

Beyond Difference in Reaction Time: Understanding Neuronal Activity during the Preparatory Period of the Decision Process

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Abstract

■ Even the simplest perceptual tasks are executed with significant interindividual differences in accuracy and RT. In this work, we used the diffusion decision model and multi-electrode EEG signals to study the impact of neuronal activity during the preparatory period on the following decision process in an attention task. Two groups were defined by fast and slow responses during the performance of control trials. A third, control group performed the same experiment but with instructions defining signal for response execution. We observed that the fast-responding group had a shorter duration of nondecision

processes (describing both stimulus encoding and response preparation) preceded by lower power of the frontal upper alpha (10–15 Hz) and central beta (21–26 Hz) activities during the preparatory period. To determine whether these differences were followed by a shortening of the early perceptual or late motor process, we analyzed lateralized readiness potential (LRP). The time from LRP onset until response execution (LRP-RT interval) was similar in all three groups, enabling us to interpret shortening of nondecision time as reflecting faster stimulus encoding. ■

INTRODUCTION

Perceptual decisions are composed of two phases: identification of the stimulus and selection of a specific behavioral response. Even the most basic decisions depend on sequential sampling to determine stimulus identity because stimuli representations are inherently variable and noisy. Numerous studies have investigated the neuronal correlates of simple perceptual decisions in animals (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Newsome, Britten, & Movshon, 1989) and humans (Philiastides & Sajda, 2006; VanRullen & Thorpe, 2001; Thorpe, Fize, & Marlot, 1996). In these studies, the decision process was often characterized by two behavioral measures: RT and accuracy. Such an approach has an intrinsic limitation in that it oversimplifies decision making as an indivisible process. In contrast to this approach, sequential sampling models describe perceptual decisions as an interplay of multiple independent processes (e.g., stimulus-encoding, evidence accumulation, establishing decision threshold, and preparation of response) that allow for searching of their underpinnings in electrophysiological signals.

There are several sequential sampling models available (for a review, see Ratcliff & Smith, 2004). One of the most prominent models is the diffusion decision model (DDM) proposed by Ratcliff (1978). DDM was originally developed to describe memory retrieval (Ratcliff, 1978). It was later successfully applied to simple perceptual

decisions (e.g., color judgment; Voss, Rothermund, & Voss, 2004; Ratcliff, 2002) as well as lexical decisions (Ratcliff, Gomez, & McKoon, 2004) and—after some expansions—for decisions in conflict tasks (Ulrich, Schröter, Leuthold, & Birngruber, 2015; Hübner, Steinhauser, & Lehle, 2010). DDM has also been used to examine interindividual differences in studies on aging (Ratcliff, Thapar, & McKoon, 2001), sleep deprivation (Ratcliff & Van Dongen, 2009), and hypoglycemia (Geddes et al., 2010).

Recently, efforts have been made to determine physiological mechanisms that underlie constituent subcomponents of the decision process (Nunez, Gosai, Vandekerckhove, & Srinivasan, 2019; Nunez, Vandekerckhove, & Srinivasan, 2017; Ratcliff, Philiastides, & Sajda, 2009; Philiastides, Ratcliff, & Sajda, 2006). For instance, the amplitude of a late (~300-msec poststimulus) positive occipital potential recorded during a classification task has been shown to reflect the amount of available perceptual evidence (Ratcliff et al., 2009; Philiastides et al., 2006). Other studies using target detection (Kelly & O'Connell, 2013; O'Connell, Dockree, & Kelly, 2012) and oddball tasks (Twomey, Murphy, Kelly, & O'Connell, 2015) demonstrated that the classical P3 displayed all properties of an evidence accumulation marker. These properties include sensitivity for stimulus quality (i.e., sensory evidence strength), the trial-to-trial correlation between maximal amplitude and RTs, and dynamics resembling accumulation to bound process predicted by the model. In support of these observations, Mueller, White, and Kuchinke (2017) showed that the P3 amplitude (referred to by the authors as “late

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positive complex”) was positively related to individual differences in the efficacy of evidence accumulation that was measured with DDM during the performance of a lexical task. While evidence accumulation is probably the most investigated subcomponent of the decision process, the studies on its neuronal substrates are still sparse. Synthesis of the literature is also hindered by the diversity of applied experimental paradigms and the variety of methods used for data analysis.

Even less is known about the neuronal processes engaged in the realization of other subcomponents specified by DDM—the time of nondecisional processes (describing both the basic stimulus encoding and motor response preparation) and the decision criterion (representing the amount of evidence required for a decision to be made). Electrophysiological studies attempting to identify neuronal processes altered by manipulation of decision criterion despite similar analytical approaches provided inconsistent results. Past research divided time spent on task into two periods delineated by the onset of the lateralized readiness potential (LRP). The period from stimulus onset until LRP onset (S-LRP interval) was used as an approximation of the stimulus processing span. The time from LRP onset until response execution (LRP-RT interval) was used as an approximation of the motor processes span. Osman et al. (2000) used the Eriksen flanker task and observed a shortening of the LRP-RT interval after verbal instructions emphasizing the speed of responses over their accuracy. Two other studies used a response deadline to promote either fast or accurate responses (Rinkenauer, Osman, Ulrich, Muller-Gethmann, & Mattes, 2004; van der Lubbe, Jaśkowski, Wauschkuhn, & Verleger, 2001). These studies observed a shortening of LRP-RT interval in the subset of the examined tasks (i.e., Eriksen flanker task, choice-by-location task, and Simon task), but in the other tasks (i.e., line discrimination, lexical task), S-LRP interval was shortened under speed demand. Based on these results, the authors concluded that shifts of decision criterion result in task-dependent effects and could be, at least partially, reduced to the shortening of motor processes (Rinkenauer et al., 2004). This conclusion was contradictory to the assumptions of DDM that consider the establishment of decision criterion as occurring solely at the premotor stage of decision making. Importantly, none of the abovementioned physiological studies evaluated DDM or any kind of sequential sampling model on their data. The successful manipulation of decision criterion was inferred indirectly from the faster RTs accompanied by worse performance under “speed” when compared to “accuracy” instruction.

Although the foundations of the decision process described above are dependent mostly on the properties of the task (e.g., stimulus quality, task difficulty, time for response preparation), their course can be additionally modulated by the information available before the task onset. Depending on its type, this information can be utilized during different preparatory processes such as focusing perception (e.g., via anticipatory attention), promoting

future motor response preparation, or optimizing decision criterion (e.g., by trading off between speed and accuracy of responses). The need for such research has been recognized by Curl and White (2019), who recently studied the impact of prior information on the subcomponents of the decision process. Specifically, the authors analyzed the impact of different types of cues such as alerting (informing participants about the time of the target stimulus appearance) and orienting (informing participants about the time and location of the target stimulus appearance) on the decision process during the following task. The presence of orienting but not alerting cues led to the liberalization of the decision criterion (i.e., a decrease of information required to make a decision). Both the alerting and orienting cues resulted in the shortening of nondecision time. This shortening was hypothesized to reflect faster stimulus encoding rather than differences in motor processes because the former is more likely to be affected by the stimulus predictability. Unfortunately, their study recorded only behavioral data. To the best of our knowledge, our current experiment pioneers the research on the relation between electrical neuronal activity preceding task performance and the different components of the decision process as assessed by the DDM. While the application of DDM became a standard in the neuroimaging data using fMRI technique (for a review see Mulder, van Maanen, & Forstmann, 2014), it is still rare in the electrophysiological literature, especially in studies not directly devoted to decision making.

We used behavioral and electrophysiological measures to address the question of how neuronal activity during the preparatory period corresponds to different subcomponents of a decision process. We analyzed data from participants performing the task with distinct behavioral strategies characterized by fast and slow responses resulting in bimodal distribution of RTs in the control trials (for a similar observation, see Ruge, Braver, & Meiran, 2009). In addition to these two groups, we included a third control group that was presented with the manipulated task instructions in which participants were asked to respond after the offset of target stimulus (as in experiments employing the “response signal” method aiming to manipulate decision criterion; Reed, 1973). We focused on EEG activity recorded before task execution taking advantage of a specific construction of our paradigm that included long (2–5 sec) cueing periods. In addition, similar to previous studies, we analyzed LRP as an indicator of motor response preparation. To distinguish the effects of duration of nondecision processes (stimulus encoding and response preparation) and evidence accumulation, we evaluated DDM on the behavioral data and compared estimated parameters values between groups. The decision criterion was included in the model but not further discussed because of insufficient number of trials for its precise estimation.

Our results show that the groups implementing different strategies during perceptual decision making (as manifested in RTs and decision diffusion modeling) differed in their

neuronal activity not only during the decision process, as was previously shown, but already long before the onset of the stimulus that required decision making. The application of a DDM supplemented with LRP analysis allowed us to determine that observed electrophysiological difference (i.e., lower alpha activity over frontal cortex during cueing period) was followed by a shorter time on stimulus encoding during task execution.

METHODS

Participants

In the main experiment, we examined 49 participants performing the attention and control trials with standard instruction (see below). After the initial analysis of behavioral data, these participants were assigned to one of the two groups based on performance in the control trials (i.e., RT faster or equal to/slower than 0.8 sec, respectively): “fast-responders” ($n = 34$, two women; mean age = 24.74 years, $SD = 3.08$ years) and “slow-responders” ($n = 15$, six women; mean age = 24.09 years, $SD = 1.97$ years). To control for the difference in time spent on stimulus processing, a third group “slowed-by-instruction-responders” ($n = 15$, three women; mean age = 29.02 years, $SD = 5.93$ years) was included in the study. This group performed the task with different instructions (see below). All participants were right-handed and without any history of psychological or neurological disease. The small number of women reflects the composition of the students at the Military University of Technology, where recruitment was performed. The experiment was approved by the local ethics committee. All participants provided written informed consent for participation in the study.

Experimental Paradigm

Each experimental session included two types of trials referred to as attention ($n = 48$) and control ($n = 48$). Each trial consisted of a preparatory period (2, 3, 4, or 5 sec selected with uniform probability) that was followed

by a task execution period (1.8 sec). The variable and long duration of the preparatory period demanded sustained attention and allowed us to study preparatory processes in isolation from task execution or stimulus encoding (Figure 1).

In the attention trials, the cue (a 4×4 matrix of homogeneously tilted bars surrounded by a green frame) determined one of the four to-be-searched orientations (left-tilted/right-tilted/vertical/horizontal). The cue was continuously presented on the screen during the preparatory period to reduce working memory load. After the preparatory period, the target stimulus (a 4×4 matrix of differently oriented bars without the frame) was presented for 0.8 sec. In 50% of the trials, one of the bars in the target stimulus had the same orientation as presented in the cue. Participants responded with their right index finger/button if they thought that such a bar was present and with their left index finger/button if they thought it was absent.

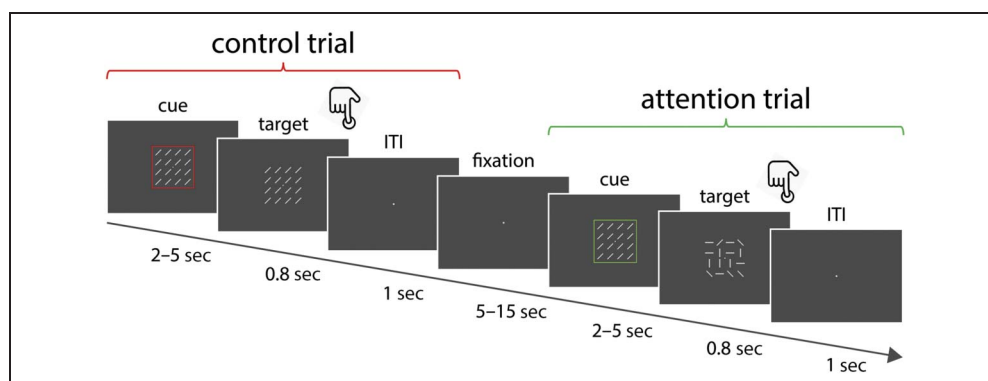
In control trials, the cue (a 4×4 matrix of left- or right-tilted bars surrounded by a red frame) directly coded the correct response. After the preparatory period, the target stimulus (identical matrix but without the frame) was presented. Participants responded with their right index finger/button if the bars were right-oriented and left index finger/button if the bars were left-oriented.

In both the attention and control trials, responses were registered during the target stimulus presentation (0.8 sec) or within the 1-sec intertrial interval after the target stimulus presentation. All stimuli were presented in the central visual field, and the fixation point was visible throughout the whole trial. Trials were interspersed with 5-sec long fixation periods ($n = 24$). The order of trials and fixation periods was pseudorandom and determined using a genetic algorithm (*Optimise Design GA*; Wager & Nichols, 2003) with the restriction that there could be no more than three fixation periods in a row. Stimulus appearance and timing were controlled with Presentation software (Neurobehavioral Systems, Inc.).

Before the start of the task, participants were shown instructions on the computer screen and completed a short training exercise. Participants started the experiment only

Figure 1. Experimental schema. Presented are as follows: a simple control trial composed of cue stimulus surrounded by a red frame and target stimulus composed of same orientation bars; fixation period; and demanding attention trial composed of cue stimulus surrounded by a green frame and a target stimulus, requiring search of an element with orientation presented in the cue among heterogeneously oriented bars.

The responses (indicated with a hand icon) could be provided during the target stimulus presentation (0.8 sec) or the following intertrial interval (ITI; 1 sec).



after reaching at least 60% accuracy on the training exercise. Because a participant's attention rapidly declines with time spent on the task, the experiment lasted only ~12 min and was divided into two halves separated by a 30-sec break.

Manipulation by Instruction

Two different sets of instructions were used. First, fast- and slow-responders groups were given the same standard instruction ("respond as fast and as accurately as possible"). We refer to this as "Instruction I." This instruction did not unequivocally determine the time in which response should be provided. Second, participants in the slowed-by-instruction control group were asked to withhold their response until stimulus offset ("respond after target stimulus offset"). We refer to this as "Instruction II." This instruction was aimed to recreate the behavior observed in the slow-responders group and resembled an experimental technique known as "response signal" introduced by Reed (1973) to study speed-accuracy tradeoff (SAT).

Behavioral Data Analysis and DDM Fit

We calculated performance-related statistics (percent of correct responses and their mean RTs) separately for control and attention trials. We analyzed behavioral measures with one-way ANOVAs with Group (fast-responders vs. slow-responders vs. slowed-by-instruction-responders) as the between-subjects factor. Greenhouse-Geisser correction was applied when the data did not meet the assumption of sphericity. ANOVAs were computed using IBM SPSS Statistics 23. ANOVA results were deemed to be significant when $p \leq .05$. Post hoc tests were performed with independent-samples t tests to determine significant pairwise comparisons. Bonferroni correction was used to correct for multiple comparisons (for three comparisons $p \leq .0167$).

To enable the interpretation of between-group differences in task performance in more physiological terms, RTs of correct and erroneous attention trials were submitted to DDM analysis (Voss & Voss, 2007; Ratcliff, 1978). Because of complete congruency of cue and target stimuli in control trials enabling advanced preparation of response, these trials did not require the decision process after stimulus onset and thus could not be included in the model. The application of DDM allowed the decomposition of behavioral data into four basic components approximated by independent parameters. In the model parameter, t_0 denotes the duration of nondecisional processes embracing early perception (i.e., stimulus encoding) and postdecisional motor processes (i.e., response preparation and execution). Parameter ν corresponds to the efficiency of evidence accumulation (i.e., the amount of information about stimulus acquired in a given time). The parameter a defines the amount of information required by the participant to provide a response (i.e., the "decision criterion"). When the value of a is large, the response strategy

promotes slow but accurate responses (conservative response criterion). When the value of a is small, faster but more error-prone responses are promoted (liberal decision criterion). The last source of variability assumed by the DDM is reflected by the additional z parameter that represents response preference before the start of stimulus processing (i.e., bias). For example, if the experimental design is not balanced, participants might favor decisions corresponding to the more frequent condition. When the model is used for estimation of correct and erroneous responses, there should be no response bias and the relative starting point has to be fixed to 0.5 (as recommended by Voss, Voss, & Lerche, 2015). Model fit was performed with the fast-dm program (<https://www.psychologie.uni-heidelberg.de/ae/meth/fast-dm/>) estimating model parameters in a single step, by using a Simplex downhill search to optimize the concordance between the predicted and the empirical distributions (see Voss & Voss, 2007, for details). Since we modeled RT distributions of correct and erroneous responses, the value of parameter z was set to 0.5. Thus, we run a rather parsimonious DDM with three free parameters (t_0 , ν , and a) and a fixed parameter z set to 0.5. Trials with no response ($M = 2.73$, $SD = 3.92$) were excluded from the analysis. Goodness of model fit was assessed with maximum likelihood criterion, because this method was proved to be the most efficient in estimating parameter values on limited number of trials (Lerche, Voss, & Nagler, 2017). It was also shown that maximum likelihood criterion is sensitive to data contamination by responses provided without decision process, for example, because of guesses (fast contaminants) or attentional lapses (slow contaminants). Therefore, the analysis was conducted after additional, strict control for possible RT contaminants (i.e., after exclusion of trials in which RT was farther from the mean than 2 SD s). Only single trials were removed based on this criterion; an average number of trials remaining in the analysis was $n = 44.27$ ($SD = 2.81$) and did not differ between groups, $F(61, 2) = 0.441$, $p = .645$. According to recommendations provided by Lerche et al. (2017) for a one-drift three-parameter model, this number should be sufficient for high-precision estimation of t_0 values ($n < 24$ as requisite for high precision) and average precision of parameter ν estimation ($n = 26$ for minimum and $n = 78$ for high precision). The same recommendations imply that the number of trials in our task may not suffice for reliable estimation of parameter a (requisite number of trials $n = 55$). We decided to keep parameter a free in the model but withhold from the interpretation of results obtained for this parameter. An alternative model with two free parameters and parameter a set to 1 provided virtually the same results regarding between-group differences in t_0 , and ν parameters, however, showed a poor fit to empirical data (data not shown). Concordance of empirical and predicted data was verified visually, by plotting the predicted and empirical correctness and RTs of each participant. For the latter, values of the first, second, and third quartile of RTs from correct responses were compared with the

corresponding values from the predicted RT distribution for each participant (for similar approach see Voss, Rothermund, Gast, & Wentura, 2013, Appendix B). The values of average fit index and for parameters $t0$ and v were subsequently compared between groups with one-way ANOVAs in the same manner as the behavioral measures described above.

EEG Data Acquisition

During EEG recordings, participants were seated in an electrically shielded and sound-attenuated room. Two variants of electrodes montage were used. EEG was continuously recorded from 64 or 128 scalp sites using a 128-channel amplifier (Quick Amp; Brain Products). Electrodes were positioned according to the 10–10 and 10–5 systems, respectively (Oostenveld & Praamstra, 2001), and mounted on an elastic cap (ActiCAP and EASYCAP). Electrode impedance was kept below 10 k Ω (verified after task completion). The reference electrode was placed at FCz or Cz location, depending on the montage. The ground electrode was placed at the Fpz location. Only electrodes present in both montages, $n = 61$, were included in the analysis. The sampling rate was 500 Hz or 1000 Hz, respectively.

EEG Data Analysis

The EEG data, event markers, and locations of the electrodes were imported from BrainVision Analyzer to EEGLAB using the *bva-io* plug-in. The signal recorded with a 1000-Hz sampling rate was down-sampled to 500 Hz. Data were filtered within 0.1–70 Hz. Line noise was removed using a notch filter (48–52 Hz). Data were cleaned automatically using the artifact subspace reconstruction method (Mullen et al., 2015), as implemented in the *clean_rawdata* plug-in. We used the following configuration: threshold for flat channels set to 5 sec; high-pass filter with frequencies of transition-start and transition-end set to 0.25 Hz and 0.75 Hz, respectively, for removal of slow drifts (for the analysis of LRP, high-pass filters were disabled to avoid distortion of low-frequency components); parameters for artifactual channels removal (e.g., because of extensive line noise or movement) set to: < 0.8 for correlation with other channels and 4 SD s for amplitude variation; and *clean_asr* function with standard deviation threshold set to 10, as recommended by Chang, Hsu, Pion-Tonachini, and Jung (2020). Removal of data windows in which signal quality was too low to be properly cleaned was disabled to preserve the continuity of data. Signals from channels polluted by artifacts were rejected ($M = 2.5$, $SD = 2.41$) and interpolated using spherical interpolation method implemented in the *pop_interp* function. To enable the joint analysis of all participants, data were rereferenced to average with the signal from on-line reference electrodes (FCz or Cz) restored.

Continuous data were epoched into time frames extending from 1 sec before cue onset to 1 sec after the target

stimulus onset. Five-second-long segments were selected from fixation periods. Epochs were classified as contaminated by artifacts and excluded from further analysis based on their spectral properties: if mean power, in the 22- to 50-Hz range, computed across all channels and epochs exceeded ± 3 SD s from the average power for a given participant. The procedure ran iteratively until no epochs exceeded the threshold. The cleaning procedure resulted in the removal of $\sim 7.38\%$ of all epochs (including 7.26% of attention trials, 6.85% of control trials, and 8.69% of fixation periods).

Time-frequency signal decomposition was performed using wavelet transform implemented in the *newtimef* EEGLAB function. The analysis was performed for the frequency range 1–30.5 Hz with window length increasing with frequency by a factor of 0.5 (starting from one cycle per window for the lowest frequency). Spectral power was expressed as a percent change of baseline activity (Grandchamp & Delorme, 2011) allowing to compare the power of different frequencies (each frequency being normalized by itself) as well as discarding differences between participants in overall EEG power (e.g., resulting from interindividual differences in skull thickness or scalp impedance). Fixation periods were used for the assessment of baseline activity. The first fixation period was discarded from the analysis because it constituted the first trial in the experiment and could be nonrepresentative. Spectrograms were computed from all data available for subsequent seconds of anticipation (i.e., the cue–stimulus presentation). We did this in the following manner: For the 1st and 2nd second, we used data from all cue durations; for the 3rd second, we used data from 3-, 4-, 5-sec long cues and so on. We then averaged signals across cue durations. The first and last half-second of anticipation for each trial duration was discarded from the statistical analysis of anticipatory activity because the assessment of power during this period would require averaging over time windows comprising cue and target stimulus onset, respectively, and thus would be contaminated (for the lowest frequency of 1-Hz window length was equal to 1 sec).

Statistical comparison of oscillatory brain activity during the anticipation period was performed using cluster permutation tests (Maris & Oostenveld, 2007) as implemented in the *ft_freqstatistics* and *ft_timelockstatistics* functions. To verify if the three groups differ in electrical activity during the anticipation period, one-way ANOVA was conducted for average activity in each frequency at every channel. The obtained single-point statistics were thresholded at $p = .05$ and data points with significant difference, which are aligned in space or frequency domain, formed clusters. To measure cluster statistics, we used weighted cluster mass combining effect intensity and extent (Hayasaka & Nichols, 2004). The same steps were performed on the permuted data with 1000 randomizations (Montecarlo method) and compared with empirical data. When the probability of obtaining cluster statistics observed in the empirical data was equal or lower than 0.05, the results

were deemed significant. Subsequently, to identify pairs of groups whose signals differed significantly from each other, post hoc *t* tests were performed on activity averaged across the frequency range and electrodes constituting significant clusters. Bonferroni correction was used to correct for multiple comparisons (for three comparisons $p \leq .0167$).

For the analysis of LRP, preprocessed data were imported to the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) using the *eeglab2fieldtrip* function and cut into epochs extending from 0.5 sec before to 0.25 sec after the button press. LRP was computed according to the equation: $1/2 * ((ERP_{contra_R} - ERP_{ipsi_R}) + (ERP_{contra_L} - ERP_{ipsi_L}))$, where $ERP_{contra_R/L}$ and $ERP_{ipsi_R/L}$ stands for ERP recorded at selected electrodes lying on the hemisphere contralateral/ipsilateral to the responding hand (right = R or left = L), as implemented in the *ft_lateralized-potential* function. The LRP was baseline corrected using 0.4 sec before the target stimulus onset. To control for the impact of extreme cases in the group analysis, LRP data for each participant were divided by the standard deviation of signal values in the baseline period and expressed in *z* scores (for a similar approach see Delorme, Miyakoshi, Jung, & Makeig, 2015; Makeig et al., 2004). The procedure did not alter the shape of ERPs. Magnitude and latency of LRP were measured using *geterpvalues* from the ERPLAB plug-in with measurement options *arean/fareanlat* for magnitude/latency. As a measure of latency, we used fractional latency (i.e., latency at which the component reached 0.5 of its total magnitude as recommended by Luck, 2004). For visualization purposes, ERP data were low-pass filtered with a 30-Hz filter. Magnitude and latency of LRP were compared between groups with one-way ANOVAs. Subsequently, to identify pairs of groups whose signals differed significantly from each other, post hoc *t* tests were performed with Bonferroni correction for multiple comparisons (for three comparisons $p \leq .0167$).

RESULTS

Behavioral Data

Initial analysis of behavioral data from the main experiment ($n = 49$) revealed that variability of the average RT in control trials ($M = 0.62$ sec, $SD = 0.33$ sec) was larger than in attention trials ($M = 1.15$ sec, $SD = 0.18$ sec). This was an unexpected outcome taking into account that mean RTs were longer in attention trials. Further exploration revealed that participants presented with identical instruction ("Instruction I") voluntarily adopted distinct behavioral strategies resulting in a bimodal distribution of RTs in control trials (Figure 2A, top). The analysis of average RTs for each participant confirmed the separation of two subgroups (Figure 2B). The majority of the participants (34 of 49; referred to as "fast-responders") spontaneously engaged in a strategy characterized by fast RTs in simple, control trials ($M = 0.41$ sec, $SD = 0.08$ sec) and slower RTs in

demanding, attention trials ($M = 1.03$ sec, $SD = 0.14$ sec; $t(33) = -24.62$, $p < .001$; Figure 2C). The rest of the participants performing the task with the same instruction ($n = 15$; referred to as "slow-responders"), regardless of task difficulty, responded always after stimulus offset ($M = 1.09$ sec, $SD = 0.12$ sec in control trials and $M = 1.29$ sec, $SD = 0.07$ sec in attention trials; $t(14) = -7.17$, $p < .001$; Figure 2C). Notably, although the distribution of RTs for attention trials did not significantly differ from unimodal (Figure 2A, bottom), fast-responders (defined according to their performance in control trials) were also significantly faster in attention trials than the slow-responders, $t(47) = -6.68$, $p < .001$ (Figure 2C).

Since the analyzed behavioral strategies were distinguished post hoc based on RT distributions, to dissociate effects of different response strategy from the results of response speed (i.e., responding as fast as possible or withholding response until target stimulus offset), another group of participants ($n = 15$; referred to as "slowed-by-instruction-responders") performed the same paradigm but preceded by explicit instruction to respond after target stimulus offset ("Instruction II"). Explicit manipulation of instruction successfully recreated behavior of slow-responders in attention trials (slowed-by-instruction group $M = 1.30$ sec, $SD = 0.08$ sec; $t(28) = 0.20$, $p = .843$; Figure 2C). In control trials, responses of the group with Instruction II were slower ($M = 1.19$ sec, $SD = 0.09$ sec) than responses of slow-responders, $t(28) = 2.62$, $p = .014$ (Figure 2C).

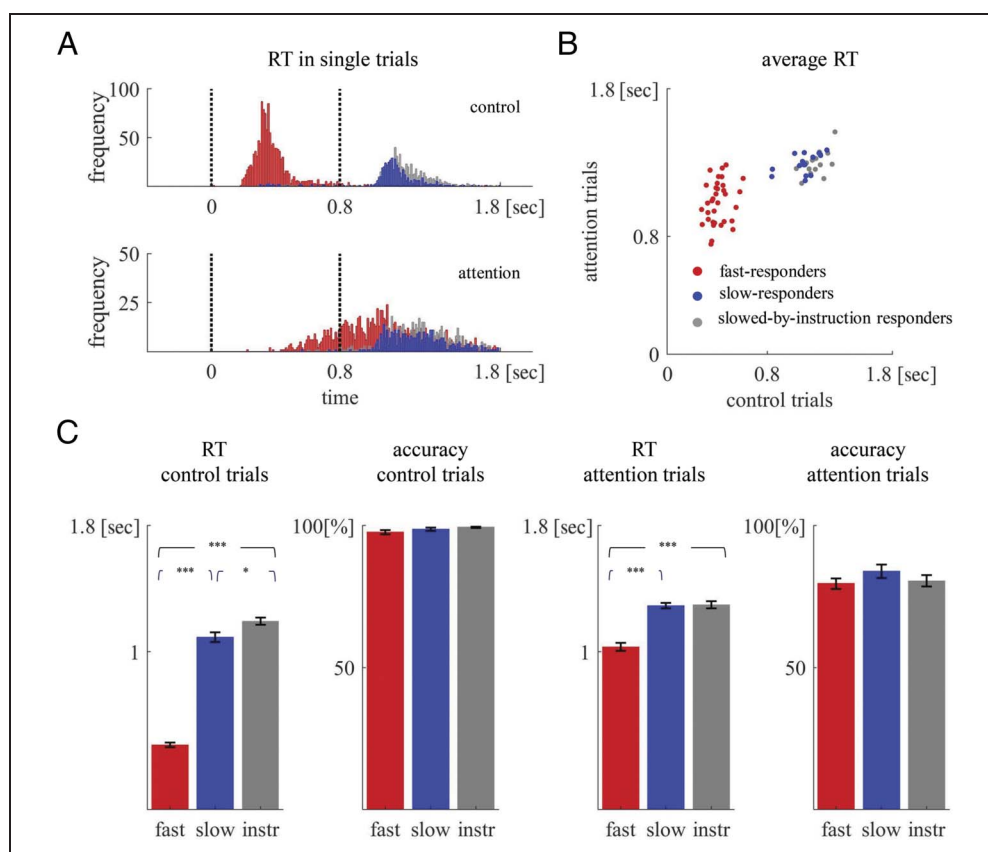
Accuracy in the control trials was in all groups at the ceiling level, $F(2, 61) = 1.51$, $p = .230$; fast-responders: $M = 97.73\%$, $SD = 4.24\%$; slow-responders: $M = 98.75\%$, $SD = 2.20\%$; slowed-by-instruction-responders $M = 99.44\%$, $SD = 0.95\%$. Accuracy in demanding, attention trials was overall lower but also did not differ significantly between the three groups, $F(2, 61) = 1$, $p = .374$; although performance was slightly better in slow-responders: $M = 83.89\%$, $SD = 9.27\%$ than in fast-responders: $M = 79.54\%$, $SD = 10.97\%$; and slowed-by-instruction group: $M = 80.56\%$, $SD = 7.94\%$. Lack of significant difference in performance of fast-responders and both slow-responding groups indicated that these groups did not simply differ in their resolution of SAT (in which case faster responses should be accompanied with more errors). To verify which subcomponents of decision process are reflected in observed differences in RTs and accuracy, we evaluated DDM on our data.

DDM Fit

A DDM with three free parameters ($t0$, v , and a ; see Methods section) and one fixed parameter ($z = 0.5$) was fit to the behavioral data from attention trials to model the distribution of correct and erroneous responses. Average model fit was assessed by statistical comparison of fit index (mean goodness of fit 12.47, $SD = 17.32$;

Figure 2. Behavioral data for groups employing different strategies. (A) Distribution of RTs in single trials for all participants pooled together. Vertical lines at 0 and 0.8 sec represent the onset and offset of the target stimulus. (B) Average response times in attention and control trials for individual participants form two separate clusters corresponding to participants pursuing different behavioral strategies despite identical instruction (Instruction I). Two participants exhibited an unstable strategy with both slow and fast responses in the control condition (two data points between the central mass of both clusters). Since they fulfilled the criterion of mean RT in control trials (≥ 0.8 sec), they were included in the analysis as slow-responders. However, all the analyses repeated after their exclusion provided virtually the same results. (C) Between-group comparison of performance in control and attention trials. Error bars represent *SEM*.

Colors indicate the results of participants employing different strategies: red = fast-responders, blue = slow-responders, gray = participants presented with Instruction II (slowed-by-instruction-responders). The significance of post hoc comparisons is marked with asterisks: *** $p \leq .001$, * $p \leq .05$. Fast, slow, instr = refer to average results for fast, slow, and slowed-by-instruction groups.



$F(2,61) = 6.95$, $p = .002$, Figure 3A bottom right). The analysis revealed that model fit was worse for fast-responders (bigger values of fit index) than for slow-responders ($p > .001$) and, although to a lesser extent, than for slowed-by-instruction group ($p = .015$). The two slow-responding groups did not differ significantly ($p \geq .542$). Subsequently, we visually inspected goodness of fit by plotting predicted and empirical values of accuracy and mean RT in the first, second, and third quartile (Voss et al., 2015; Voss, Nagler, & Lerche, 2013). The plots revealed considerable similarity between empirical and predicted data (Figure 3B). The model provided accurate predictions of response correctness, slightly underestimated RTs for the first quartile and overestimated ones for the third quartile (see the distance between data points and line of perfect fit). The discrepancies were overall small, indicating sufficiently good model fit in all three groups.

A comparison of DDM parameters is summarized in Figure 3A. Groups implementing different strategies differed most prominently in the duration of nondecision processes (parameter t_0 ; $F(2, 61) = 59.84$, $p < .001$) with slow-responders ($M = 0.94$, $SD = 0.08$) and slowed-by-instruction groups ($M = 0.96$, $SD = 0.14$) spending more time on encoding and/or response preparation/execution

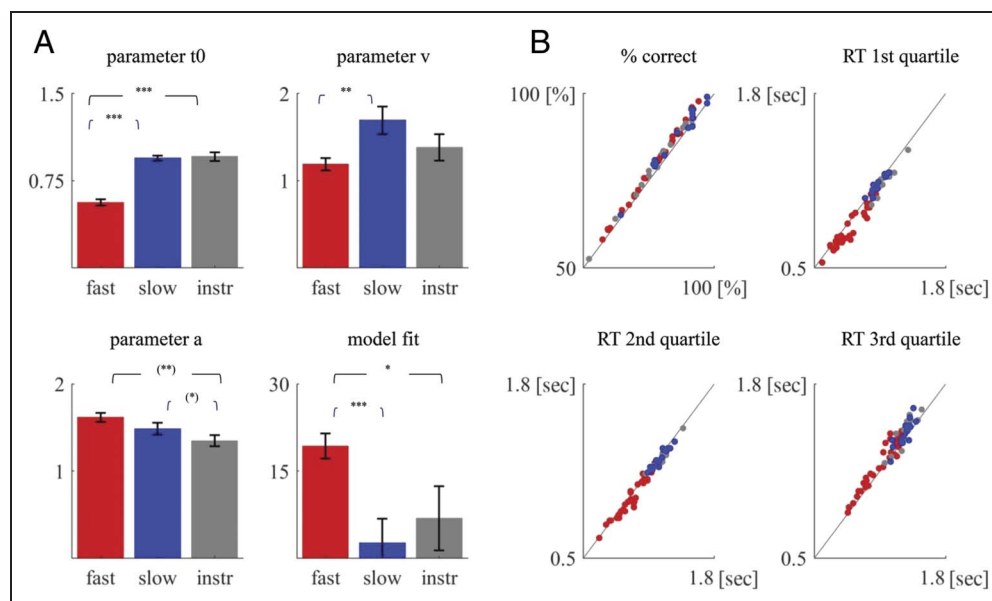
than fast-responders ($M = 0.56$, $SD = 0.16$; with $p < .001$ for both post hoc comparisons).

Despite the similarity in the percent of correct responses, the compared groups differed in the efficacy of evidence accumulation (parameter v ; $F(2, 61) = 5.14$, $p = .009$). Slow-responders had significantly bigger values of this parameter ($M = 1.69$, $SD = 0.62$) than fast-responders ($M = 1.19$, $SD = 0.42$, post hoc comparison $p = .002$) and, although not significantly, than participants provided with slowing instruction ($M = 1.38$, $SD = 0.58$, post hoc comparison $p = .167$), implying more efficient processing of the target matrix. This difference may reflect systematic differences in some cognitive abilities between fast- and slow-responders, which predisposed individual participants to embrace one or another strategy (for more details see Discussion section).

We did not compare statistically the values of parameter a because the number of trials available in our experiment could be insufficient for its reliable estimation (for more details, see Methods section).

In conclusion, analysis of behavioral results revealed that: (i) shorter RTs in fast-responding group than in both slow-responding groups can be, at least partially, explained by shorter time spent on nondecision processes

Figure 3. Estimation of DDM parameters and model fit. (A) The average value of diffusion model parameters (t_0 , v , a) and goodness of model fit estimated for performance in attention trials in groups with different behavioral strategies. Error bars represent *SEM*. (B) Relation of the empirical versus predicted data (percentage of correct responses and RTs for first, second, and third quartile), each dot represents a single participant. The majority of data points lie close to the line of perfect congruency (gray line). Different groups of participants are plotted with different colors: red = fast-responders, blue = slow-responders, gray = slowed-by-instruction-responders. Significance of post hoc comparisons is marked with asterisks: * $p \leq .05$; ** $p \leq .01$; *** $p \leq .001$. For consistency of the report, we show also the significance for parameter a (in brackets), which is not further interpreted (see Methods section). Fast, slow, instr = refer to average results for fast, slow, and slowed-by-instruction groups.



(stimulus encoding and/or response preparation); (ii) slow-responders had better efficacy of stimulus processing than fast-responders—which was reflected in their slightly better performance.

Activity during the Anticipation Period

Previous studies of electrophysiological correlates of decision process focused mostly on its execution part (Nunez et al., 2017; Ratcliff et al., 2009). Markedly less is known about the impact of preparatory processes on the following decision. The long (2–5 sec) cueing period in our paradigm allowed us to compare the anticipatory neuronal activity between groups employing different behavioral strategies. Similarly to previous studies (Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Sauseng, Klimesch, Stadler, et al., 2005), we observed that all groups exhibited a profound decrease of alpha power (8–15 Hz) that lasted throughout the entire cueing period of attention trials. This depression of alpha oscillations (in relation to the fixation period) indicated preparatory neuronal activity taking place in participants from all experimental groups during the presentation of the cue stimulus (Figure 4A).

To reveal whether groups employing different task performance strategies differed in the oscillatory activity before the onset of the target, we ran an exploratory ANOVA analysis for all frequencies (1–30.5 Hz) and channels. The analysis revealed that the averaged activities of the three groups differed over frontal and central sites in the frequency range 10.5–30.5 Hz (cluster $p = .044$; single comparison $p \leq .05$; Figure 4B). The obtained cluster of significant between-group differences comprised different activities from a wide range of frequencies including frequencies above 20 Hz, which are susceptible to the

contamination by muscle activity (Whitham et al., 2007; Goncharova, McFarland, Vaughan, & Wolpaw, 2003). To reject the possibility that observed between-group difference reflects muscle-related activity overlaying EEG signal, we plotted values of F statistic averaged across all electrodes constituting the cluster for all subsequent frequencies. If the difference between groups was because of muscle activity, we would expect an increase of average F statistic value with increasing frequency. We observed that the between-group difference was maximal in the range of 10.5–15 Hz followed by the second peak between 21 and 26 Hz (the frequency ranges exhibiting maximal between-group difference are marked in Figure 4C with black arrows and vertical, shaded areas; the entire frequency range constituting the cluster of significant between-group differences is marked with a black dotted line). In the next step, we reran analogical analysis on the averaged activity for upper alpha (10–15 Hz) and beta (21–26 Hz) bands, which revealed distinct topographies of the two activities (Figure 4D, F).

The cluster representing a significant between-group difference in the upper alpha activity ($p = .020$, single electrode $p \leq .05$; Figure 4D, first plot) was localized over the frontal region and was relatively symmetrical. The frequency range of 10–15 Hz fits well with the previous reports showing that event-related desynchronization (ERD) of alpha activity was not a unitary phenomenon and could be further differentiated into slow (7–10 Hz) and fast (10–13.5 Hz) sub-bands (for a review, see Klimesch, Doppelmayr, & Hanslmayr, 2006). ERD in lower alpha band was attributed to general attentional demands of the task, whereas ERD in the upper alpha band was attributed to “sensory-semantic processes” in the long-term memory system (Klimesch et al., 2006). The second

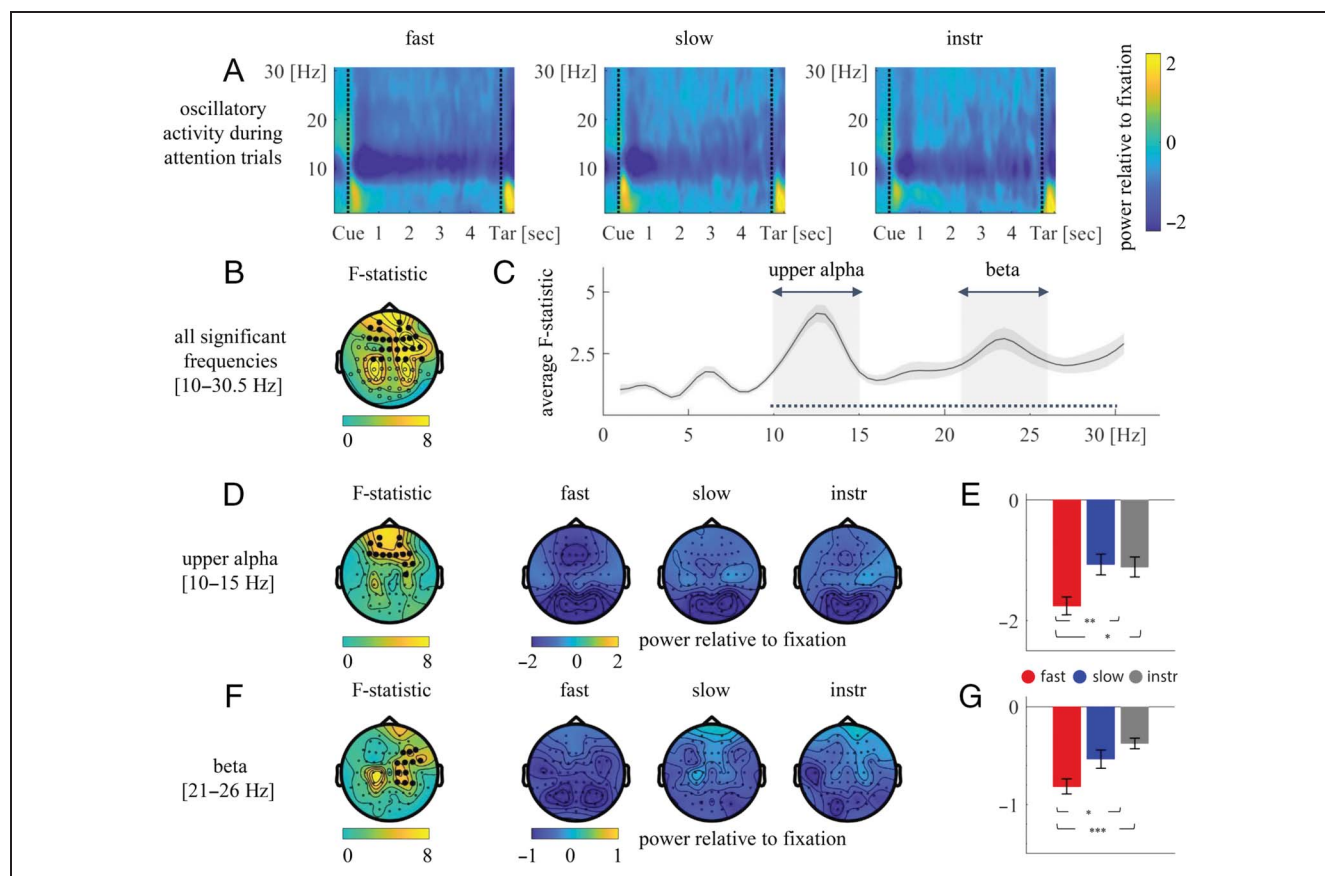


Figure 4. Between-group differences in the oscillatory activity during anticipation of attention task. (A) EEG power averaged across all channels ($n = 61$). Vertical lines on time axes at 0 and 5 sec represent cue and target stimulus onset, respectively. Data from different cue durations were aggregated and averaged, excluding first and last 0.5 sec of anticipation time because of their possible contamination by the responses to cue and target stimuli, respectively (see Methods section). From left to right plotted are results for fast-responders (fast), slow-responders (slow), and slowed-by-instruction-responders (instr). (B) Distribution of significant between-group difference in oscillatory activity (F -test map). Marked with bold black dots is a cluster of recording sites for which average power during the anticipation period was significantly different between the compared groups (for the cluster $p \leq .05$, for single electrode $p \leq .05$). (C) F statistics averaged across all channels comprising significant clusters (marked in B) plotted for subsequent frequencies. The shaded area represents the SEM . The black dotted-line over the horizontal axis marks the frequency range comprising a significant cluster. Two local maxima corresponding to upper alpha (10–15 Hz) and beta (21–26 Hz) bands are marked by shaded areas. (D, F) Topographic maps of upper alpha (10–15 Hz) and beta (21–26 Hz) bands relate to power during the anticipation period (0.5–4.5 sec after cue onset) of the attention task. From left to right: F -test map, topography of selected band power in fast-responders, slow-responders, and slowed-by-instruction group. Marked with bold black dots are recording sites for which average power was significantly different between the compared groups (cluster $p \leq .05$, single electrode $p \leq .05$). (E, G) Average ERD of upper alpha and beta bands for the clusters of frontal and right central electrodes, respectively (marked by bold black dots in D and F). Error bars represent SEM . The significance of post hoc comparisons is marked with asterisks: *** $p \leq .001$, ** $p \leq .01$, * $p \leq .05$. Fast, slow, instr = refer to average results for fast-responders, slow-responders, and slowed-by-instruction groups.

maximum of between-group difference (cluster $p = .039$, single electrode $p \leq .05$; Figure 4F, first plot) corresponded to beta band activity (21–26 Hz) and was localized over the right motor cortex. Although a similar cluster of smaller spatial extent was also visible over the left motor cortex, it was spatially disconnected from the main effect and, by itself, too small to reach significance. Note that participants responded with their left hand to indicate that the searched stimulus was not present in the target matrix. Bigger activity over the right motor cortex could thus reflect participants' tendency to report that the searched element was not present (as confirmed by bigger number of misses than false alarms in all three groups, all $p \leq .006$). Altogether, the obtained results revealed that beta band activity over the motor cortex was

differently modulated in groups employing different strategies.

To verify which pairs of groups significantly differ in their upper alpha and beta activity, we extracted average power across electrodes expressing between-group differences for post hoc comparisons. The analysis for upper alpha (Figure 4E) revealed that its power during anticipation period was significantly smaller over the frontal region in fast-responders ($M = -1.75$, $SD = 0.86$) than in slow-responders ($M = -1.07$, $SD = 0.66$; $p = .009$) and slowed-by-instruction group ($M = -1.11$, $SD = 0.64$; $p = .013$). There was no difference between the two slow-responding groups ($p = .858$). Analogical analysis run for beta frequency range (Figure 4G) revealed that fast-responders had lower activity in this frequency range over

right central and fronto-central regions ($M = -0.82$, $SD = 0.45$) than the slowed-by-instruction group ($M = -0.37$, $SD = 0.21$; $p < .001$) and lower than slow-responders ($M = -0.54$, $SD = 0.36$; $p = .041$), although this difference was not significant after correction for multiple comparisons. Again, there was no difference in this frequency range between the two slow responding groups ($p = .156$). Scalp topography of this effect suggests that this activity was related to movement preparation.

In summary, we found that groups employing different strategies during task execution had different oscillatory activity already at the time of the preceding preparatory period. The between-group difference comprised a wide frequency range 10.5–30.5 Hz and was localized over frontal and central regions. A more detailed analysis revealed that obtained clusters comprised two distinct effects with different topographies and frequency characteristics. The first effect was characterized by lower power in the upper alpha range (10–15 Hz) over frontal sites in fast-responders compared to the two slow responding groups. The group order of this effect closely resembled the pattern of group differences exemplified by RTs as well as $t0$ parameter of diffusion model (compare bar graph in Figure 4E with Figures 2C and 3A). The second effect involved significantly lower beta (21–26 Hz) band power over the motor cortex during the anticipation period in fast-responders than in the slowed-by-instruction group with a moderate decrease of power in slow-responders. Because of its scalp localization over the motor cortex (Figure 4F), this effect suggests a difference in activation of motor system preceding the appearance of the target, which was smaller in the two slow-responding groups. Especially, in the slowed-by-instruction group, which was explicitly asked to postpone their responses after stimulus offset, the high level of motor cortex activity during cueing period might be detrimental for the performance resulting in failures in postponing the response until target stimulus offset.

Response Preparation

Analysis of oscillatory activity during the anticipation period revealed that the group with significantly shorter duration of nondecision processes (parameter $t0$) during task performance had the biggest ERD in the upper alpha band over frontal sites during the anticipation period. Unequivocal interpretation of this result is precluded because this parameter describes in the model a set of two, distinct processes: initial stimulus encoding and preparation of the motor response. Fortunately, according to the DDM, these two processes are separated by a decision process that occurs in between. Thus, it should be possible to disentangle them by analyzing stimulus-locked and response-locked activities, for early-perceptual and late-motor processes, respectively. Because of large between-group differences in RTs, we did not perform stimulus-locked analysis. Instead, we focused on response-locked activity and compared its dynamics between groups.

To this end, we identified electrodes that recorded significantly different signals depending on the responding hand in all three groups and their equivalents in the other hemisphere (marked on Figure 5A with white dots). For these electrodes, we computed LRP as the difference between ERP courses recorded in the hemisphere contralateral and ipsilateral to the responding hand (for details see Methods section) separately for groups employing different strategies. We compared their magnitudes and latencies (the time at which the component reached half of its total magnitude). A similar estimate was applied in previous research that reported shortening of LRP-RT interval when the task was performed under the time pressure (Rinkenauer et al., 2004; van der Lubbe et al., 2001).

Despite the limited number of trials, we observed demonstrable lateralization of activity, visible as a more negative potential over the hemisphere contralateral to the responding hand (Figure 5A).

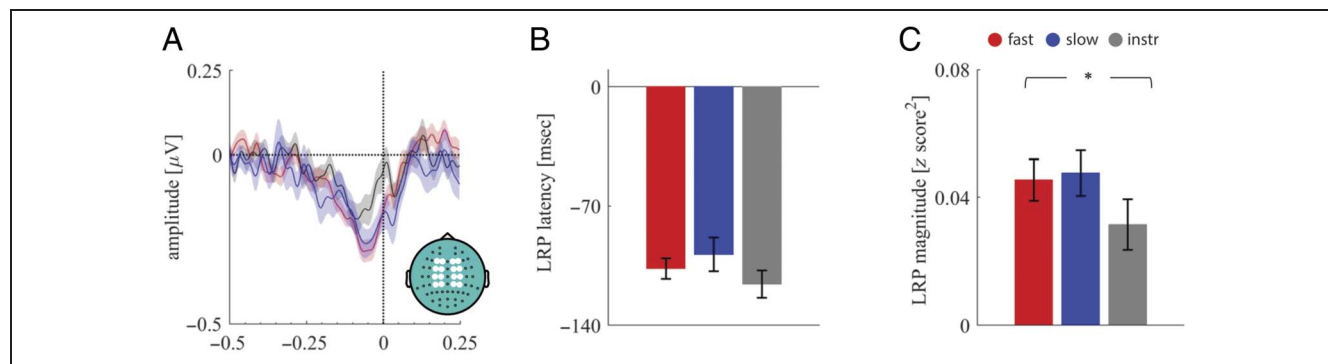


Figure 5. Analysis of response-locked ERPs in the attention task. (A) Time course of the LRP for attention trials computed from the selected electrodes (marked with white dots) in the three compared groups. Shaded areas mark SEM. The vertical, dotted line marks the time of the button press. (B) The latency of LRP measured as time at which it reached 0.5 of its total magnitude. (C) The magnitude of LRP measured as an average area of negativity (Potential \times Time) preceding button press (from -0.3 to 0 sec). Error bars represent SEM. The significance of post hoc comparisons is marked with an asterisk ($p \leq .05$). Data for groups employing different strategies are represented with colors: red = fast-responders; blue = slow-responders; gray = slowed-by-instruction-responders.

One-way ANOVA conducted for the latency of LRPs revealed that the compared groups did not differ with respect to the duration of motor preparation in attention trials, $F(2, 61) = 0.931, p = .400$ (Figure 5B). However, the same analysis performed for the magnitude of LRPs revealed significant between-group differences (Group effect, $F(2, 61) = 3.9, p = .025$; Figure 5C). Post hoc comparisons indicated that, in attention trials, the slowed-by-instruction group ($M = 0.03, SD = 0.02$) had significantly smaller LRP than fast-responders ($M = 0.07, SD = 0.04; p = .012$). The magnitude of LRPs in slow-responders was in between the two other groups ($M = 0.05, SD = 0.04$) and did not differ significantly from neither of them (for comparison with fast-responders $p = .166$ and with slowed-by-instruction group $p = .271$).

The obtained result enabled us to discard the hypothesis that fast- and slow-responding groups differed in the motor response preparation. Thus, we interpret the between-group difference in the duration of nondecision processes (estimated by $t0$ parameter) as a result of speeding of early perceptual processes (i.e., stimulus encoding) in fast-responders.

DISCUSSION

In this study, we compared behavior and neuronal activity of three groups of participants: fast-responders (characterized by fast responses in control trials and the fastest responses in the attention trials), slow-responders (who, regardless of trial type, spontaneously postponed their responses until stimulus offset), and slowed-by-instruction group (explicitly asked in the instruction to postpone their responses until the stimulus offset). By evaluation of the DDM, we were able to describe these behavioral strategies in terms of between-group differences in the independent components comprising the decision process. We show that fast-responders spent the shortest time on nondecision processes (had the smallest value of parameter $t0$), whereas slow-responders were most efficient in evidence accumulation (had the largest value of parameter ν). Because we did not find any between-group differences in the duration of LRP-RT interval, we discarded the hypothesis that fast-responders had more efficient motor processes and concluded that different duration of nondecision processes should be assigned to the speeding of stimulus encoding in the fast-responding group. Faster stimulus encoding was preceded by a more profound ERD in the upper alpha (10–15 Hz) range over the frontal region during the anticipation period. In addition, we observed between-group differences in beta activity (21–26 Hz) over the motor cortex, with the smallest beta band power in fast responders, moderate in slow-responders, and the largest in the slowed-by-instruction group.

Within the analyzed anticipation period, we did not find any electrophysiological indices, which would

exhibit the same between-group pattern as efficacy of evidence accumulation (parameter ν). The relevant changes were found, however, by previous studies during task execution. In particular, P3 wave has been repeatedly reported as reflecting this parameter of DDM (Kelly & O'Connell, 2013; O'Connell et al., 2012). Because of the large difference in RTs between groups compared in our analyses, we did not compute target stimulus-locked ERPs. In previous reports (e.g., Schmiedek, Oberauer, Wilhelm, Süß, & Wittmann, 2007), interindividual differences in the efficacy of evidence accumulation were shown to be related to various measures of cognitive abilities such as working memory, reasoning, and psychometric speed. In fact, assignment to fast- or slow-responders was not randomized but established post hoc based on the strategy employed in the control trials. Thus, it is likely that affiliation to a fast- and slow-responders group reflects some cognitive abilities or temperamental traits that predisposed a particular individual to embrace one strategy rather than another. These potential confounds were controlled by an introduction of the third slowed-by-instruction group presented with instruction to postpone their responses until stimulus offset (slowed-by-instruction-responders). This group successfully recreated behavior of slow-responders (no differences in the values of RTs for attention trials or parameter $t0$), proving that the control was adequate.

Neuronal Activity during the Anticipation Period

The neuronal activity in the widely defined alpha range (8–15 Hz) has long been discussed in the context of anticipatory processes (Klimesch et al., 2006; Thut et al., 2006; Sauseng, Klimesch, Stadler, et al., 2005). The general finding was that, before the onset of the expected stimulus, alpha power decreased over regions subsequently engaged in its processing. A decrease in alpha power (conventionally described with the term ERD) was also shown to reflect an increase in cortical excitability (Romei, Rihs, Brodbeck, & Thut, 2008), possibly because of desynchronization of cortical columns engaged in information processing. We found that the group with more prominent decrease in upper alpha (10–15 Hz) power over the frontal cortex during the anticipation period had shorter duration of nondecision processes (smaller value of $t0$ parameter) during subsequent decision making. Because this parameter concurrently described early perceptual and late motor processes, additional reasoning was needed to ascertain which one of them was responsible for the observed shortening of nondecision time. A similar duration of LRP-RT interval for fast- and slow-responding groups allowed us to assign differences in $t0$ parameter to the early stages of perception (i.e., a shorter time required for stimulus encoding).

Previous EEG studies postulated that decreased upper alpha activity over the frontal cortex was related to the

activation of the frontoparietal network in tasks engaging executive functions (Sauseng, Klimesch, Stadler, et al., 2005; Sauseng et al., 2002). Sauseng, Klimesch, Schabus, and Doppelmayr (2005) asked participants to learn eight abstract figures consisting of black bars that differed with regard to some physical features (e.g., length, width, number, orientation). After training, participants undertook two tasks: first, a retrieval task in which they were asked to recall the appearance of the figures and, second, a manipulation task in which they had to compare indicated figures with respect to a particular feature (e.g., length). Upper ($\sim 10\text{--}13$ Hz) but not lower ($\sim 7\text{--}10$ Hz) alpha power largely decreased over frontal and parietal sites during the manipulation task and exhibited a small increase of power during the retrieval task. In addition, signal synchronization between frontal sites in the upper alpha range decreased, indicating functional activation within this region during performance of the manipulation task (Sauseng, Klimesch, Schabus, et al., 2005). The authors concluded that the observed decrease in upper alpha power indicated activation of the frontoparietal network constituting neuronal substrate of the central executive system.

Converging evidence was provided by an fMRI study on task switching (Ruge et al., 2009). Similarly to our division into fast- and slow-responders groups, Ruge et al. (2009) observed spontaneous occurrence of two subgroups of participants (showing a bimodal distribution of RTs in a simple trials and unimodal distribution in a demanding trials; see Figure 2 in Ruge et al., 2009). These authors proposed that the two observed strategies resulted from the difference in the preparation of the motor response and called them “high-readiness” and “low-readiness” groups. Direct comparison of brain activity between the two groups showed that, during the cueing period, the “high-readiness” group had increased activity in a medial frontal cortex (specifically in dorsal ACC, corresponding to Brodmann’s area 32; Ruge et al., 2009). This effect was present not only in simple trials in which preparation of response was possible in advance but also in demanding trials in which the correct response was not known in advance. The presence of the effect in both types of trials as well as the localization of the difference outside motor areas argued against a purely motoric explanation of the difference observed between groups. Ruge et al. proposed that difference in activation within the medial frontal cortex was related to the voluntarily employed strategies that differed in the weighting of benefits and costs when the optimal behavior was not evident (i.e., in demanding trials, a higher level of motor readiness would increase the preparatory efforts and only slightly shorten RT, whereas in simple trials, it would decrease demands for response selection). Although direct comparison of these results to our data is impossible because of methodological differences, similar localization of the differential activity supports our hypothesis of the source of anticipatory upper alpha activity within the frontal cortex. In contrast to Ruge

et al. (2009), in our data, the between-group difference could not be reduced to the preparatory motor processes. The use of DDM allowed us to relate the anticipatory decrease of alpha power with early perception (i.e., stimulus encoding). However, as this change was recorded over the frontal region, it could not reflect an original causing activity, as such should be localized over the visual cortex. Instead, we probably observed a supramodal control mechanism that, in turn, affected the activity of visual and/or other sensory cortices.

The question remains by which mechanism the supramodal centers localized in the frontal cortex (e.g., the hubs of the frontoparietal network; Sauseng, Klimesch, Schabus, et al., 2005) may affect stimulus encoding. One such possible mechanism was described by Iemi, Chaumon, Crouzet, and Busch (2017), who showed that, during decreased alpha activity, participants more likely reported perception of the near-threshold stimulus, regardless of its actual presence (increase in hits and false alarms rates). To explain this effect, the authors tested two hypotheses: first, a shift in perception threshold (unspecific increase of sensitivity to signal as well as noise) and, second, a shift in response strategy (i.e., increased tendency to affirmative responses). In an artful experiment applying two-interval tasks requiring either stimulus detection or discrimination of stimulus orientation, Iemi and Busch (2018) were able to assign a decrease of alpha power with changes in early perception (i.e., lowering of perception threshold) and not with response making strategy. The topography of this effect was set in the fronto-central region and shifted shortly before the stimulus onset to parieto-occipital sites (see Figure 3C in Iemi & Busch, 2018). Although Iemi et al. investigated the effects of spontaneous fluctuations of alpha power, they proposed that the same mechanism of a general increase in sensitivity could occur during the decrease of alpha power induced by a cue in experiments investigating anticipatory attention (see discussion in Iemi et al., 2017). Accordingly, Sauseng, Klimesch, Stadler, et al. (2005) used the Posner task and showed that, if a stimulus is preceded by an informative cue (e.g., centrally located arrow indicating likely localization of the following stimulus), alpha power decreased over the contralateral parieto-occipital region. Cue-induced, spatially specific deployment of perceptual bias to the probable location of target stimulus can be beneficial for performance in detection tasks and serve as a mechanism of attention focus. However, the hypothesis that similar mechanisms underlie spontaneous and voluntary shifts of alpha power requires confirmation in future studies.

In our study, we took advantage of the application of the DDM, which enabled us to investigate the role of anticipatory alpha power on the individual subcomponents of subsequent stimulus processing within a single experiment. In line with the observations of Iemi and Busch (2018), our results suggest that a decrease in upper alpha power over the frontal cortex before the onset of the target stimulus is followed by a perceptual bias as revealed by

shorter stimulus-encoding time. It can be hypothesized that this effect results from the descending modulation of visual cortex activity implemented by frontal and prefrontal cortices.

Preparation of Motor Response

To control for the effects of response speed, we tested a group of participants who were presented with slightly altered task instruction (Instruction II—see Methods section) than the two spontaneously emerged groups (fast- and slow-responders). The Instruction II explicitly asked participants to postpone their response until the target stimulus offset resembling an experimental technique known as “response signal.” The method was introduced by Reed (1973) to study SAT. This technique of SAT manipulation is less popular than commonly applied instructions emphasizing speed or accuracy of responses (for a comprehensive comparison of different approaches, see Heitz, 2014).

In our data, we observed similar durations of the LRP-RT intervals for fast- and both slow-responding groups, despite a profound difference in their RTs. This result is not surprising because our attention task did not allow for the prior preparation of responding hand, which was chosen after the analysis of the target stimulus matrix (response with the right hand if the cue bar was present in the matrix and with the left hand if it was absent). However, it is important to note that, although the selection of a specific response required the same amount of time in all three groups, the general level of activation of the motor system was different, as reflected in the beta ERD during the anticipation period.

In fact, we observed a significant difference in beta (21–26 Hz) band activity over right and less pronounced symmetric effect over left, central regions. This observation followed the results of Ruge et al. (2009) who found stronger activation of the premotor cortex (specifically of its dorsal part, corresponding to Brodmann’s area 6) in their “high-readiness” group. In our data, ERD in beta range changed gradually from the biggest in the fast-responding group, medium in slow-responders to the smallest in the slowed-by-instruction group. The difference in beta ERD was maximal between fast-responders and slowed-by-instruction group, which was included in our study to experimentally recreate behavior observed post hoc in slow-responders. In this group, explicitly asked to postpone responses until target stimulus offset, the high level of motor system activation, was not only unnecessary (as in the case of slow-responders) but even adverse because it might result in the increased number of premature responses.

Participants who postponed their reactions according to the explicit instruction (slowed-by-instruction-responders) had smaller magnitude of LRP than two remaining groups. Since slowed-by-instruction group did not differ in duration of nondecision processes (parameter t_0) from slow-responders and in efficacy of evidence accumulation

(parameter v) from fast-responders, we hypothesized that observed difference in LRP magnitude may reflect difference in decision criterion—a third subcomponent of decision process. In line with this hypothesis, Sangals, Sommer, and Leuthold (2002) who studied utilization of precues during response preparation using pay-offs as a method of inducing time pressure observed that LRP amplitude but not LRP-RT interval was affected by time pressure (i.e., bigger LRP amplitude for participants disposed to respond faster). Thus, shortening of LRP-RT interval is not a necessary and sufficient condition of speeded response and it depends on the involved mechanism (e.g., shorter response preparation, faster evidence accumulation or lower decision criterion).

Our hypothesis that magnitude of LRP rather than its duration may reflect the level of decision criterion is at odds with previous electrophysiological studies on SAT, which often reported shortening of LRP-RT interval under speed instruction (Rinkenauer et al., 2004; van der Lubbe et al., 2001; Osman et al., 2000). However, recent behavioral studies have demonstrated that commonly employed instructions emphasizing speed versus accuracy of responses evoke, as intended, shift in decision criterion but also shortening of the nondecision time (Dutilh et al., 2019; Arnold, Bröder, & Bayen, 2015; Voss et al., 2004). The observed interdependence of these two subcomponents is not a flaw of the DDM as the subcomponents can be differentiated in simulations performed on the surrogate data (Lerche & Voss, 2018). Instead, the joint changes of nondecisional process and decision criterion should be attributed to the lack of discriminant validity of the experimental method (i.e., providing participants with verbal instructions emphasizing speed or accuracy of responses) or may result from a more general inability of participants to independently adjust these two subcomponents of decision process. Most importantly, because LRP is generated within the motor system (Praagstra, Stegeman, Horstink, & Cools, 1996), reported shortening of LRP-RT interval could reflect the shortening of nondecisional processes (specifically motor response preparation) and be unrelated to the shift of decision criterion. Therefore, neuronal correlates of decision criterion would remain to be determined.

Conclusions

In this study, we demonstrated the impact of preparatory processes on the subcomponents of decision process, as described by DDM. To this aim, we compared the neuronal activity of three groups of participants recorded during few seconds long cueing period preceding performance of the task requiring perceptual decision making. We found that the group characterized by decreased power of upper alpha band over frontal cortex during the preparatory period spent significantly shorter time on nondecision processes, involving stimulus encoding and motor response preparation. Analysis of LRP enabled us to ascribe this difference to the quicker perception of the target

stimulus because there were no differences in motor preparation between the compared groups.

We proposed also that the observed upper alpha ERD paralleled activation of higher control regions of the frontal cortex, which facilitated activity of the visual cortex during stimulus processing, leading to perceptual bias (a mechanism recently proposed by Iemi & Busch, 2018). In addition, we observed increased preparatory ERD of beta band localized over the motor cortex in fast-responders group. We interpreted this activity as reflecting general readiness of the motor system for responding, similarly to the hypothesis proposed by Ruge et al. (2009).

It should be noticed that the conclusions of our study are limited to the between-group differences as we analyzed the between-group data. All reported effects are related to the behavioral strategies voluntarily adopted or induced by instruction alterations. Thus, they likely reflect qualitative and not quantitative differences between analyzed groups. Further investigations, with larger number of trials, are needed to determine the neuronal indices of within-participant fluctuations of behavior. Finally, because of limited number of trials, which prevented us from reliable estimation of parameter α , we were unable to verify previous findings on electrophysiological correlates of decision criterion. Studies with larger number of trials, employing DDM concurrently with electrophysiological recordings, are needed to address this issue.

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REFERENCES

- Arnold, N. R., Bröder, A., & Bayen, U. J. (2015). Empirical validation of the diffusion model for recognition memory and a comparison of parameter-estimation methods. *Psychological Research*, 79, 882–898. **DOI:** <https://doi.org/10.1007/s00426-014-0608-y>, **PMID:** 25281426, **PMCID:** PMC4534506
- Britten, K. H., Newsome, W. T., Shadlen, M. N., Celebrini, S., & Movshon, J. A. (1996). A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Visual Neuroscience*, 13, 87–100. **DOI:** <https://doi.org/10.1017/S095252380000715X>, **PMID:** 8730992
- Chang, C.-Y., Hsu, S.-H., Pion-Tonachini, L., & Jung, T.-P. (2020). Evaluation of artifact subspace reconstruction for automatic artifact components removal in multi-channel EEG recordings. *IEEE Transactions on Biomedical Engineering*, 67, 1114–1121. **DOI:** <https://doi.org/10.1109/TBME.2019.2930186>, **PMID:** 31329105
- Curl, R. A., & White, C. N. (2019). Cueing effects in the attentional network test: A spotlight diffusion model analysis. *Journal of Vision*, 19, 107c. **DOI:** <https://doi.org/10.1167/19.10.107c>
- Delorme, A., Miyakoshi, M., Jung, T.-P., & Makeig, S. (2015). Grand average ERP-image plotting and statistics: A method for comparing variability in event-related single-trial EEG activities across subjects and conditions. *Journal of Neuroscience Methods*, 250, 3–6. **DOI:** <https://doi.org/10.1016/j.jneumeth.2014.10.003>, **PMID:** 25447029, **PMCID:** PMC4406779
- Dutilh, G., Annis, J., Brown, S. D., Cassey, P., Evans, N. J., Grasman, R. P. P., et al. (2019). The quality of response time data inference: A blinded, collaborative assessment of the validity of cognitive models. *Psychonomic Bulletin & Review*, 26, 1051–1069. **DOI:** <https://doi.org/10.3758/s13423-017-1417-2>, **PMID:** 29450793, **PMCID:** PMC6449220
- Geddes, J., Ratcliff, R., Allerhand, M., Childers, R., Wright, R. J., Frier, B. M., et al. (2010). Modeling the effects of hypoglycemia on a two-choice task in adult humans. *Neuropsychology*, 24, 652–660. **DOI:** <https://doi.org/10.1037/a0020074>, **PMID:** 20804253
- Goncharova, I. I., McFarland, D. J., Vaughan, T. M., & Wolpaw, J. R. (2003). EMG contamination of EEG: Spectral and topographical characteristics. *Clinical Neurophysiology*, 114, 1580–1593. **DOI:** [https://doi.org/10.1016/S1388-2457\(03\)00093-2](https://doi.org/10.1016/S1388-2457(03)00093-2), **PMID:** 12948787
- Grandchamp, R., & Delorme, A. (2011). Single-trial normalization for event-related spectral decomposition reduces sensitivity to noisy trials. *Frontiers in Psychology*, 2, 236. **DOI:** <https://doi.org/10.3389/fpsyg.2011.00236>, **PMID:** 21994498, **PMCID:** PMC3183439
- Hayasaka, S., & Nichols, T. E. (2004). Combining voxel intensity and cluster extent with permutation test framework. *Neuroimage*, 23, 54–63. **DOI:** <https://doi.org/10.1016/j.neuroimage.2004.04.035>, **PMID:** 15325352
- Heitz, R. P. (2014). The speed–accuracy tradeoff: History, physiology, methodology, and behavior. *Frontiers in Neuroscience*, 8, 150. **DOI:** <https://doi.org/10.3389/fnins.2014.00150>, **PMID:** 24966810, **PMCID:** PMC4052662
- Hübner, R., Steinhauser, M., & Lehle, C. (2010). A dual-stage two-phase model of selective attention. *Psychological Review*, 117, 759–784. **DOI:** <https://doi.org/10.1037/a0019471>, **PMID:** 20658852
- Iemi, L., & Busch, N. A. (2018). Moment-to-moment fluctuations in neuronal excitability bias subjective perception rather than strategic decision-making. *eNeuro*, 5, ENEURO.0430-17.2018. **DOI:** <https://doi.org/10.1523/ENEURO.0430-17.2018>, **PMID:** 29911179, **PMCID:** PMC6002263

- Iemi, L., Chaumon, M., Crouzet, S. M., & Busch, N. A. (2017). Spontaneous neural oscillations bias perception by modulating baseline excitability. *Journal of Neuroscience*, 37, 807–819. **DOI:** <https://doi.org/10.1523/JNEUROSCI.1432-16.2016>, **PMID:** 28123017, **PMCID:** PMC6597018
- Kelly, S. P., & O'Connell, R. G. (2013). Internal and external influences on the rate of sensory evidence accumulation in the human brain. *Journal of Neuroscience*, 33, 19434–19441. **DOI:** <https://doi.org/10.1523/JNEUROSCI.3355-13.2013>, **PMID:** 24336710, **PMCID:** PMC6618757
- Klimesch, W., Doppelmayr, M., & Hanslmayr, S. (2006). Upper alpha ERD and absolute power: Their meaning for memory performance. *Progress in Brain Research*, 159, 151–165. **DOI:** [https://doi.org/10.1016/S0079-6123\(06\)59010-7](https://doi.org/10.1016/S0079-6123(06)59010-7), **PMID:** 17071229
- Lerche, V., & Voss, A. (2018). Speed–accuracy manipulations and diffusion modeling: Lack of discriminant validity of the manipulation or of the parameter estimates? *Behavior Research Methods*, 50, 2568–2585. **DOI:** <https://doi.org/10.3758/s13428-018-1034-7>, **PMID:** 29542062
- Lerche, V., Voss, A., & Nagler, M. (2017). How many trials are required for parameter estimation in diffusion modeling? A comparison of different optimization criteria. *Behavior Research Methods*, 49, 513–537. **DOI:** <https://doi.org/10.3758/s13428-016-0740-2>, **PMID:** 27287445
- Luck, S. J. (2004). Ten simple rules for designing ERP experiments. In T. C. Handy (Ed.), *Event-related potentials: A methods handbook*. Cambridge, MA: MIT Press.
- Makeig, S., Delorme, A., Westerfield, M., Jung, T.-P., Townsend, J., Courchesne, E., et al. (2004). Electroencephalographic brain dynamics following manually responded visual targets. *PLoS Biology*, 2, e176. **DOI:** <https://doi.org/10.1371/journal.pbio.0020176>, **PMID:** 15208723, **PMCID:** PMC423146
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164, 177–190. **DOI:** <https://doi.org/10.1016/j.jneumeth.2007.03.024>, **PMID:** 17517438
- Mueller, C. J., White, C. N., & Kuchinke, L. (2017). Electrophysiological correlates of the drift diffusion model in visual word recognition. *Human Brain Mapping*, 38, 5616–5627. **DOI:** <https://doi.org/10.1002/hbm.23753>, **PMID:** 28758287, **PMCID:** PMC6866948
- Mulder, M. J., van Maanen, L., & Forstmann, B. U. (2014). Perceptual decision neurosciences—A model-based review. *Neuroscience*, 277, 872–884. **DOI:** <https://doi.org/10.1016/j.neuroscience.2014.07.031>, **PMID:** 25080159
- Mullen, T. R., Kothe, C. A. E., Chi, Y. M., Ojeda, A., Kerth, T., Makeig, S., et al. (2015). Real-time neuroimaging and cognitive monitoring using wearable dry EEG. *IEEE Transactions on Biomedical Engineering*, 62, 2553–2567. **DOI:** <https://doi.org/10.1109/TBME.2015.2481482>, **PMID:** 26415149, **PMCID:** PMC4710679
- Newsome, W. T., Britten, K. H., & Movshon, J. A. (1989). Neuronal correlates of a perceptual decision. *Nature*, 341, 52–54. **DOI:** <https://doi.org/10.1038/341052a0>, **PMID:** 2770878
- Nunez, M. D., Gosai, A., Vandekerckhove, J., & Srinivasan, R. (2019). The latency of a visual evoked potential tracks the onset of decision making. *Neuroimage*, 197, 93–108. **DOI:** <https://doi.org/10.1016/j.neuroimage.2019.04.052>, **PMID:** 31028925
- Nunez, M. D., Vandekerckhove, J., & Srinivasan, R. (2017). How attention influences perceptual decision making: Single-trial EEG correlates of drift-diffusion model parameters. *Journal of Mathematical Psychology*, 76, 117–130. **DOI:** <https://doi.org/10.1016/j.jmp.2016.03.003>, **PMID:** 28435173, **PMCID:** PMC5397902
- O'Connell, R. G., Dockree, P. M., & Kelly, S. P. (2012). A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. *Nature Neuroscience*, 15, 1729–1735. **DOI:** <https://doi.org/10.1038/nn.3248>, **PMID:** 23103963
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011, 156869. **DOI:** <https://doi.org/10.1155/2011/156869>, **PMID:** 21253357, **PMCID:** PMC3021840
- Oostenveld, R., & Praamstra, P. (2001). The five percent electrode system for high-resolution EEG and ERP measurements. *Clinical Neurophysiology*, 112, 713–719. **DOI:** [https://doi.org/10.1016/S1388-2457\(00\)00527-7](https://doi.org/10.1016/S1388-2457(00)00527-7), **PMID:** 11275545
- Osman, A., Lou, L., Muller-Gethmann, H., Rinkenauer, G., Mattes, S., & Ulrich, R. (2000). Mechanisms of speed–accuracy tradeoff: Evidence from covert motor processes. *Biological Psychology*, 51, 173–199. **DOI:** [https://doi.org/10.1016/S0301-0511\(99\)00045-9](https://doi.org/10.1016/S0301-0511(99)00045-9), **PMID:** 10686365
- Philastides, M. G., Ratcliff, R., & Sajda, P. (2006). Neural representation of task difficulty and decision making during perceptual categorization: A timing diagram. *Journal of Neuroscience*, 26, 8965–8975. **DOI:** <https://doi.org/10.1523/JNEUROSCI.1655-06.2006>, **PMID:** 16943552, **PMCID:** PMC6675324
- Philastides, M. G., & Sajda, P. (2006). Temporal characterization of the neural correlates of perceptual decision making in the human brain. *Cerebral Cortex*, 16, 509–518. **DOI:** <https://doi.org/10.1093/cercor/bhi130>, **PMID:** 16014865
- Praamstra, P., Stegeman, D. F., Horstink, M. W. I. M., & Cools, A. R. (1996). Dipole source analysis suggests selective modulation of the supplementary motor area contribution to the readiness potential. *Electroencephalography and Clinical Neurophysiology*, 98, 468–477. **DOI:** [https://doi.org/10.1016/0013-4694\(96\)95643-6](https://doi.org/10.1016/0013-4694(96)95643-6), **PMID:** 8763506
- Ratcliff, R. (1978). A theory of memory retrieval. *Psychological Review*, 85, 59–108. **DOI:** <https://doi.org/10.1037/0033-295X.85.2.59>
- Ratcliff, R. (2002). A diffusion model account of response time and accuracy in a brightness discrimination task: Fitting real data and failing to fit fake but plausible data. *Psychonomic Bulletin & Review*, 9, 278–291. **DOI:** <https://doi.org/10.3758/BF03196283>, **PMID:** 12120790
- Ratcliff, R., Gomez, P., & McKoon, G. (2004). A diffusion model account of the lexical decision task. *Psychological Review*, 111, 159–182. **DOI:** <https://doi.org/10.1037/0033-295X.111.1.159>, **PMID:** 14756592, **PMCID:** PMC1403837
- Ratcliff, R., Philastides, M. G., & Sajda, P. (2009). Quality of evidence for perceptual decision making is indexed by trial-to-trial variability of the EEG. *Proceedings of the National Academy of Sciences, U.S.A.*, 106, 6539–6544. **DOI:** <https://doi.org/10.1073/pnas.0812589106>, **PMID:** 19342495, **PMCID:** PMC2672543
- Ratcliff, R., & Smith, P. L. (2004). A comparison of sequential sampling models for two-choice reaction time. *Psychological Review*, 111, 333–367. **DOI:** <https://doi.org/10.1037/0033-295X.111.2.333>, **PMID:** 15065913, **PMCID:** PMC1440925
- Ratcliff, R., Thapar, A., & McKoon, G. (2001). The effects of aging on reaction time in a signal detection task. *Psychology and Aging*, 16, 323–341. <https://doi.org/10.1037/0882-7974.16.2.323>, **PMID:** 11405319
- Ratcliff, R., & Van Dongen, H. P. A. (2009). Sleep deprivation affects multiple distinct cognitive processes. *Psychonomic Bulletin & Review*, 16, 742–751. **DOI:** <https://doi.org/10.3758/PBR.16.4.742>, **PMID:** 19648462, **PMCID:** PMC2797337
- Reed, A. V. (1973). Speed–accuracy trade-off in recognition memory. *Science*, 181, 574–576. **DOI:** <https://doi.org/10.1126/science.181.4099.574>, **PMID:** 17777808

- Rinkenauer, G., Osman, A., Ulrich, R., Muller-Gethmann, H., & Mattes, S. (2004). On the locus of speed-accuracy trade-off in reaction time: Inferences from the lateralized readiness potential. *Journal of Experimental Psychology: General*, *133*, 261–282. **DOI:** <https://doi.org/10.1037/0096-3445.133.2.261>, **PMID:** 15149253
- Romei, V., Rihs, T., Brodbeck, V., & Thut, G. (2008). Resting electroencephalogram alpha-power over posterior sites indexes baseline visual cortex excitability. *NeuroReport*, *19*, 203–208. **DOI:** <https://doi.org/10.1097/WNR.0b013e3282f454c4>, **PMID:** 18185109
- Ruge, H., Braver, T., & Meiran, N. (2009). Attention, intention, and strategy in preparatory control. *Neuropsychologia*, *47*, 1670–1685. **DOI:** <https://doi.org/10.1016/j.neuropsychologia.2009.02.004>, **PMID:** 19397862, **PMCID:** PMC2674875
- Sangals, J., Sommer, W., & Leuthold, H. (2002). Influences of presentation mode and time pressure on the utilisation of advance information in response preparation. *Acta Psychologica*, *109*, 1–24. **DOI:** [https://doi.org/10.1016/S0001-6918\(01\)00045-2](https://doi.org/10.1016/S0001-6918(01)00045-2), **PMID:** 11766138
- Sauseng, P., Klimesch, W., Gruber, W., Doppelmayr, M., Stadler, W., & Schabus, M. (2002). The interplay between theta and alpha oscillations in the human electroencephalogram reflects the transfer of information between memory systems. *Neuroscience Letters*, *324*, 121–124. **DOI:** [https://doi.org/10.1016/S0304-3940\(02\)00225-2](https://doi.org/10.1016/S0304-3940(02)00225-2), **PMID:** 11988342
- Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *International Journal of Psychophysiology*, *57*, 97–103. **DOI:** <https://doi.org/10.1016/j.ijpsycho.2005.03.018>, **PMID:** 15967528
- Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., et al. (2005). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, *22*, 2917–2926. **DOI:** <https://doi.org/10.1111/j.1460-9568.2005.04482.x>, **PMID:** 16324126
- Schmiedek, F., Oberauer, K., Wilhelm, O., Süß, H.-M., & Wittmann, W. W. (2007). Individual differences in components of reaction time distributions and their relations to working memory and intelligence. *Journal of Experimental Psychology: General*, *136*, 414–429. **DOI:** <https://doi.org/10.1037/0096-3445.136.3.414>, **PMID:** 17696691
- Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, *381*, 520–522. **DOI:** <https://doi.org/10.1038/381520a0>, **PMID:** 8632824
- Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). α -band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*, *26*, 9494–9502. **DOI:** <https://doi.org/10.1523/JNEUROSCI.0875-06.2006>, **PMID:** 16971533, **PMCID:** PMC6674607
- Twomey, D. M., Murphy, P. R., Kelly, S. P., & O'Connell, R. G. (2015). The classic P300 encodes a build-to-threshold decision variable. *European Journal of Neuroscience*, *42*, 1636–1643. **DOI:** <https://doi.org/10.1111/ejn.12936>, **PMID:** 25925534
- Ulrich, R., Schröter, H., Leuthold, H., & Birngruber, T. (2015). Automatic and controlled stimulus processing in conflict tasks: Superimposed diffusion processes and delta functions. *Cognitive Psychology*, *78*, 148–174. **DOI:** <https://doi.org/10.1016/j.cogpsych.2015.02.005>, **PMID:** 25909766
- van der Lubbe, R. H. J., Jaśkowski, P., Wauschkuhn, B., & Verleger, R. (2001). Influence of time pressure in a simple response task, a choice-by-location task, and the Simon task. *Journal of Psychophysiology*, *15*, 241–255. **DOI:** <https://doi.org/10.1027//0269-8803.15.4.241>
- VanRullen, R., & Thorpe, S. J. (2001). The time course of visual processing: From early perception to decision-making. *Journal of Cognitive Neuroscience*, *13*, 454–461. **DOI:** <https://doi.org/10.1162/08989290152001880>, **PMID:** 11388919
- Voss, A., Nagler, M., & Lerche, V. (2013). Diffusion models in experimental psychology: A practical introduction. *Experimental Psychology*, *60*, 385–402. **DOI:** <https://doi.org/10.1027/1618-3169/a000218>, **PMID:** 23895923
- Voss, A., Rothermund, K., Gast, A., & Wentura, D. (2013). Cognitive processes in associative and categorical priming: A diffusion model analysis. *Journal of Experimental Psychology: General*, *142*, 536–559. **DOI:** <https://doi.org/10.1037/a0029459>, **PMID:** 22866687
- Voss, A., Rothermund, K., & Voss, J. (2004). Interpreting the parameters of the diffusion model: An empirical validation. *Memory & Cognition*, *32*, 1206–1220. **DOI:** <https://doi.org/10.3758/BF03196893>, **PMID:** 15813501
- Voss, A., & Voss, J. (2007). Fast-dm: A free program for efficient diffusion model analysis. *Behavior Research Methods*, *39*, 767–775. **DOI:** <https://doi.org/10.3758/bf03192967>, **PMID:** 18183889
- Voss, A., Voss, J., & Lerche, V. (2015). Assessing cognitive processes with diffusion model analyses: A tutorial based on fast-dm-30. *Frontiers in Psychology*, *6*, 336. **DOI:** <https://doi.org/10.3389/fpsyg.2015.00336>, **PMID:** 25870575, **PMCID:** PMC4376117
- Wager, T. D., & Nichols, T. E. (2003). Optimization of experimental design in fMRI: A general framework using a genetic algorithm. *Neuroimage*, *18*, 293–309. **DOI:** [https://doi.org/10.1016/s1053-8119\(02\)00046-0](https://doi.org/10.1016/s1053-8119(02)00046-0), **PMID:** 12595184
- Whitham, E. M., Pope, K. J., Fitzgibbon, S. P., Lewis, T., Clark, C. R., Loveless, S., et al. (2007). Scalp electrical recording during paralysis: Quantitative evidence that EEG frequencies above 20 Hz are contaminated by EMG. *Clinical Neurophysiology*, *118*, 1877–1888. **DOI:** <https://doi.org/10.1016/j.clinph.2007.04.027>, **PMID:** 17574912