 h, nor had consumed alcohol in the last 24 h. Participants were

493   paid an institution-approved amount for participating in the experiment. Experimental design

494   and procedure were approved by the UCL research ethics committee, and followed the

495   principles of the Declaration of Helsinki.

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496   *Behavioural task and procedure.*

497   Participants were placed in an electrically shielded chamber, 55 cm in front of a computer

498   screen (60 Hz refresh rate). After signing the consent form, the experimental procedure was

499   explained and the EEG cap was set up. The behavioural task was as follows: participants

500   were instructed to look at a fixation cross in the middle of the screen. The colour of the

501   fixation cross changed slowly and continuously throughout the trial. This colour always

502   started from 'black' and then gradually changed to other colours in a randomised order. The

503   fixation cross changed colour gradually (e.g., from green to pink), taking 2.57 s. The fixation

504   cross was initially black, but the sequence of colours thereafter was random. At the same

505   time, participants waited for a display of randomly moving dots (displayed within a circular

506   aperture of 7º of diameter with a density of 14.28 dots/degree, initially moving with 0%

507   coherence with a speed of 2º/s (Desantis, Waszak, & Gorea, 2016; Desantis, Waszak,

508   Moutsopoulou, & Haggard, 2016), to move coherently (step change to 100% coherence)

509   towards the left or right. They responded with the left or right hand by pressing a left or right

510   arrow key on a keyboard, accordingly. The change in dot motion coherence happened

511   abruptly. Correct responses were rewarded (2p). Conversely, participants lost money (-1p)

512   for giving a wrong answer (responding with the left hand when dots were moving to right or

513   vice versa), for responding before dots start moving, or not responding within 2 s after dot

514   motion. The trial was interrupted while such error feedback was given. Importantly, the time

515   of coherent movement onset was drawn unpredictably from an exponential distribution (min

516   = 2 s, max = 60 s, mean = 12 s), so waiting was sometimes extremely long. However, this

517   wait could be avoided by a 'skip' response (see later). Participants could lose time by

518   waiting, but receive a big reward (2p) if they responded correctly, or could save time by

519   'skipping' but collect a smaller reward (1p) (Fig. 1A). The experiment was limited to one

520   hour, so using the skip response required a general understanding of the trade-off between

521   time and money. Participants were carefully informed in advance of the rewards for

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522   responses to dot motion, and for skip response, and were clearly informed that the

523   experiment had a fixed duration of one hour.

524   There were two blocked conditions, which differed only in the origin of the skip response. In

525   the 'self-initiated' condition blocks, participants could skip waiting if they chose to, by

526   pressing the left and right response keys simultaneously. The skip response saved time, but

527   produced a smaller reward (1p) than a response to dot motion. Each block consisted of 10

528   trials. To ensure consistent visual attention, participants were required to monitor the colour

529   of the fixation cross, which cycled through an unpredictable sequence of colours. At the end

530   of each block they were asked to classify the number of times the fixation cross turned

531   'yellow', according to the following categories : never, less than 50%, 50%, more than 50%.

532   They lost money (-1p) for giving a wrong answer. At the end of each block, participants

533   received feedback of total reward values, total elapsed time, and number of skips. They

534   could use this feedback to adjust their behaviour and maximise earnings, by regulating the

535   number of endogenous 'skip' responses.

536   In the 'externally-triggered' condition blocks, participants could not choose for themselves

537   when to skip. Instead, they were instructed to make skip responses by an external signal.

538   The external signal was an unpredictable change in the colour of the fixation cross to 'red'

539   (Fig. 1B). Participants were instructed to make the skip response as soon as they detected

540   the change. The time of the red colour appearance was yoked to the time of participant's

541   own previous skip responses in the immediately preceding self-initiated block, in a

542   randomised order. For participants who started with the externally-triggered block, the timing

543   of the red colour appearance in the first block only was yoked to the time of previous

544   participant's last self-initiated block. The colour cycle of the fixation cross had a random

545   sequence, so that the onset of a red fixation could not be predicted. The fixation cross

546   ramped to 'red' from its previous colour in 300 ms. Again, a small reward (1p) was given for

547   skipping. The trial finished and the participant lost money (-1p) if s/he did not skip within 2.5

548   s from beginning of the ramping colour of the fixation cross. The 'red' colour was left out of

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549   the colour cycle in the self-initiated blocks. To control for any confounding effect of attending

550   to the fixation cross, participants were also required to attend to the fixation cross in the self-

551   initiated blocks and to roughly estimate the number of times the fixation cross turned 'yellow'

552   (see previous). Each externally-triggered block had 10 trials, and after each block feedback

553   was displayed. Each self-initiated block was interleaved with an externally-triggered block,

554   and the order of the blocks was counterbalanced between the participants. The behavioural

555   task was designed in Psychophysics Toolbox Version 3 (Brainard, 1997).

556   *EEG recording.*

557   While participants were performing the behavioural task in a shielded chamber, EEG signals

558   were recorded and amplified using an ActiveTwo Biosemi system (BioSemi, Amsterdam,

559   The Netherlands). Participants wore a 64-channel EEG cap. To shorten the preparation time

560   we recorded from a subset of electrodes that mainly covers central and visual areas: F3, Fz,

561   F4, FC1, FCz, FC2, C3, C1, Cz, C2, C4, CP1, CPz, CP2, P3, Pz, P4, O1, Oz, O2. Bipolar

562   channels placed on the outer canthi of each eye and below and above the right eye were

563   used to record horizontal and vertical electro-oculogram (EOG), respectively. The Biosemi

564   Active electrode has an output impedance of less than 1 Ohm. EEG signals were recorded

565   at a sampling rate of 2048 Hz.

566   *EEG preprocessing.*

567   EEG data preprocessing was performed in Matlab (MathWorks, MA, USA) with the help of

568   EEGLAB toolbox (Delorme & Makeig, 2004). Data were downsampled to 250 Hz and low-

569   pass filtered at 30 Hz. No high-pass filtering and no detrending were applied, to preserve

570   slow fluctuations. All electrodes were referenced to the average of both mastoid electrodes.

571   Separate data epochs of 4 s duration were extracted for self-initiated and externally-

572   triggered skip actions. Data epochs started from 3 s before to 1 s after the action. To avoid

573   EEG epochs overlapping each other any trial in which participants skipped earlier than 3 s

574   from trial initiation was removed. On average, 5% and 4% of trials were removed from the

575   self-initiated and externally-triggered conditions, respectively.

576   RP recordings are conventionally baseline-corrected using a baseline 2.5 until 2 s before

577   action. This involves the implicit assumption that RPs begin only in the 2 s before action

578   onset (Shibasaki & Hallett, 2006), but this assumption is rarely articulated explicitly, and is in

579   fact questionable (Verbaarschot, Farquhar, & Haselager, 2015). We instead took a baseline

580   from -5 ms +5 ms with respect to action onset. This choice avoids making any assumption

581   about how or when the RP starts. To ensure this choice of baseline did not capitalize on

582   chance, we performed parallel analyses on demeaned data (effectively taking the entire

583   epoch as baseline), with consistent results (see Figure. S2). Finally, to reject non-ocular

584   artefacts, data epochs from EEG channels (not including EOG) with values exceeding a

585   threshold of ±150 μv were removed. On average 7% and 8% of trials were rejected from

586   self-initiated and externally-triggered conditions, respectively. In the next step, Independent

587   Component Analysis (ICA) was used to remove ocular artefacts from the data. Ocular ICA

588   components were identified by visual inspection. Trials with artefacts remaining after this

589   procedure were excluded by visual inspection.

590   *EEG analysis.*

591   Preliminary inspection showed a typical RP-shaped negative-going slow component that

592   was generally maximal at FCz. Therefore, data from FCz was chosen for subsequent

593   analysis. Time series analysis was performed in Matlab (MathWorks) with the help of the

594   FieldTrip toolbox (Oostenveld et al., 2010). We measured two dependent variables as

595   precursors of both *self-initiated* and *externally-triggered* skip actions: mean RP amplitude

596   across trials and variability of RP amplitudes across and within trials (measured by SD). To

597   compare across-trials SD between the two conditions, data epochs were divided into four

598   500 ms windows, starting 2 s before action onset: [-2, -1.5 s], [-1.5, -1 s], [-1, -0.5 s], [-0.5, 0

599   s]. All p-values were Bonferroni corrected for four comparisons. To get a precise estimate of

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600   the standard error of the difference between conditions, paired-samples t-tests were

601   performed on jack-knifed data (Efron & Stein, 1981; Kiesel, Miller, Jolicoeur, & Brisson,

602   2008). Unlike the traditional methods, this technique compares variation of interest across

603   subsets of the total sample rather than across individuals, by temporarily leaving each

604   subject out of the calculation. In addition, we also performed cluster-based permutation tests

605   on SD (Maris & Oostenveld, 2007). These involve a priori identification of a set of electrodes

606   and a time-window of interest, and incorporate appropriate corrections for multiple

607   comparisons. Importantly, they avoid further arbitrary assumptions associated with selecting

608   specific sub-elements of the data of interest, such as individual electrodes, time-bins or ERP

609   components. The cluster-based tests were performed using the following parameters: time

610   interval = [-2 - 0 s relative to action], minimum number of neighbouring electrodes required =

611   2, number of draws from the permutation distribution = 1000.

612   To measure variability of RP amplitudes within each individual trial, the SD of the EEG signal

613   from FCz was measured across time in a 100 ms window. This window was applied

614   successively in 30 time bins from the beginning of the epoch (3 s prior to action) to the time

615   of action onset. We used linear regression to calculate the slope of the within-trial SD as a

616   function of time (Figure. 6A). This was performed separately for each trial and each

617   participant. Slopes greater than 0 indicate that EEG within the 100 ms window becomes

618   more variable with the approach to action onset. Finally, we compared slopes of this within-

619   trial SD measure between self-initiated and externally-triggered conditions in a multilevel

620   model with single trials as level 1 and participants as level 2 variables. Multilevel analysis

621   was performed in R (R Core Team, Vienna, Austria).

622   Time-frequency analysis was performed with custom written Matlab scripts. The

623   preprocessed EEG time series were decomposed into their time-frequency representation by

624   using Complex Morlet wavelet with 20 frequencies, ranging linearly from 5 to 30 Hz. The

625   number of wavelet cycles increased from 3 to 7 in the same number of steps used to

626   increase the frequency of the wavelets from 5 to 30 Hz. Power at each trial, each frequency

627   and each time point was measured by convolving the raw time series with the wavelet and

628   squaring the resulting complex number. The power at each frequency and each time point

629   was then averaged across trials for each participant. Edge artefacts were removed by

630   discarding the first and last 500 ms of the epoch. Baseline time window was defined as the

631   first 500 ms of the epoch (after removal of edge artefacts: 2.5 - 2 s prior to skip action).

632   Changes in power during action preparation was subsequently expressed as the percentage

633   of change relative to the average power during the baseline time window, across time at a

634   specific frequency. Baseline normalisation was performed by using the following equation:

$$percentage_{tf} = 100 \; \frac{power_{tf} - \overline{baseline_f}}{\overline{baseline_f}}$$

635

636   Values > 0 indicates that power at a specific frequency (f) and a specific time (t) is higher

637   relative to the average power at the same frequency during the first 500 ms of the epoch.

638   Finally, we asked whether percentage change in power relative to baseline differs between

639   self-initiated and externally-triggered skip conditions in the beta band (15 – 30 Hz). Beta

640   band Event-related Desynchronization (ERD) during action preparation is a well-established

641   phenomenon (Bai, Mari, Vorbach, & Hallett, 2005; Doyle, Yarrow, & Brown, 2005;

642   Pfurtscheller & Lopes da Silva, 1999). Beta power was calculated in a 500 ms window

643   starting from 1 s and ending 0.5 s prior to skip action. We avoided analysing later windows

644   (e.g., 0.5 - 0 s prior to action) to avoid possible contamination from action execution following

645   presentation of the red fixation cross that cued externally-triggered responses. The average

646   normalised power across all pixels within the selected window was then calculated for each

647   participant and compared across conditions using paired-samples t-tests.

648   *Modelling and simulations.*

649 All simulations were done in Matlab (MathWorks). We used a modified version of the Leaky

650 Stochastic Accumulator Model (Usher & McClelland, 2001), in which the activity of

651 accumulators increases stochastically over time but is limited by leakage.

$$\delta x = (I - kx)\Delta t + c\xi\sqrt{\Delta t}$$

652 Where I is drift rate, k is leak (exponential decay in x), ξ is Gaussian noise, c is noise scaling

653 factor, and Δt is the discrete time step (we used $\Delta t = 0.001$). This leaky stochastic

654 accumulator has been used previously to model the neural decision of 'when' to move in a

655 self-initiated task (Schurger et al., 2012). In that experiment, I was defined as the general

656 imperative to respond (with a constant rate). This imperative, if appropriately small in

657 magnitude, moves the baseline level of activity closer to the threshold, but not over it. Thus,

658 imperative alone does not trigger action, but does increase the likelihood of a random

659 threshold-crossing event triggering action. In the original model, c was assumed to be

660 constant and was fixed at 0.1. In a departure from the original model, we assumed that the

661 noise scaling factor could change linearly from an initial value of c_1 to a final value of c_2,

662 during action preparation. Consequently, Δc was defined as the magnitude of change in the

663 noise scaling factor during the trial.

$$\Delta c = c_2 - c_1$$

664 A negative Δc means that signal becomes less noisy as it approaches the threshold for

665 action. Therefore, the modified model in our experiment had five free parameters: I, k, c_1, c_2

666 and threshold.

$$\delta x = (I - kx)\Delta t + c_t\xi\sqrt{\Delta t}$$

667 Where c_t is noise scaling factor at time t. The threshold was expressed as a percentile of the

668 output amplitude over a set of 1000 simulated trials (each of 50,000 time steps each).

669 Epochs of simulated data were matched to epochs of actual EEG data by identifying the

670 point of first threshold crossing event within each simulated trial and then extracting an

671 epoch from 3000 time steps before to 1000 time steps after the threshold crossing.

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672   Parameter estimation for self-initiated skip action was performed by fitting the model against

673   the *real mean* RP amplitude of each participant in self-initiated condition. First, 1000 unique

674   trials of Gaussian noise, each 50,000 time steps, were generated for each participant and

675   were fed into the model. The initial values of the model's parameters were derived from

676   previous studies (Schurger et al., 2012). The output of the model was then averaged across

677   trials and was down sampled to 250 Hz to match the sampling rate of the real EEG data. A

678   *least squares* approach was used to minimise root mean squared deviation (RMSD)

679   between the *simulated* and *real* mean RP, by adjusting the free parameters of the model for

680   each participant (by using the MATLAB 'fminsearch' function). Note that this procedure

681   optimised the model parameters to reproduce the mean RP, rather than individual trials.

682   To fit the model to our externally-triggered skip condition, we fixed the threshold of each

683   participant at their best fitting threshold from the self-initiated condition. We wanted to keep

684   the threshold the same in both conditions so that we could test the effect of changing noise

685   levels for a given threshold. Importantly, we also fixed the value of c_1 at its optimal value

686   form the self-initiated condition. By using this strategy, we can ask how noisiness of the

687   signal *changes*, from its initial value, and we can compare this change in noise between

688   conditions. We additionally performed parallel simulations without the assumption of a

689   common initial noise level, and obtained essentially similar results. Specifically Δc in the all-

690   parameter-free model (mean= 0.02, SD = 0.06) was similar to the Δc in the model with c_1

691   and threshold fixed (mean= 0.02, SD = 0.05). The remaining parameters (l, k, c_2) were

692   optimised by minimising the deviation between the *simulated mean* RP and the *real mean*

693   RP in externally-triggered condition.

694   Finally, we tested the model on the across-trial variability of RP epochs, having *fitted* the

695   model parameters to the mean RP. All parameters of the model were fixed at each

696   participant's optimised values for the self-initiated condition, and for the externally-triggered

697   condition respectively. The model was run 44 times (22 participants, x 2 conditions) with the

698   appropriate parameters, and 1000 separate trials were generated, each corresponding to a

33

699   putative RP exemplar. The Gaussian noise element of the model ensured that these 1000

700   exemplars were non-identical. The standard deviation across trials was calculated from

701   these 1000 simulated RP exemplars, for each participant and each condition. Importantly,

702   this procedure fits the model to each participant's *mean* RP amplitude, but then tests the fit

703   on the *standard deviation* across the 1000 simulated trials. Finally, to assess similarity

704   between the real and predicted SD reduction, the predicted SD in self-initiated and

705   externally-triggered conditions was plotted as a function of time and the area between the

706   two curves was computed. We then compared the area between the SD curves in a 2 s

707   interval prior to self-initiated and externally-triggered conditions for all participants' simulated

708   data, and actual data (Figure 5), using Pearson's correlation.

709   **Author Contributions**

710   Conceptualization, N.K., P.H., A.S., and A.D.; Methodology, N.K. and A.S.; Software, N.K.

711   and A.D.; Formal Analysis, N.K., L.Z., and P.H.; Investigation, N.K., L.Z.; Writing-original

712   draft, N.K., Writing-review & editing, P.H., A.S., Supervision, P.H. and A.S.

713   **Acknowledgement**

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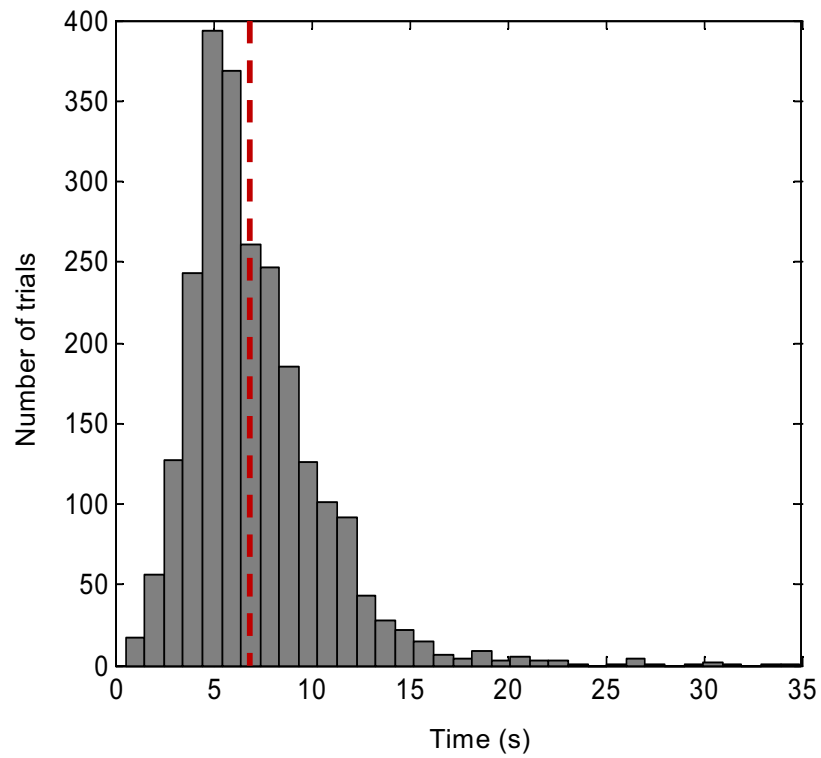
Supplementary Figures & Tables

Figure S1. Histogram of waiting times before skip actions in self-initiated condition, across all trials and all participants. The dashed red line shows the average waiting time.
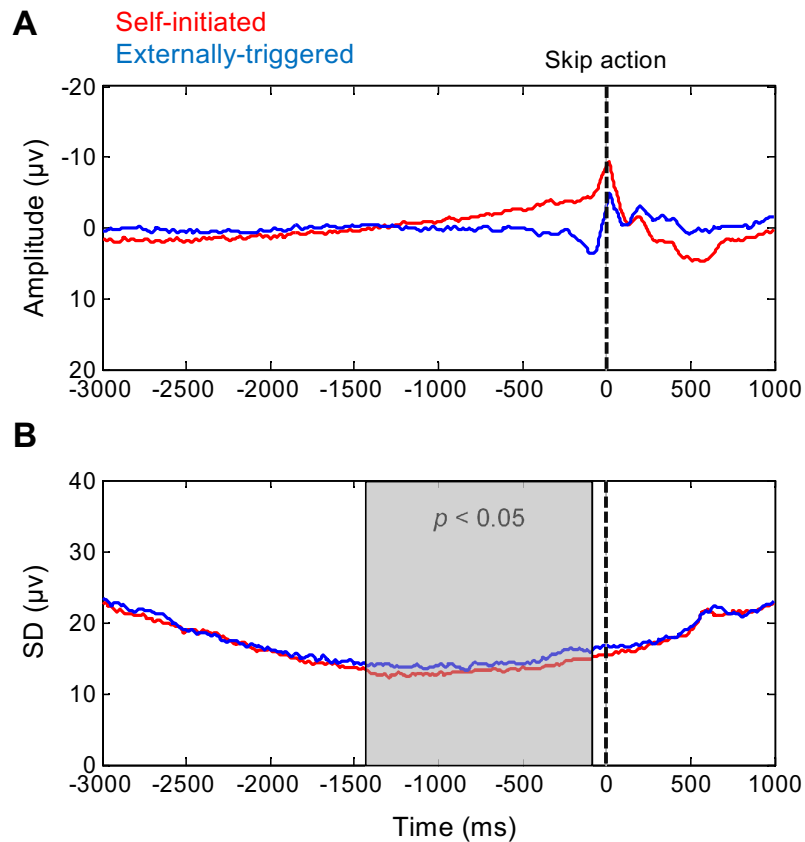
Figure S2. Demeaned EEG activity prior to skip actions. The red and blue lines represent self-initiated and externally-triggered skips, respectively. Data is time-locked to the skip action (black vertical line), and is baselined to the mean of entire epoch (i.e., demeaned), and recorded from FCz electrode. A. Grand average RP amplitude. B. Standard deviation across trials averaged across participants. Shaded area show significant clusters across central electrodes, detected by cluster-based permutation test. Whereas baselining to a limited time window forces a low SD within the baseline time window, and a progressive rise in SD with temporal distance before or after the baseline, the use of a broad baseline time window, as here, reduces this artefactual effect of baseline-correction on variability of time-locked data. Nevertheless, the difference in SD between conditions remains significant.

time=[-2 -1.9] time=[-1.9 -1.8] time=[-1.8 -1.7] time=[-1.7 -1.6] time=[-1.6 -1.5]

time=[-1.5 -1.4] time=[-1.4 -1.3] time=[-1.3 -1.2] time=[-1.2 -1.1] time=[-1.1 -1]

time=[-1 -0.9] time=[-0.9 -0.8] time=[-0.8 -0.7] time=[-0.7 -0.6] time=[-0.6 -0.5]

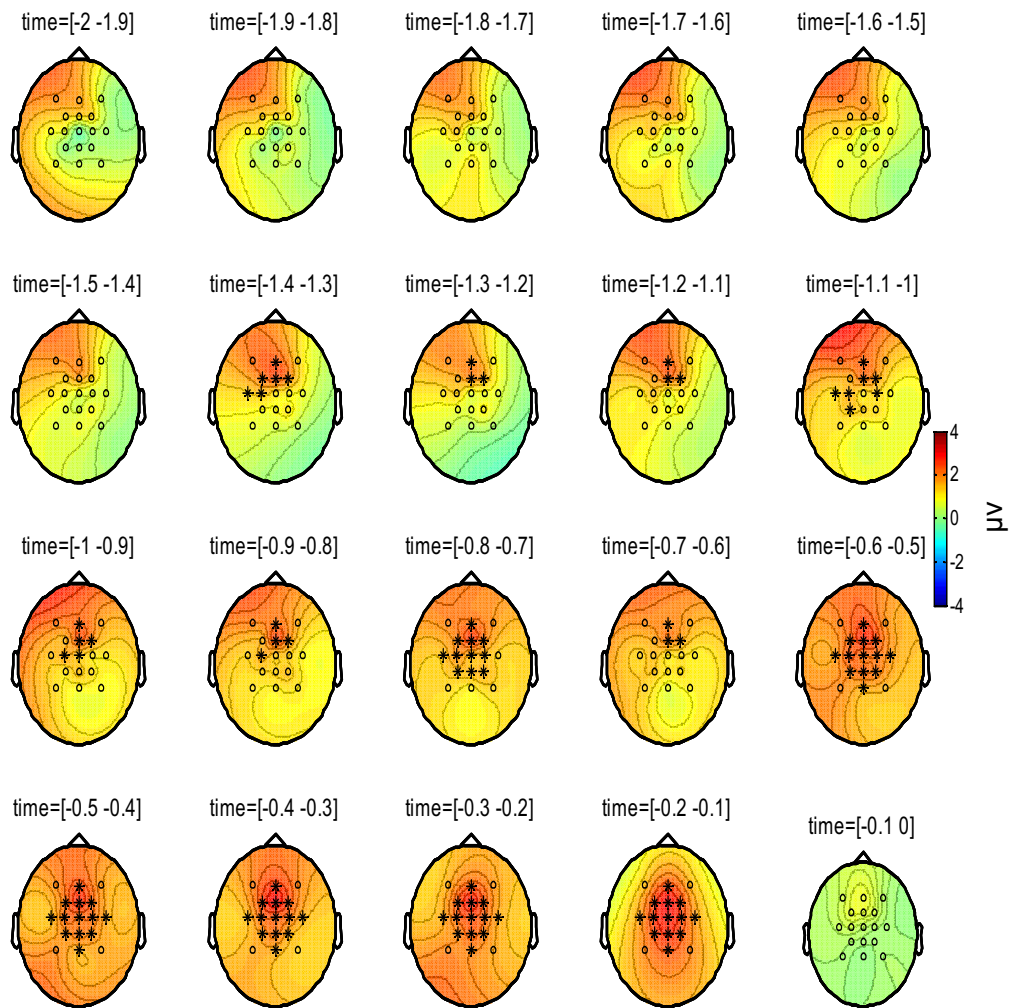time=[-0.5 -0.4] time=[-0.4 -0.3] time=[-0.3 -0.2] time=[-0.2 -0.1] time=[-0.1 0]

Figure S3. Topography of the difference in SDs between self-initiated and externally-triggered conditions. Small circles represent EEG electrodes across which the permutation test was performed. Electrodes that showed significant difference between conditions have been marked *. The time interval (s) is indicated above each subplot.
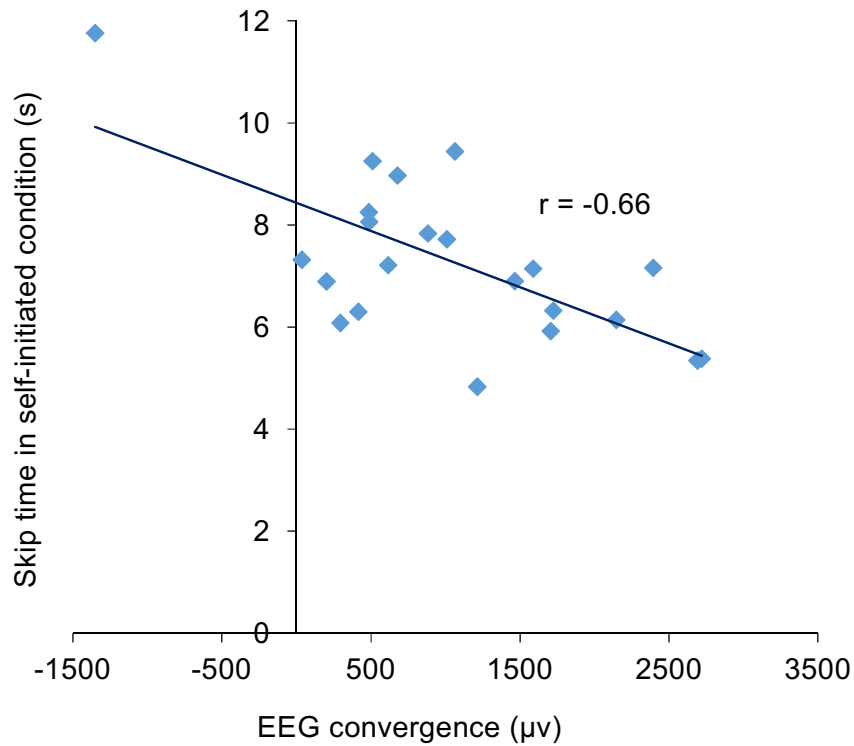
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Figure S4. Correlation between participants' mean waiting time (s) before skipping in the self-initiated condition and EEG convergence. EEG convergence was measured by subtracting the area under the SD curve in self-initiated from the externally-triggered condition. There was a significant negative correlation between waiting time and EEG convergence (Pearson's r = -0.66, p < 0.01).
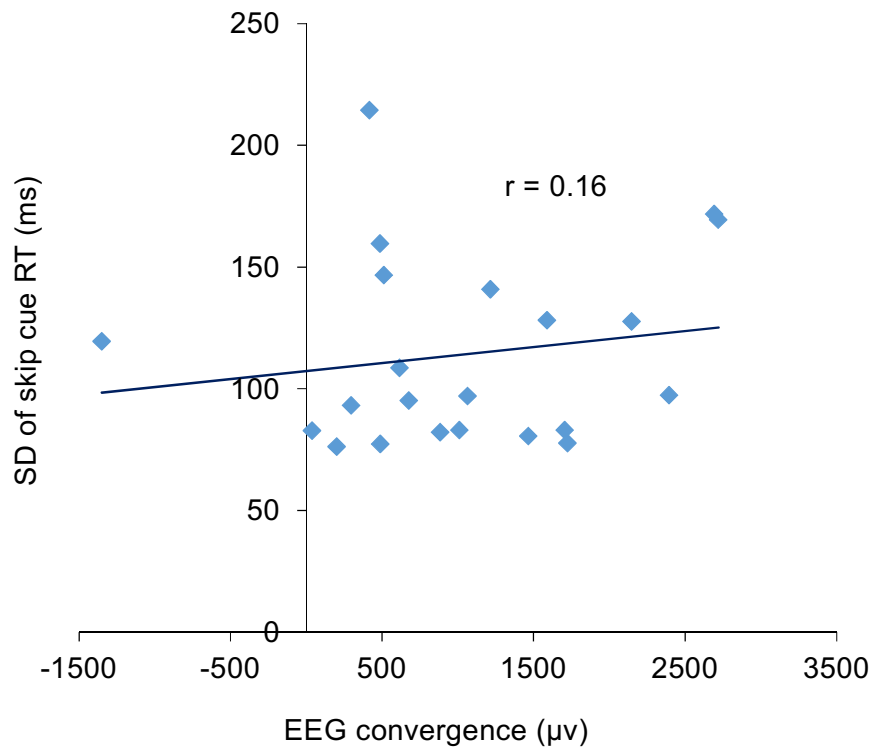
Fig S5. No significant correlation (Pearson's r = 0.16, p = 0.46) across participants between standard deviation of each participant's RT to externally-triggered skip cues (ms), and EEG convergence. EEG convergence was measured by subtracting the area under the SD curve in self-initiated from the externally-triggered condition.

Subject	Mean wait (s): self-initiated	Mean wait (s): externally-triggered	SD self-initiated	SD externally-triggered
1	11.76	12.09	6.82	6.79
2	5.38	5.76	2.27	2.30
3	6.14	6.45	4.58	4.61
4	7.16	7.45	3.25	3.22
5	8.25	8.39	4.57	3.97
6	7.21	7.70	3.22	3.27
7	5.92	6.20	1.66	1.67
8	7.83	8.16	3.20	3.23
9	6.08	6.48	1.26	1.20
10	6.32	6.54	2.96	2.68
11	5.34	5.85	1.00	1.01
12	6.89	7.28	2.72	2.70
13	4.83	5.23	1.83	1.82
14	8.06	8.23	2.66	2.54
15	8.97	9.44	3.60	3.60
16	9.25	9.66	5.85	5.91
17	6.30	6.81	2.69	2.61
18	7.72	8.14	2.53	2.57
19	6.90	7.16	2.94	2.93
20	7.32	7.80	2.40	2.62
21	9.44	9.85	2.93	2.94
22	7.14	7.73	4.74	5.19

Table S1. Mean and standard deviation of waiting time before skipping in self-initiated and externally-triggered conditions.

Drift (l)	Leak (k)	Initial noise (c_1)	Final noise (c_2)	Threshold	Change in noise (Δc)
0.04	-0.18	0.08	0.01	0.10	-0.07
0.11	0.55	0.12	0.13	0.14	0.00
0.11	0.57	0.13	0.11	0.18	-0.02
0.11	0.52	0.12	0.12	0.17	0.00
0.09	0.23	0.19	0.14	0.41	-0.05
0.01	0.38	0.23	0.13	0.42	-0.10
0.10	0.50	0.14	0.13	0.20	-0.01
0.12	0.62	0.10	0.14	0.08	0.04
0.11	0.57	0.11	0.13	0.11	0.01
0.02	0.27	0.25	0.12	0.44	-0.13
0.08	0.14	0.21	0.13	0.38	-0.08
0.11	0.53	0.12	0.12	0.13	0.01
0.09	0.11	0.21	0.12	0.35	-0.09
0.06	0.17	0.21	0.12	0.39	-0.09
0.07	0.28	0.19	0.14	0.36	-0.05
0.11	0.53	0.12	0.11	0.12	-0.01
0.11	0.54	0.12	0.12	0.13	0.01
0.08	0.22	0.18	0.12	0.29	-0.06
0.11	0.60	0.12	0.13	0.09	0.01
0.11	0.53	0.12	0.12	0.13	0.01
0.17	0.59	0.18	0.24	0.74	0.06
0.11	0.55	0.13	0.12	0.15	0.00

Table S2. Optimum parameters for self-initiated skip action. The values were detected by fitting the model against the mean RP amplitude of each participant in self-initiated condition. Δc was measured by subtracting the initial noise level (c_1) from the final noise level (c_2).

Drift (l)	Leak (k)	Initial noise (c_1)	Final noise (c_2)	Threshold	Change in noise (Δc)
0.09	0.42	0.08	0.10	0.10	0.02
0.11	1.01	0.12	0.21	0.14	0.09
0.10	0.35	0.13	0.13	0.18	0.00
0.16	0.70	0.12	0.16	0.17	0.04
0.12	0.48	0.19	0.18	0.41	-0.01
0.10	0.48	0.23	0.17	0.42	-0.05
0.09	0.26	0.14	0.07	0.20	-0.06
0.17	0.93	0.10	0.24	0.08	0.13
0.18	0.44	0.11	0.19	0.11	0.08
0.05	0.44	0.25	0.22	0.44	-0.03
0.10	0.38	0.21	0.17	0.38	-0.04
0.19	0.72	0.12	0.15	0.13	0.03
0.10	0.41	0.21	0.18	0.35	-0.03
0.08	0.54	0.21	0.17	0.39	-0.04
0.12	0.51	0.19	0.23	0.36	0.05
0.16	0.87	0.12	0.15	0.12	0.04
0.18	0.69	0.12	0.16	0.13	0.04
0.10	0.45	0.18	0.15	0.29	-0.03
0.21	0.75	0.12	0.17	0.09	0.05
0.17	0.77	0.12	0.20	0.13	0.09
0.10	0.61	0.18	0.20	0.74	0.01
0.16	0.58	0.13	0.16	0.15	0.03

Table S3. Optimum parameters for externally-triggered skip action. The values were detected by fitting the model against the mean RP amplitude of each participant in externally-triggered condition. Δc was measured by subtracting the initial noise level (c_1) from the final noise level (c_2). c_1 and the threshold were fixed at their optimum values in self-initiated condition (see materials and methods for more details)