Cortical beta power reflects a neural implementation of decision boundary collapse in a speeded flanker task

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Abstract

A prominent account of decision-making assumes that information is accumulated until a fixed response threshold is crossed. However, many decisions require weighting of information appropriately against time. Collapsing response thresholds are a mathematically optimal solution to this decision problem. However, evidence in favour of dynamic response thresholds and a neural implementation thereof is sparse. Here we combined predictions of a multistage drift diffusion model (DDM) and lateralization of movement selective EEG beta power (BPL) as a neural proxy of a decision signal to provide inside into this issue. We analysed a large dataset (n=863) from a speeded flanker task and data from an independent confirmation sample (n=119). We show that a DDM with collapsing decision thresholds captured participants behaviour better than a model with fixed thresholds. Previous research suggests that BPL over motor cortices reflects features of a decision signal and that its peak may serve as a neural proxy for the decision threshold. The modelled decision signal and BPL convergently support the assumption of collapsing decision thresholds, whereby the peak of the decision process decreased with increasing response times.

Introduction

We often make decisions under time pressure, precluding extensive evidence accumulation

in favour of or against choice alternatives. Imagine, for example, a basketball player who must

trade off the accuracy of a shoot against the amount of available time as a defender

approaches. Psychology and neuroscience have successfully utilized sequential sampling

models such as the drift-diffusion model (DDM) to understand the underpinnings of decision-

making Ratcliff et al. (2016). DDMs assume that motor executions of decisions are triggered

when the accumulated evidence for one option/alternative crosses a response threshold.

Traditionally, diffusion models assume a time-invariant decision policy, which is reflected in

fixed decision boundaries. However, as in the example above, this assumption may be ill-

posed on situations where decisions must be made under time pressure. Consequently, more

recently, diffusion models with collapsing decision bounds gained popularity (Hawkins,

Forstmann, et al., 2015; Palestro et al., 2018; Ratcliff et al., 2016). Here, as time passes,

decisions are triggered at decreasing decision thresholds. This facilitates terminating decision

making when no solution can be reached within the desired time frame.

While collapsing decision boundaries are a mathematically optimal solution to the

decision problem, except for some evidence in monkeys (Purcell & Kiani, 2016), no neural

data has confirmed a neural implementation of dynamic boundaries yet (Hanks &

Summerfield, 2017; Thura & Cisek, 2017). It has recently been suggested that the motor

cortex is involved in the decision-making process by continually sampling information in

favour or against response options (Cisek & Kalaska, 2005; Pape & Siegel, 2016). In the EEG,

this process is reflected in beta band (13-25 Hz) activity over centroparietal electrodes. It has

been shown that beta power over the contralateral motor-cortex decreases before any overt

action and even reflects imaginary movements (Kuhn et al., 2006). The difference in beta

power between both motor-cortices may thus encode the relative evidence in favour of

respective response options in a lateralised fashion (Donner et al., 2009; Pape & Siegel, 2016),

or, put more broadly, decisions in action-space (Cisek & Kalaska, 2005; Hunt et al., 2013). In

this line of research, we recently demonstrated that model parameters of a multistage drift-

diffusion model and the lateralisation of EEG beta power convergently show a complex

interplay that facilitates behaviour adaptations after erroneous responses in a flanker task

(Fischer et al., 2018). Specifically, suppression of distracting evidence, together with increased

response thresholds appear to cause slower and more accurate post-error responses. Based

on this work demonstrating a remarkable similarity of the time course of the decision variable

in the DDM and the beta power lateralization (BPL) over motor cortex, we argue that the BPL

peak around response time can serve as a proxy for response thresholds.

Here, we follow-up on this argumentation and investigate whether BPL can

demonstrate a plausible neural mechanism for collapsing decision thresholds in a large

sample of 863 healthy participants. We complemented our previous multistage DDM (Fischer

et al., 2018) by an additional free parameter that allowed decision bounds to collapse

according to a cumulative Weibull distribution. As depicted in Figure 1D, this model makes

distinct predictions about the decision threshold depending on speed: later decisions are

made at a lower threshold. We hypothesized that this decision threshold collapse would also

be reflected in a decreased BPL peak for slower responses. Indeed, we found that the

extended DDM provides a better fit for the data. This model predicts decision threshold

differences due to boundary collapse over time. This is confirmed in the beta band signal,

where slower responses show a decreased BPL peak. These data suggest that peak BPL

around response time, may serve as a neural proxy for the decision threshold. Taken together,

model predictions and their independently measured neuronal proxies in beta power

convergently support the assumption of collapsing decision thresholds.

4   **Results and Discussion**

Eight hundred and sixty-three healthy subjects performed a speeded arrow-version of an

Eriksen flanker task while EEG was recorded. Participants were instructed to respond as

quickly and accurately as possible to the direction of a centrally presented arrow (see Figure

1A). To elicit a large proportion of response errors, we presented distracting flanking stimuli

in visual proximity and slightly ahead in time (83 ms) of the imperative, central target

stimulus. On incongruent stimulus sets a mismatch between the flanker and target arrow

directions induced conflicting response tendencies. The response conflict was further

enhanced by manipulation of stimulus distances among each other (close and far,

Danielmeier et al. (2009)) and response-stimulus intervals (short and long, Danielmeier and

Ullsperger (2011)). To increase time-pressure, we kept the response stimulus intervals (RSIs)

and the response window of 1200 ms rather short. Behavioural analyses of this task confirmed

that general behaviour effects were in accordance with typical results seen in flanker tasks.

They reflected interference effects, with slower (ΔRT = + 62 ms, t(862) = -81.79, p < .001, d =

1.03, BF_{10} > 100) and more erroneous (Δaccuracy = 20%, t(862) = 96.18, p < .001, d = 3.44,

BF_{10} > 100) responses on incongruent trials, whereby these effects interacted with flanker

distance. Moreover, all error-related behavioural adaptations associated with cognitive

control (post-error slowing (PES), post-error increase in accuracy (PIA), post-error reduction

of interference (PERI)) were present. Overall participants responded accurately (mean

accuracy > 85%) and errors were committed at faster RTs compared to hits (see Fischer et al.,

2018 for a detailed description of these results).

An extended DDM with collapsing decision boundaries captures task behaviour best

We have previously shown that an extended multistage conflict DDM captures these

behavioural effects (Fischer et al., 2018). In brief, this model assumes that choice options are

mutually exclusive, so that a single decision variable is reflecting both decision options.

Features of the DDM are depicted in Figure 1C and D. On every trial, the decision can be

randomly biased slightly to one response option (startpoint variance, sz). The height of the

boundary parameter (a) determines how much evidence accumulation is required to cross

the boundary and trigger a response. The non-decision-time-parameter (T_{er}), reflects the time

from actual flanker onset until the information can be used to influence the decision process,

which in our model can vary from trial to trial (st). During flanker-only presentation, evidence

was accumulated in the direction of the flankers (83 ms). After target onset, evidence

accumulation is driven by the direction of the target. We previously demonstrated that a

model that allowed for trial-by-trial weighting of the distractor-driven diffusion (simulating

an attentional process suppressing the influence of the flankers) explained participants'

behaviour best (Fischer et al., 2018). Comparisons of model estimates fitted to either post-

error or post-correct trials revealed that post-error adaptations are facilitated by a complex

interplay of multiple mechanisms: suppression of distracting evidence, response threshold

increase, and reduction of evidence accumulation. Our DDM is very similar to previously

introduced DDMs that model behavioural effects in conflict task suggesting that drift rates

varies over time (e.g., the dual-stage (Hubner et al., 2010) or the shrinking spotlight model

(White et al., 2011)). Here, we use a simplified version of these DDMs, that only assumes that

attention shifts from flankers to the target once the target is on screen and that these two

stages of information processing can differ from each other (f) which should be different on

each trial (sf). Therefore, we did not have to simulate two processes (stimulus and response

selection - dual-stage (Hubner et al., 2010))) nor assume a shrinking function for the

attentional spotlight (shrinking spotlight model (White et al., 2011)). In addition, our task

design differs slightly from the designs used by Hubner et al. (2010) and White et al. (2011)

such that flanker stimuli alone precede the presentation of the full target-flanker stimulus

array which renders our simplification plausible. Moreover, it should be noted that we do not

exclude that separate racing accumulators are a valid model of speeded decision-making

under conflict. Yet, we previously demonstrated that the approximation in our DDM which

assumes that evidence for response A counteracts evidence for response B, is valid and

compatible with the neural signal reflected in BPL (Fischer et al., 2018). To investigate

whether dynamic decision boundaries explain subjects' behaviour better, we complemented

our multistage DDM by an additional free parameter that scaled decision bound collapse

according to a cumulative Weibull distribution (see Supplementary Figure 1 for illustration of

different boundary dynamics). As can be seen in Figure 1C, this model makes a specific

prediction: later decisions are formed at a lower threshold. Model comparison (Figure 2A - I)

revealed that our data is better described by the collapsing bound model than by the original

models with fixed bounds (described in the method section). This indicates that individuals

apply a discounting function that decreases decision thresholds when time is running out (i.e.,

the response window of 1200 ms closes). Overall, the model provided a good fit to the data.

Specifically, the model captured correct vs. error RT quantiles for congruent and incongruent

trials and conflict related accuracies (Figure2 F-I). While the full fixed boundary model (DDM3)

also provided a good fit to the data (Figure2 B-E), the collapsing boundary model appears to

capture the human data slightly better in later quantiles. Parameter recovery studies suggest

that this model was capable to reliably recover parameters that generated synthetic data (see

Supplementary Figure 3). To characterise predictions of the collapsing boundary DDM we

simulated 5000 individual trials using the mean of the best fitting individual parameters (see

Supplementary Table 1). When averaged across trials in a median-split analysis, the decision

signal shows clear response threshold differences, whereby fast responses show a higher

threshold (Figure 3E). Interestingly, our results are at odds with previous research identifying

evidence in favour of standard DDMs with fixed bounds in humans (Hawkins, Forstmann, et

al., 2015; Hawkins, Wagenmakers, et al., 2015; Ratcliff et al., 2016). In these studies, other

decision-making tasks were used (i.e., random dot motion, brightness discrimination, dot

separation) and DDMs treat (perceptual) interference trials as trials on which drift rates are

low to capture the increased RT and uncertainty on (error)-trials. However, lower drift rates

per trial cannot produce fast errors. Yet, fast errors are a hallmark of speeded reaction time

tasks, like our flanker task. Here, fast errors arise from an interaction of distractor-driven

biasing and trial-wise pre-lateralization of the decision variables as well as noise during

stimulus processing (Fischer et al., 2018). Moreover, in contrast to most other decision-

making tasks, after flanker and target presentation (which was only presented for 33 ms in

our task) no further information could be sampled to inform decisions. Thus, decision policies

might be task-dependent and affected by various factors. It is also possible, that mild

collapsing decision boundaries were present in previous investigations, but not clearly

identifiable in model fit comparison (Murphy et al., 2016). Specifically, Murphy et al. (2016)

argue that several popular fixed thresholds DDMs include variability parameters, that are able

to capture similar behavioural effects as in dynamic boundary DDMs (e.g., Brown &

Heathcote, 2008; Murphy et al., 2014), which precludes discrimination between the two

model classes. Indeed, our fixed boundary model (DDM3) included variance parameters and

captured subjects' behaviour well. On average, the boundary collapse in DDM4 was mild (see

Figure 1D) and, hence, only affected a small percentage of trials. The differences between

fixed and dynamic boundary models therefore may exert a hard-to-detect influence on

likelihood estimates in small samples and with methods commonly used for model

comparison (e.g., summed BICs). Yet, predictions of different sequential sampling model

classes can be highly informative to differentiate between different mechanistic accounts. In

this line of thought, we also considered a different kind of dynamic decision model. In this

model, decision making under time pressure is facilitated by an urgency signal (Cisek et al.,

2009; Hanks et al., 2014). Here, an urgency signal that increases with decision time is used as

a multiplicative gain of the diffusion and noise (DDM5; see Supplementary Figure 1 and 2A

for an illustration). Both dynamic DDMs capture RT quantiles and accuracies better than the

time-invariant models (Supplementary Figure 2B) but make distinct predictions regarding the

response threshold. While the collapsing bound model predicts that slower responses are

made at lower decision boundary thresholds, the urgency model would predict similar

decision boundaries for slow vs. fast responses (Supplementary Figure 2D). We test the neural

plausibility of these accounts in the next section.

Figure 1. Task information, model features and predictions.

(A) In the flanker task either congruent or incongruent flankers (four surrounding arrows) in proximity or further away from the central target (inlet) are presented on each trial. Congruent stimuli usually yield faster responses (green) compared to incongruent stimuli, which lead to delayed responses (orange) or induce fast errors (red) **(B)**. **(C-D)** Illustration of the multi-stage DDMs based on simulated single trial decision processes. On a given trial, the decision can be randomly biased to favour one response (startpoint variance, $sz_{(t)}$). The first stage of the respective model consisted of a pre-stimulus zero-mean baseline for which the value is determined by the start-point ($z_{(t)}$) (Stage 1). After flanker presentation (0 ms), visual processing and motor execution times are captured by the non-decision time (T_{er}) parameter, which can vary from trial to trial (st). In this period the decision process randomly

drifts away from the start point (Stage 2). The next stage represents a noisy diffusion in flanker direction ($f_{(t)}$) for the duration of the SOA which again can vary from trial to trial (sf) (Stage 3 - flanker diffusion). After flanker diffusion, stage 4 models the consecutive diffusion into the correct response direction with drift rate $v_{(t)}$ with trial-to-trials variance (sv). Longer RTs for incongruent correct trials are due to an initial drift away from the correct response (orange decision process). Error likelihood increases when the baseline is shifted towards the flanker direction and $f_{(t)}$ is higher on a given trial resulting in an early crossing of decision boundaries (red decision process). As a result, errors are usually faster on incongruent trials. Finally, Stage 5 models the return to baseline of the decision variable, akin to an Ornstein-Uhlenbeck process. The height of the boundary parameter (a) determines how much evidence accumulation is required to cross the boundary and trigger a response. Which can either be fixed **(C)** or collapse with increasing decision time **(D)**. To simulate the temporal evolution of the single trial decision process depicted in **(C)** and **(D)** we used the mean maximum likelihood parameters from the group fit obtained for DDM3 and DDM4.

Figure 2. Drift-diffusion model fits and model validation.

(A) Cumulated approximated Bayesian Information Criterion (aBIC) scores over participants of each candidate model. Higher values indicate a better fit of the models to the behavioral data. Results indicate that the dynamic bound model (DDM4) provides the best fit to the data. Protected exceedance probabilities (pEP) similarly favor DDM4. **(B − I)** shows quantile fits of the model (**B-D** DDM3, orange; **F-H** DDM4, green) against human RT data (light blue) and **(E and I)** shows model and human accuracy (**E** DDM4; **F** DDM3). In all conditions (congruent & incongruent correct as well as incongruent error), both models capture the RT data in each quantile, suggesting a good fit to the data. However, the collapsing boundary model appears to capture the variance in the data better (particularly in the later RT quantiles). **(J)** The collapsing boundary model included nine free parameters. In addition to the standard-parameters (DDM3) reflecting drift rate (v), flanker weighting (f), boundary (a), and non-decision time (Ter), and variance parameters that determined how much standard-parameters varied from trial-to-trial (sv, sz, st, sf), the dynamic boundary model included the free parameter k that scaled the boundary collapse that increases with the duration of the decision See Supplementary Table 1 for more details on the Maximum likelihood parameters of three best fitting DDMs. **(K)** shows simulated boundary collapse (details on the simulation procedure can be found in the methods). **(B - J)** boxes = interquartile range (IQR), o = median, - = mean, whiskers =1.5 × IQR, grey dots = outlier.

Figure 3. Response-locked power spectra, beta power, and DDM decision variable.

(A) Shows the result of a single-trial regression analysis comparing responses with the left and right

hand, while controlling for congruency, flanker distance, response stimuli intervals (RSI), following RSI,

trial number, and log transformed RT. Data suggests, that Beta power more strongly decreases when

a response is given with the contralateral compared to the ipsilateral hand. This effect was most

pronounced over the electrodes C3/4 and CP3/4. Beta power lateralization signal **(C)** is composed of

the activity-difference recorded over contralateral and ipsilateral motor cortices **(B)**. **(D - G)** shows

neural stimulus processing locked to response separated by response speed, congruence, accuracy,

and previous accuracy. First, we show that in BPL as well as modelled signal a lateralisation towards

the given response is pronounced for fast response **(D & H)**. Importantly, BPL at response execution

is reduced for later responses. This observation confirms dynamically changing decision bounds within

a trial and is also reflected in the modelled signal **(H)**. In addition, when comparing RT-matched correct

congruent and incongruent trials, we found a significant difference at response execution **(E)**.

Exploratory analysis of the lateralised signal (see Supplementary Figure 4) demonstrated that this

effect is caused by reduced activation (i.e., increased beta power) of the ipsilateral hemisphere on

congruent trials compared to incongruent ones. This likely reflects enhanced motoric readiness caused

by the flanker stimuli. This effect is not captured by the DDM signal **(I)** because it does not include

threshold differences between trials. When comparing RT-matched correct and error responses **(F &**

K), we demonstrate that both conditions are associated with similar thresholds in BPL. This effect is

similarly reflected in the modelled DDM signal. Finally, we demonstrate that BPL at response execution

is increased on response matched post error trials **(G)**. This may reflect strategic decision policy

adaptations to increase accuracy after errors (Fischer et al., 2018; Murphy et al., 2016). Again, this

effect is not reflected in the modelled DDM signal because this model does not include threshold

differences between trials **(K)**. *Note.* Contours in **(A)** represent significant clusters after cluster-based

permutation testing (Maris & Oostenveld, 2007). Shades in **B-K** represent 99.9% CIs. Grey

backgrounds in indicate significant time-points after Bonferroni correction. In **H-F** we rectified the

modeled diffusion signal to always plot the unchosen response up and the chosen response down. For

details about the simulation see Methods.

Cortical beta power lateralization reflects neural implementation of decision boundary

collapse

Next, we tested the hypotheses that the response-locked BPL represents a neural

implementation for decision boundary collapse. First, we confirmed that beta power

decreased more at centro-parietal electrodes contralateral to the initiated response (see

Figure 3A-C), suggesting that BPL reflects differential motor activation (Donner et al., 2009;

Pfurtscheller, 1981). When averaged across trials in a median-split analysis, differences in BPL

are clearly evident in the response locked data, where fast responses show a higher BPL (i.e.,

higher decision boundary; fast RT: -0.13 (SD: .003) vs. slow RT: -0.10 (SD: .003); $t(862) = -9.58$,

$p < .001$, $d = 0.25$, $BF_{10} > 100$, see Figure 3D). The representation of RT is similarly reflected in

the modelled DDM signal (Figure 2H). Thus, collapsing boundaries are confirmed by response-

locked BPL, indicating that humans make use of a discounting function to decide earlier to

fulfil a time criterion. To confirm this finding on a single-trial level we regressed task-related

behavioural factors onto measured individual single-trial BPL at response execution (button

press ±12ms). This allows to control for other task factors that may additionally influence BPL

but are not of primary interest for this short report (but see Supplementary Figure 4 for more

details on these results). The regression analyses confirmed that BPL was decreased (i.e.,

boundary collapse) for slower RTs ($t(862) = 13.26$, $p < .001$, $d = 0.45$, CI [0.46, 0.62], $BF_{10} >$

100, see Figure 4A). Plotting the RT quantiles against the BPL at response execution confirms

a boundary collapse that closely resembles a sigmoidal function (Figure 4B). In an explorative

analysis, we split the regression analysis by ipsilateral (hemisphere that does not induce the

choice on the current trial) and contralateral hemispheres to better understand which

hemisphere drives RT-related BPL decreases (see Figure 4C). Results indicate that threshold

decreases are partly due to slightly stronger decreases in beta power over the contralateral

hemisphere (contralateral: $t(862) = 5.13$, $p < .001$, $d = 0.17$, CI [.19, .42], $BF_{10} = 1.57e^{+4}$ vs.

ipsilateral: $t(862) = -3.68$, $p < .001$, $d = 0.12$, CI [-.33, -.10], $BF_{10} = 32.10$). In the averaged beta

power signal, this effect is partly explained by a reduction of beta power over the contralateral

hemisphere (Figure 4D left), while on average beta power decrease over the ipsilateral

hemisphere is barely changed when responses are given later in a trial (Figure 4D right).

However, the effect is stronger when the relative signal per trial is investigated, than when

either of the hemispheres beta power is analyzed alone (contrast contralateral against BPL

effect: $t(862) = 3.87$, $p < .001$, $d = 0.23$, $BF_{10} = 63.47$). These data suggest that peak BPL,

coinciding with the motor response, may be an especially valid marker of response threshold

modulations. However, it should be noted, that this assumption may be limited to speeded

forced-choice tasks with short reaction times and evidence accumulation (Rogge et al., 2022).

Specificity of the effects to the beta frequency range

Similarly to BPL, lateralization in the alpha (8 −12 Hz, APL) and µ (8–14 Hz, MuPL) frequency

band over the motor cortex has been related to a variety of decision processes, such as

decision formation and preparation (e.g., Donner et al., 2009; Pape & Siegel, 2016; Rogge et

al., 2022) or urgency of a decision (Murphy et al., 2016). In a control analyses we therefore

aimed to establish specificity of our effects to the beta frequency range. First, we confirm that

sensorimotor alpha and µ power similarly reflected response-related signals and that this was

specifically lateralised to the active motor cortex (see Figure 3A and Supplementary Figure 5).

Yet, effects are smaller and peak slightly after responses are made (Supplementary Figure B

and D). To quantify the effect differences on a single-trial level, we regressed response speed

onto measured individual single-trial APL and MuPL at response execution while controlling

for other task factors (see Supplementary Figure 6 for details). Results revealed that, response

speed is similarly reflected in movement selective alpha and μ suppression, but that this effect

is more pronounced in the beta frequency range (BPL vs. APL: .54 (.04) vs. .23 (0.04); t(862) =

6.43, p < .001, d = 0.26, BF_{10} > 100; BPL vs. MuPL: .54 (.04) vs. .28 (.04); t(862) = 6.15< .001, d

= 0.26, BF_{10} > 100). In addition to the alpha and µ frequency band, an opposite effect was

present for lateralization in the theta frequency band (4–8 Hz) with a similar topography (see

see Figure 3A and Supplementary Figure 5 and 6), which is not further interpreted in this

report.

Conclusion and implications for beta power function in the decision process

Here, we show convergent evidence from motor preparation signals and behavioural modelling that dynamic decision thresholds facilitate termination of decision-formation under high time pressure. Taken together, our results extend previous work on BPL as a neural signal that carries important features of a decision variable (Donner et al., 2009; Fischer et al., 2018; O'Connell & Kelly, 2021). Recent work has suggested that beta power suppression around response contralateral to the chosen hand reaches a highly similar level, irrespective of urgency or response speed, suggesting a fixed response threshold (Corbett et al., 2023; Feuerriegel et al., 2021; Kelly et al., 2021; Murphy et al., 2016; Steinemann et al., 2018). In line with this account, it has been suggested the beta power over the right and left motor cortex is reflecting two race-to-(response-)threshold motor preparation signals (Corbett et al., 2023; Kelly et al., 2021; O'Connell et al., 2012). Under time-pressure, speeding is facilitated by an urgency signal that independent but in addition to evidence, drives the signal towards the response threshold (Cisek et al., 2009; Corbett et al., 2023; Hanks et al., 2014; Murphy et al., 2016; Steinemann et al., 2018). Our results challenge this interpretation, suggesting that response thresholds are dynamic and that peak BPL (i.e., the relative beta signal), coinciding with the motor response, may be an especially valid marker of response threshold modulations. In an independent confirmation sample (n = 119) collected at a different site, but using the same study protocol, we replicated all key findings (see supplementary results). Thus, in this study we provide strong, converging evidence for the existence of time-dependent within-trial response threshold adjustments. How can this discrepancy in findings be explained? One factor that likely contributes to the differences is the nature of our task. In our task, after flanker (83ms) and target presentation (which was only presented for 33 ms in our task) no further information could be sampled to inform decisions. In contrast, other studies typical use paradigms in which evidence can be accumulated until the response is

made (e.g., random dot motion paradigms). Hence, the differences in findings may highlight

that decision policies may not be generalized across tasks. It is also possible, that within-trial

adjustments of response thresholds are small. Here, we draw inference from a large sample

and likely have the power to detect even small time-depended changes. Supporting this

argument, on average the bound collapse in our behaviour model is small. In addition, beta

amplitudes vary quite widely across groups and thus small effects might be difficult to detect

in smaller samples. Indeed, even our confirmation sample is considerably larger than in

average EEG studies. Finally, our results do not exclude the possibility of an urgency signal as

suggested by Thura and Cisek (2017). It may be, that instead of increasing the gain in the

decisions process, the urgency signal in the globus pallidus modulates decision thresholds in

the cortex. Yet, this argumentation remains speculative.

Taken together, our results relate to previous work investigating how movement-

selective beta power facilitates dynamic decision policy adjustments to facilitated task

demands at hand and suggest, that collapsing response thresholds may be one mechanism

via which fast-paced decisions under time-pressure can be achieved.

2 **Figure 4. Single-trial regression on beta-power lateralization at response.**

(A) Results of a single-trial regression analysis on BPL at response (mean ± 12ms surrounding button press). This analysis confirms collapsing decision boundaries on a single-trial level while controlling for other task factors that potentially influence BPL. **(B)** BPL raw values for RT quantiles plotted against BPL at response. Fitting the mean values trajectory confirms boundary collapse that closely resembles a sigmoidal function (black line expressed with: ymin = -0.13, ymax = -0.09, x0 = 4.89, and slope = 0.49, adjusted R^2 = .95). **(C)** Display results of separate regression analyses on beta power split by ipsilateral (hemisphere that does not induce the choice on the current trial) and contralateral hemispheres. RT related BPL decrease is partly due to slightly more decreases over the contralateral hemisphere. In the averaged beta power signal, this effect is partly explained by a reduction of beta power over the contralateral hemisphere **(4D left)**, while on average beta power over the ipsilateral hemisphere is barely changed when responses are given later in a trial **(D right)**. **(A)** boxes= interquartile range (IQR), o = median, - = mean, whiskers =1.5 × IQR, grey dots = outlier. Error bars reflect standard error of the mean. **(A and C)** depicts mean within participants t-values, and statistics are results of t-tests of individual within-subject regressions against zero. RSI reflects the response-stimulus interval, NLD the distance from the last break in the task, and trial the general time on task.

Materials and methods

Participants

Eight hundred ninety-five healthy young adults were recruited into the study. After exclusion of participants due to low task performance, recording failures, or poor data quality, 863 participants remained for subsequent analyses. The mean age of the sample including 434 female and 429 male participants was 24.2 years (range: 18–40). A detailed description of the sample characteristics and exclusion criteria can be found in Fischer et al. (2018).

Task

We employed a speeded arrow version of the Eriksen flanker paradigm in that participants were encouraged to respond as quickly and correctly as possible to the direction of the target arrow presented in the centre of the screen. The target could point either to the right or the

left side, requiring a corresponding response with the right or left thumb. We additionally

modulated response-stimulus intervals (short = 250ms, long = 700ms) as well as the distance

between the imperative central and distracting flanker arrows (far distance: 6.5° and 4°, and

close 3.5° and 1.75° visual angle). In total the task comprised 1,080 trials (see Fischer et al

2018, for more details on the task). A short response window of 1200ms and short RSIs

ensured high-time pressure.

Drift-diffusion model and model comparison.

Features of the multi-stage sequential sampling models one to three, and general fitting

procedures were exactly as described by Fischer et al. (2018). The description is adapted from

therein. We used a multi-stage sequential sampling model to simulate participants' RT and

accuracy distributions and the decision process giving rise to these. This discrete diffusion

model simulates decisions as a Wiener process with stepwise increments according to a

Gaussian distribution with mean v (called drift rate) and variance s on every trial. Here, v

reflects the speed of evidence accumulation and s the system's noise, which scales all other

parameters and is usually fixed (here to 0.1). The step size for all models was set to 1ms.

Responses are triggered when the diffusion reaches a criterion (boundary, determined by the

free parameter ± a). We assumed that there was no bias in response selection over the task,

because we had an equal number of left and right responses. However, individual trials were

allowed to start with a random bias towards one response (start-point variability, parameter

sz). We used symmetrical boundaries which were defined as left-hand responses when the

positive boundary was reached first, and as right-hand responses when the negative

boundary was reached first (see Figure 1B for more details). The non-decision time was

modelled as another free parameter T_{er}. The stages of the model per trial were defined as a

zero-mean baseline until flanker onset, a noisy diffusion with v = 0 during the non-decision

time, a diffusion driven by the flanker direction between flanker and target onset (83 ms) with

drift = vt × ft, and the target phase thereafter with drift = **vt** and the direction of the target.

Single-trial values **vt** and **ft** were determined according to Gaussian variance parameters **sv**

and **sf**. For display purposes, in Figure. 2F, we modelled a consecutive return of the decision

variable to baseline similar to an Ornstein-Uhlenbeck process to facilitate comparisons

between model and BPL. To speed up the model fitting procedure, we did neither simulate

baseline periods nor return to baseline during the fitting because these have no effect on

model predictions. We compared four different variants of the DDM by fitting their

parameters to RT and accuracy data observed in the group of 863 participants using quantile

maximum likelihood statistics (Heathcote et al., 2004) and differential evolution algorithms

(Price et al., 2005). Additionally, we used a mixture model assuming 2% outliers that were

distributed uniformly over the full range of RTs in correct and error responses. This

downweighs the impact of possible outliers on model parameters. DDM model 1 used the

same drift rate during flanker and target processing, thus not allowing for suppression of

distractors (parameter **f** fixed to 1). DDM model 2 fixed parameter **f** which suppressed flanker

processing when below the value of 1. DDM model 3 furthermore included trial-by-trial

variance in **f** modelled as a zero-mean Gaussian distribution with variance **sf**. The fourth DDM

model extended DDM model 3 to allow for a dynamic decision boundary collapse according

to a Weibull distribution scaled by the free parameter **k**. Here, the dynamic boundary **u** at

time **t** was calculated as follows:

$$u_t = a - \left(1 - \exp - \left(\frac{t}{k}\right)^s\right) * \frac{a}{2}$$

In this equation, a represents the initial boundary value and k scales the Weibull distribution (see Supplementary Figure 1 for illustration of the impact of this parameter on boundary dynamics). The shape parameter s was fixed at 3, to impose a "late collapse" decision strategy. This value/shape was informed by results from a previous study in a large human sample (Hawkins, Forstmann, et al., 2015).

For model comparison, we first computed approximated BIC values (aBIC; akin to White et al. (2011)). Next, we used these individual aBIC values to computed protected exceedance probabilities, which gives the probability that one model was more likely than any other model of the model space (Rigoux et al., 2014).

To simulate the temporal evolution of the modelled diffusion signal depicted in Figure 3 we used the mean maximum likelihood parameters from the group fit obtained for DDM 4. For this simulation, we computed 5000 simulated trials.

EEG processing

EEG was recorded at 500Hz from 60 Ag/AgCl sintered electrodes with A1 as reference channel and an electrode placed over the sternum as the ground electrode arranged in the extended 10-20 system using BrainAmp amplifiers (Brain Products, Gilching, Germany). Impedances were kept below 5 kΩ. Pre-processing of the EEG data was done under Matlab 2021b (The MathWorks, Natick, MA) and the EEGlab 13 toolbox (Delorme & Makeig, 2004) using custom routines as described previously (Fischer et al., 2018). Pre-processing steps included: (1) Filtering (0.5 Hz high- and 42 Hz low-pass filter), (2) re-referencing to common average, (4) Segmentation into stimulus-

locked epochs spanning −1.5 to 2 s relative to target onset, (5) automatic epoch rejection. Here,

epochs contaminated with artefacts were rejected using a dynamically adjusted rejection

threshold to remove at least 1 trial separately for error and correct responses and maximally

5% per condition (average number of rejected epochs: 41, range 11–53). (6) removal of blink,

eye-movement, and other, less homogenous artefact components (average number of removed

components = 3.4, range 1–14) using adaptive mixture independent component analysis (AMICA;

Palmer et al., 2012). Finally, we extracted response-locked epochs spanning from −1 to 1 s from

the stimulus-locked epochs.

EEG analyses

First, we convolved the artefact free response-locked EEG signal, with a series of complex

Morlet wavelets between 13 and 25 Hz. We used 20 linear steps and a wavelet width of six

cycles. Data were then log-transformed and normalized. When comparing the averaged signal

over contralateral (electrodes C3/CP3 for right and C4/CP4 for left) and ipsilateral (electrodes

C3/CP3 for left and C4/CP4 for right) motor cortices, we show an overall decrease in beta

power around 300ms prior to the response, which was followed by a consecutive increase in

beta power (i.e., beta rebound) around 400ms post response (Figure 3c). To confirm the

lateralisation of the signal to the hemisphere initiating a response, we used single-trial

multiple robust regression. Here, we regressed the factor response hand (-1 = left, 1 = right)

onto the convolved signal across the collapsed frequency range of 13–25 Hz for every

electrode and time point, while controlling for unspecific task effects. Noise-Regressors

included: congruency, flanker distance, RSI, following RSI, trial number, and log transformed

RT. This analysis confirmed response related beta band lateralisation, whereby beginning

around 100ms before response onset, beta power decreased over the sensorimotor cortex

contralateral to the response. This was reflected in a positive covariation between response hand and the signal in the beta band which was maximal at C4/CP4, and a negative covariation at maximal at C3/CP3 (Figure 2a). We chose electrodes with a maximal effect (C3, C4, CP3, CP4) for all further analyses of lateralised beta power (BPL).

To derive BPL we subtracted beta band power over the inactive sensorimotor cortex (i.e., the electrodes side ipsilateral to the hand that gave the response in the trial) from the beta power recorded over the active (contralateral) sensorimotor cortex. This difference signal thus compares the degree of beta power reduction between both hemispheres, presumably reflecting differential motor activation (see Figure 3). To investigate single-trial associations of beta thresholds and RT, we used the response-locked single-trial signal (mean ± 12 ms) and regressed the log-transformed RT onto the beta threshold while accounting for unspecific task effects according to the following equation:

$$BPL\ Threshold\ =\ b_0 + b_1 * Congruency + b_2 * Accurancy + b_3 * RSI + b_4 *$$
$$Previous\ Accurcay + b_5 * Trial + b_6 * \log(RT) + e$$

In an explorative analysis, we used the same model to test the separate contributions of each hemisphere (ipsilateral and contralateral beta power).

Data and code availability

The conditions of our informed consent form do not permit public archiving of the raw data because participants did not provide sufficient consent. Researchers who wish to access processed and anonymized data from a reasonable perspective should contact the corresponding author. Data will be released to researchers if it is possible under the terms of

the GDPR (General Data Protection Regulation). The code of the toolbox we used for the

regression analysis can be found here: http://www.adrianfischer.de/teaching.html. The code

for the DDM models is available on request. Data and analyses scripts of the confirmation

sample can be downloaded on the Open Science Framework at [insert after acceptance for

publication].

Acknowledgments

This research was supported by the Deutsche Forschungsgemeinschaft (KL 2337/2-1 to TAK,

UL 196/3-3 to MU) and by the European Research Council (ERC) under the European Union's

Horizon 2020 research and innovation programme (ERC advanced grant agreement No

101018805 to MU).

Declaration of Competing Interest

The authors declare no conflict of interest.

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Supplementary Materials

Additional info on DDMs

Parameter	DDM3 Mean (SD)	DDM4 Mean (SD)	DDM5 Mean (SD)	boundary parameters (i.e., boundary of flat prior)
Drift rate **(v)**	4.54 (1.42)	4.23 (1.46)	4.17 (1.48)	0.01 - 8.5
Variance in drift rates **(sv)**	0.79 (0.54)	0.80 (0.54)	0.83 (0.53)	0 - 1.5
Boundary **(a)**	0.37 (0.08)	0.37 (0.07)	0.37 (0.08)	0.01 - 0.45
Variance in start points **(sz)**	0.19 (0.09)	0.17 (0.09)	0.18 (0.09)	0.05 - 0.3
Non-decision time **(T_{er})**	0.29 (0.02)	0.29 (0.02)	0.29 (0.02)	0.1 - 0.4
Variance in T_{er} **(st)**	1.14 (0.41)	1.15 (0.41)	1.15 (0.43)	0 - 2
Flanker suppression **(f)**	0.48 (0.25)	0.47 (0.27)	0.49 (0.28)	0 .1 - 1.5
Variance in **f**	0.70 (0.29)	0.75 (0.27)	0.75 (0.28)	0 - 1.5
Boundary collapse / gain parameter **(k)**	-	2.41 (0.60)	2.49 (0.59)	10e-4 - 3
(fixed) noise of within-trial diffusion **(s)**	0.1	0.1	0.1	0.1
(fixed) average start point bias **(z)**	0	0	0	0

Supplementary Table 1 - Maximum likelihood parameters of three best fitting DDMs.
The table shows the parameters obtained by fitting the models to the individual subject data. DDM3 was comprised of the standard-parameters reflecting drift rate (v), flanker weighting (f), boundary (a), and non-decision time (Ter), and variance parameters that determined how much standard-parameters varied from trial-to-trial (sv, sz, st, sf). DDM4 extended DDM3 to allow for a dynamic decision boundary collapse according to a Weibull distribution scaled by the free parameter k. In DDM5 the free parameter k is used as a multiplicative gain (urgency signal) instead of boundary collapse. In this model bounds are fixed but evidence accumulation is subject to a gain signal that increases with the duration of the decision. See Supplementary Figure 2 for examples of dynamic bound models and their relation to the scaling parameter k. In all models, diffusion noise (s) was fixed to 0.1 as commonly seen in the literature (e.g., White et al., 2011). To translate Ter values and their variance into ms they must be multiplicated by 1000 and 100 respectively. We set the bias parameter for start points (z) are set to zero for all models because the task included exactly 50% left- and right-hand responses.

Supplementary Figure 1. Illustration of different within-trial bound dynamics.
(A) Three illustrative boundary collapse trajectories depending on the scaling parameter k. Here,
smaller values are associated with faster boundary collapse. **(B)** Depicts 3 different urgency signal
trajectories. The urgency signal (orange line) is used as a multiplicative gain of the diffusion and noise.
As for the boundary collapse models, lower values of the free parameter k are associated with a
stronger urgency signal. All trial simulations used the fitted group means (see Supplementary table 1)
except the dynamic decision bound scaling factor that was set to either 1, 2 or 3. For model fitting we
applied the following hard priors for k, which can be seen as boundary parameters: [10e-4 − 3].
10

Urgency model details

We also considered a different kind of dynamic decision boundary model. In this model,

collapsing decision boundaries are facilitated via an urgency signal (Cisek et al., 2009; Hanks

et al., 2014). Here, an urgency signal that increases with decision time is used as a

multiplicative gain of the diffusion and noise (see Supplementary Figure 1 and 2A for an

illustration). The urgency signal (Gain) at a given time within a trial (t) was given by:

18
$$Gain_t = 1 + (1/(a - \left(1 - \exp - \left(\frac{t}{k}\right)^s\right) * \frac{a}{2}))$$

19 where a represents the initial boundary value and k scales the urgency signal according to an

20 inverted Weibull distribution with the shape parameter s fixed at 3.

Model comparison (Supplementary Figure 2B) and validation (Supplementary Figure 2C) revealed that our data is similarly well captured by the urgency (DDM5) and collapsing bound model (DDM4). However, when considering the trough of movement-selective beta suppression around response time as proxy for decision boundary thresholds, both dynamic decision boundary models make distinct predictions. While the collapsing bound model predicts that slower responses are made at lower decision boundary thresholds, the urgency model would predict similar decision boundaries for slow vs. fast responses (Supplementary Figure 2D). Hence, based on our robust finding, that the trough of the movement-selective beta suppression around response time is scaling with RT, we consider the collapsing bound model as more neural plausible.

Supplementary Figure 2. Model features, fit, and predictions of the urgency model.

(A) Illustration of the multi-stage DDMs based on simulated single trial decision processes. Features

of this model are the same as described in the main manuscript (Figure1 B), with the exception that

here the free parameter k is used to scale the urgency signal (orange line) that increases with decision

time. This urgency signal is used as a multiplicative gain of the noise and diffusion. **(B)** Cumulated

approximated Bayesian Information Criterion (aBIC) scores over participants of each candidate model.

Higher values indicate a better fit of the models to the behavioral data. Results indicate that the

dynamic bound model (DDM4) and the urgency model (DDM5) provides a similar fit to the data.

Protected exceedance probabilities (pEP) draw a similar picture. **(C)** shows RT quantile fits and

accuracy fits of the urgency model against human data. This model validation is suggesting a good fit

to the data. **(D)** To characterise predictions of the urgency DDM we simulated 5000 individual trials

using the mean of the best fitting individual parameters (see Supplementary Table 1). **(D)** shows the

modelled decision process locked to response separated by response speed, congruence, accuracy,

and previous accuracy. These simulations predict that decision thresholds are unaffected by these task

factors.

Supplementary Figure 3. Parameter recovery DDM4.

For parameter recovery analyses, we randomly drew model parameters out of a Gaussian distribution with mean and variance equal to the observed fitted parameters across the whole group to reduce parameter value combinations that were extremely unlikely to occur in human data. We simulated 1.000 parameter combinations and used the same differential evolution algorithm to recover the fitted models. Models that produced no errors at all or for which constraints were not met, were discarded from analysis. As in the human data, we used 5.000 trials per simulation. Plotted are ground truth (GT) parameters against the recovered parameters (plots marked in red frames). Additionally, we display the whole space of parameter combinations (maps without red borders) and distributions for each of the GT and recovered parameters. Overall, recovery studies indicate that drift-rate, response boundaries (a), non-decision time (T_{er}), flanker weighting (f), and boundary collapse (k) are independent and recoverable.

1 Supplementary EEG results

3 **Supplementary Figure 4. Single-trial regression on beta lateralisation at response.**

(A) Results of a single-trial regression analysis on BPL at response (mean ± 12ms surrounding button
press), comparing relevant task factors. **(B)** Shows raw values splits for Incongruence (congruent vs
incongruent), Accuracy (correct vs error) and Previous Accuracy (post correct vs post error). **(C)** Display
results of separate regression analyses split by ipsilateral (hemisphere that does not induce the choice
on the current trial) and contralateral hemispheres. Results indicate, that incongruent trials cause
reduced BPL (t(862) = 10.21, p < .001, d = 0.35, CI [0.31, 0.45], BF_{10} > 100). This effect is driven by
changes over the ipsilateral hemisphere where beta power was more strongly reduced on incongruent
trials. This may reflect the pre-activation of the competing response tendency. Similarly, errors were
associated with reduced BPL (t(862) = 6.52, p < .001, d = 0.22, CI [0.17, 0.32], BF_{10} > 100). This result is
partly driven by stronger increases in beta power of the contralateral hemisphere. However, it should
be noted that this effect is not evident, when comparing RT matched BPL on correct vs error trials (see
Figure 3F), which makes this effect difficult to interpret. Following errors, BPL is larger (more negative,
t(862) = -9.34, p < .001, d = -0.32, CI [-0.4, -0.26], BF_{10} > 100) which is caused by a stronger increase in
BP over the ipsilateral hemisphere. This may reflect static decision policy adaptations to increase
accuracy after errors (Fischer et al., 2018; Murphy et al., 2016). An additional interpretation is that
following errors, the unchosen response is more effectively suppressed. Error-bars reflect 99.9% CI,
(A and C) depicts mean within participants t-values, and statistics are results of t-tests of individual
within-subject regressions against zero. NDL reflects the distance from the last break in the task, and
trial the general time on task, together RSI these regressor were used as noise regressors.
20

Supplementary Figure 5. Movement selective lateralization signals across frequency bands.
(A-D) demonstrate that lateralization signals across frequencies is composed of the activity-difference
recorded over contralateral and ipsilateral motor cortices. We chose electrodes with a maximal effect

(C3, C4, CP3, CP4) for analyses of lateralised signals. Specifically, we subtracted the power in the
respective band over the inactive sensorimotor cortex (i.e., the electrodes side ipsilateral to the hand
that gave the response in the trial) from the beta power recorded over the active (contralateral)
sensorimotor cortex. This difference signal thus compares the degree of power reduction between
both hemispheres, presumably reflecting differential motor activation. Results indicate that the effect
is most pronounced in the beta band frequency.

Supplementary Figure 6. Single-trial regression on different movement selective frequency band
lateralisation signals at response.
To investigate single-trial associations of movement selective frequency band suppression around
response and RT, we used the respective lateralised response-locked single-trial signal (mean ± 12 ms)
and regressed the log-transformed RT onto the threshold while accounting for unspecific task effects.
Results indicate that that both APL (8-12 Hz) and MuPL (8-14 Hz) is decreasing (i.e., boundary collapse)
with increasing RTs (thus representing a decision threshold decrease with increasing decision time).
Moreover, an opposite effect was present for lateralization in the theta frequency band (4–8 Hz).
Error-bars reflect 99.9% CI.
10

Confirmation sample

To replicate the key findings in an independent sample, we analysed data of one hundred

nineteen subjects (mean age 22.89 years (range: 18 - 38), 70 females). These datasets were

collected at the Otto-von-Guericke University Magdeburg as part of an ongoing genetic

association study using the same approved study protocol as described in the main

manuscript. Behavioural analyses of this sample confirmed that general behaviour effects

were in accordance with typical results seen in flanker tasks. They reflected interference

effects, with slower (ΔRT = + 42 ms, $t(118)$ = -43.25, $p < .001$, d = 1.6986, $BF_{10} > 100$) and more

erroneous (Δaccuracy = 19%, $t(118)$ = 34.51, $p < .001$, d = 3.7163, $BF_{10} > 100$) responses on

incongruent trials. The overall accuracy was 86% (SD=3.94). To replicate key findings, we used

the same analyses procedures as for the main sample. Results replicate the findings for the

main sample: First, we show that the dynamic decision boundary model outperformed static

decision boundary conflict DDMs and captured conflict related RT and accuracy well (see

Supplementary Figure 7). Moreover, the EEG analysis validated our previous conclusion that

the trough of movement-selective beta suppression around response time may reflects a

collapsing decision bound (see Supplementary Figure 8).

1
Supplementary Figure 7. Model comparison and validation in the confirmation sample.
(A) Cumulated approximated Bayesian Information Criterion (aBIC) scores, protected exceedance
probabilities (pEP) and estimated model frequencies indicate that the dynamic bound model (DDM4)
provides the best fit to the data. **(B)** The drift-diffusion model (DDM) included nine free parameters.
In addition to the standard-parameters reflecting drift rate (v), flanker weighting (f), boundary (a), and
non-decision time (Ter), and variance parameters that determined how much standard-parameters
varied from trial-to-trial (sv, sz, st, sf), the dynamic boundary model included the free parameter k
that scaled the boundary collapse that increases with the duration of the decision. **(C)** shows single
trial simulations and model features based on the mean of the group best fit parameters displayed in
(B). (D–G) shows quantile fits of the model against human RT data and **(F)** shows model and human
accuracy. In all conditions (congruent & incongruent correct as well as incongruent error), the model
captures the RT data in each quantile, suggesting a good fit to the data. *Note*: boxes = interquartile
range (IQR), o = median, - = mean, whiskers =1.5 × IQR, grey dots = outlier.
15

Supplementary Figure 8. EEG results confirmation sample.

(A) Shows the result of a single-trial regression analysis comparing responses with the left and right hand, while controlling for congruency, flanker distance, response stimuli intervals (RSI), following RSI, trial number, and log transformed RT. Data suggests, that Beta power more strongly decreases when a response is given with the contralateral compared to the ipsilateral hand. This effect was most pronounced over the electrodes C3/4 and CP3/4. **(B)** Beta power lateralization signal **(Bii)** is composed of the activity-difference recorded over contralateral and ipsilateral motor cortices **(Bi)**. **(Ci)** Beta power lateralization around response time may reflects collapsing decision thresholds, whereby faster responses (based on a median split) are made at higher thresholds. This effect is partly explained by a reduction of beta power over the contralateral hemisphere **(Cii, left)**, while on average beta power

over the ipsilateral hemisphere is barely changed when responses are given later in a trial **(Cii, right).** Yet, BPL showed a stronger influence of response time than either of the hemispheres alone suggesting that it may be an especially valid marker of response threshold modulations. **(D)** Results of a single-trial regression analysis on BPL at response (mean ± 12ms surrounding button press). This analysis confirms collapsing decision boundaries on a single-trial level while controlling for other task factors that potentially influence BPL. **(E)** BPL raw values at response time plotted against GLM factors. In addition to decreases in BPL with increasing RT, we found a significant difference in BPL at response execution between congruent and incongruent trials with higher BPL for congruent trials, which might be interpreted as enhanced motoric readiness caused by the distractor stimuli. Moreover, we found that BPL at response execution was increased on post-error trials, which may reflect post-error adaptions (Fischer et al., 2018). Finally, longer response stimuli intervals (RSIs) were associated with decreased BPL. *Note.* Contours in **(A)** represent significant cluster after cluster based permutation testing (Maris & Oostenveld, 2007). Error-bars and shades reflect 99.9% CI, **(D)** depicts mean within participants t-values, and statistics are results of t-tests of individual within-subject regressions against zero. NLD reflects the distance from the last break in the task, and trial the general time on task, together RSI these regressor were used as noise regressors.

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