Beta-Band Desynchronization Reflects Competition Between Movement Plans of the Left and Right Hand

Milou van Helvert[1]
Supervisors: Leonie Oostwoud Wijdenes[1], Linda Geerligs[1], Pieter Medendorp[1]

[1] *Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, The Netherlands*

Parallel processing of multiple movement plans enables a smooth interaction with the environment. It allows for rapid switching between response alternatives, which is crucial in threatening situations. The internal representations of these response alternatives are thought to compete during movement preparation. When preparing a reaching movement towards multiple possible target locations, beta-band desynchronization is modulated by this movement plan competition. We tested whether the same applies when multiple effectors are available and we sought for neural evidence of movement plan competition related to hand use. Behavioral evidence suggests that movement plans of the left and right hand compete during hand selection, as greater ambiguity with respect to the hand to use comes with a cost, reflected in slower reaction times and movement variability. We recorded brain activity with electroencephalography (EEG) while participants (n = 17) performed a speeded hand-selection reaching task. To estimate the effect of competition between movement plans for the left and right hand, trials were included during which the hand to use was predetermined and movement plan competition was thus thought to be minimal. We focused on event-related desynchronization (ERD) in the beta band in response to a cue marking the onset of movement preparation. Results indicate that beta-band ERD is indeed modulated by competition between movement plans of the left and right hand: for reaches to the point of subjective equality, a point in space where left and right hand use is equiprobable and movement plan competition is thus thought to be maximal, beta-band ERD was smaller when participants were free to select the hand to use than when the hand to use was predetermined. These results indicate that hand selection is based on a competitive process between movement plans for the left and the right hand and underline the idea of parallel processing of multiple movement plans simultaneously. These findings provide us with valuable insight into the way the brain processes information necessary to plan goal-directed movements.

Keywords: movement preparation, effector selection, hand choice, electroencephalography, beta-band desynchronization

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Corresponding author: Milou van Helvert; **E-mail:** mvanhelvert@live.nl

Imagine having a picnic with friends and trying to reach for the orange juice. Which hand do you use to pick up the glass, your left or right hand? How does your brain make this decision? Complex environments, such as a picnic, provide us with extensive sensory information and give rise to many potential actions. The way this sensory information is processed to plan the execution of goal-directed movements has been a topic of debate. It was long believed that the brain processes information about the environment in a serial manner (Marr, 1982; Poggio, 1981). This serial processing view proposes that you first determine the goal of the movement based on sensory information, i.e., reach for and presumably drink the orange juice. After this, the brain computes a more detailed plan on how to achieve this goal by specifying, for example, which hand to use for the reaching movement and how fast and precise the movement should be.

More recently, Cisek (2007) put forward the affordance competition hypothesis. This hypothesis contradicts the serial processing view by proposing that the brain prepares multiple potential actions in parallel. The internal representations of these potential actions have been described as affordances (Gibson, 1979). The parallel processing of affordances enables continuous interaction in a complex environment and quick action in response to hazardous events (Cisek & Kalaska, 2010). Building on the affordance competition hypothesis, the brain might construct movement plans for multiple movements simultaneously. These movement plans can be based on the same computational goal, i.e., reaching for the orange juice. This goal can be achieved with different potential actions, i.e., reaches with the left hand or the right hand. The affordance competition hypothesis is underlined by the finding that having multiple action possibilities comes with a cost (Oostwoud Wijdenes, Ivry, & Bays, 2016). This cost is reflected in greater movement variability, suggesting that movement plans are indeed processed simultaneously but that processing capacity is limited. Due to this limited capacity, the parallel processing of information gives rise to a constant competition between the internal representations of potential actions, hence the name affordance competition hypothesis (Cisek, 2007; Cisek & Kalaska, 2010). This competition is eventually resolved when a certain movement plan prevails, resulting in movement.

Hand choice experiments have been used to test the affordance competition hypothesis (Oliveira, Diedrichsen, Verstynen, Duque, & Ivry, 2010). This decision process is often encountered in daily life, as most actions require moving one of the hands, and is mostly resolved unconsciously. In general, people use the hand ipsilateral to the reach goal (Bryden, Pryde, & Roy, 2000; Gabbard & Rabb, 2000). However, for reach goals close to the body midline people usually show a preference to use their dominant hand.

Oliveira et al. (2010) investigated whether hand choice evokes a competitive process between simultaneously prepared left and right hand movement plans. They hypothesized that competition between these movement plans is greatest when the decision uncertainty is greatest, i.e., when the evidence to use one hand over the other is most ambiguous. They found that reaction times of a reach were shorter if the hand to use was predetermined by the experimenter than if the hand to use was undetermined and the participants were thus free to choose the hand to use. Also, for the undetermined condition, reaction times were longer for reach directions for which the choice of left or right hand use was equiprobable. This point of equal choice is referred to as the point of subjective equality (PSE).

To examine the neural computations underlying hand choice, Oliveira et al. (2010) investigated the effect of transcranial magnetic stimulation (TMS) on the posterior parietal cortex (PPC) on hand choice. The PPC comprises the parietal reach region, a brain region associated with the planning of reaching movements. Single-pulse TMS to the left PPC increased the amount of left hand reaches and thus induced a bias in hand choice. However, TMS to the right PPC did not induce a similar bias in hand choice in the opposite direction. While the reason for this hemispheric asymmetry remains unclear, these results suggest that the PPC is part of the network involved in hand selection.

Here, we test the idea of parallel processing of movement plans for the decisions of hand choice by investigating the neural synchronization in sensorimotor regions. We will concentrate on beta-band activity (13 to 30 Hz), which has often been associated with movement preparation (Jasper & Penfield, 1949). Typically, event-related desynchronization (ERD) in the beta band is thought to reflect cortical activation and, more specifically, preparation of the execution of a movement (Pfurtscheller, 1992). However, beta-band ERD is not an undifferentiated reflection of neural activity. The level of desynchronization appears to be modulated by the level of uncertainty about the direction of the upcoming movement. Studies investigating this effect based this directional uncertainty either on the number of possible reach directions (Tzagarakis, Ince, Leuthold, & Pellizzer, 2010) or the separation of two possible reach directions in space (Grent-'t-Jong, Oostenveld, Jensen, Medendorp, & Praamstra, 2014; Grent-'t-Jong, Oostenveld, Medendorp, & Praamstra, 2015). In both cases, greater directional uncertainty corresponded to less beta-band ERD prior to the reaching movement.

Based on this information, we hypothesized that beta-band ERD is modulated in a similar way by decision uncertainty. This decision uncertainty would be based on the amount of competition between movement plans for the left and the right hand. To test this, we compared reaction times and beta-band ERD between predetermined and undetermined (freely selected) hand choice trials. Additionally, we compared reaction times and beta-band ERD for reaching movements towards target locations that evoke low competition between the left and the right hand to those associated with high competition between the hands. If movement plans are indeed prepared in parallel, we should expect more competition to result in longer reaction times (Oliveira et al., 2010) and less beta-band ERD (Grent-'t-Jong et al., 2014; Grent-'t-Jong et al., 2015; Tzagarakis et al., 2010).

Methods

Participants

Twenty participants took part in the study (5 males and 15 females, *M* = 21 years, age range 19-26 years). All participants reported to be right-handed, and this was confirmed by their responses on the Edinburgh Handedness Inventory (Oldfield, 1976). The participants had normal or corrected-to-normal vision and reported no history of neurological or psychiatric diseases or use of psychoactive medication or substances in the recent past. The ethics committee of the Faculty of Social Sciences of Radboud University Nijmegen, the Netherlands, approved the study. All participants gave written informed consent prior to the start of the study and were reimbursed for their participation in form of course credits, if applicable.

Experimental set-up

Participants performed a speeded hand-selection reaching task. Figure 1 illustrates the experimental paradigm, which is based on the task introduced by Oliveira et al. (2010). Visual stimuli were presented on a 42-inch touch monitor (Iiyama, Tokyo, Japan) with full HD resolution (1080p) and a refresh rate of 80 Hz. The room in which the task was completed was dark, except for the light emitted by the touch monitor and the monitors of the experimental computers, positioned approximately three meters away from the participant with the rear-side of the monitors facing the participant. At the start of the experiment, two start positions were presented on the touch monitor as grey disks with a diameter of 3.5 cm. These start positions were visible throughout the experiment and were positioned approximately 20 cm away from the participant's diaphragm and 9 cm on either side of the body midline. The color of these disks changed to white when touched to indicate correct placement of the participant's index fingers (Fig. 1A). A gaze fixation cross with a width of 2.5 cm was presented close to the center of the screen, 12 cm in front of the two start positions. There were five different possible cue and target positions on the screen. Colored disks with a diameter of 3.5 cm could be positioned in one of the following five directions on a semi-circular array with a 30 cm radius with its center at the fictitious point in the middle of the two starting positions: -40°, -10°, 0°, 10°, or 40°. Negative and positive directions on the semi-circle indicate positions to the left and the right of the body midline, respectively. Cue stimuli were orange and target stimuli were light blue.

The presentation of the task on the touch monitor was controlled by software that was custom-written in the Python programming language (Python Software Foundation, Beaverton, United States of America). To measure the onset of visual stimuli on the touch monitor, a photodiode was connected to the touch monitor and registered the presentation of cue and target stimuli. The output of the photodiode was recorded at 500 Hz with an electroencephalography (EEG) system (described later).

Experimental paradigm and procedure

The task of the participants was to reach with one of their index fingers towards the target as fast and accurately as possible. Participants were free to decide which hand to use for the movement in the majority of the trials. A trial was initiated by placing the two index fingers on the start positions presented on the touch monitor. After a fixed period of 1 s the cue appeared at one of the five cue positions (Fig. 1B and 1C). The duration of the presentation of the

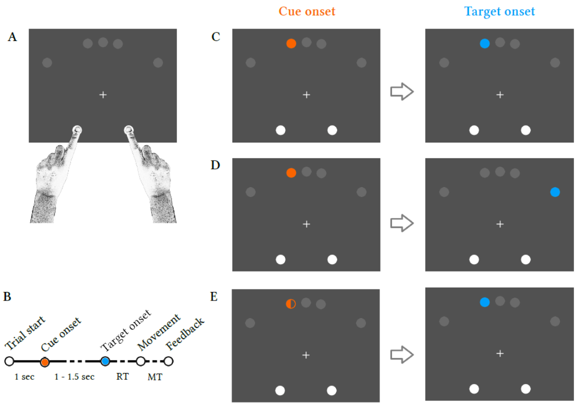

Figure 1. Illustration of the experimental set-up, paradigm, and procedure. (A) Top view of the experimental set-up (hands are not to scale relative to the set-up). Start positions (white disks), gaze fixation cross, and five potential cue and target positions (light grey disks) are shown. (B) Summary of the order of events over time for one trial. Variable periods of time are visualized with dashed lines. Reaction time and movement time are abbreviated as RT and MT, respectively. (C) Example of a correctly cued trial; the cue (orange) appeared at the same position as the target (light blue). Note that the other potential cue and target positions were not shown during the experiment. (D) Example of an incorrectly cued trial; the cue appeared at a different position than the target. (E) Example of a predetermined trial during which a modified cue stimulus instructed which hand to use. In this example, the participant was instructed to reach with the left hand.

and the participants were explicitly instructed to use the cue to prepare the movement. After the cue period the target was presented and the participants initiated the movement. The onset of the target was accompanied by a short beep sound. The cue and target could either be presented at the same position (correctly cued trials, 450 repetitions, Fig. 1C) or at different positions (incorrectly cued trials, 450 repetitions, Fig. 1D). Incorrectly cued trials were introduced to verify that the participants used the cue to prepare the reaching movement. Note that the participants were unaware of the type of trial during the cue period, as they were not provided with any other information apart from the target presented later on. When the participant touched the target it disappeared and a feedback message about the response time was presented close to the gaze fixation cross on the touch monitor. The participants were awarded with virtual points if the sum of the reaction time and the movement time was shorter than 0.7 s. This reward was implemented to motivate the participants to reach towards the target as fast as possible and therefore use the position of the cue to prepare the movement. If the sum of the reaction time and the movement time was indeed shorter than 0.7 s, the message “Well done! +1 point” was presented. Next to the feedback message, the total score of the participant was presented. If the sum of the reaction time and the movement time exceeded 0.7 s, the feedback message was “Too slow”. The feedback message disappeared when the participants placed the index finger of the hand used for the reaching movement back on the start position, thereby initiating the next trial. If the movement was initiated prior to the onset of the target, “Please wait for the target” was presented and the trial was restarted.

In one out of nine trials, the left or the right half of the cue stimulus was colored black instead of orange (predetermined trials, 100 repetitions, Fig. 1E). The orange colored half of the cue stimulus predetermined the hand to use for the reaching movement following the onset of the target. The participants were informed about these modified cue stimuli prior to the experiment and were able to dissociate the different cue stimuli during the practice trials.

All participants completed 900 trials in total. These comprised of 450 correctly cued trials (90 repetitions of each cue x target combination) and 450 incorrectly cued trials (22 or 23 repetitions of each cue x target combination). Participants were free to use the hand of their choice in 800 of these trials. In the remaining 100 trials the hand to use was predetermined (50 left hand and 50 right hand trials). The amount number of correctly cued trials was equal to the amount number of incorrectly cued trials in both the choice and the predetermined hand condition. In the predetermined hand condition, these trials were also balanced across hands. All trials were presented in a random order that differed for each participant and were subdivided in six blocks of 150 trials, separated by short breaks.

To familiarize with the experimental paradigm, participants completed 30 practice trials prior to the main experiment. Practice trials included all trial types. To make sure that participants were able to distinguish predetermined trials, the proportion of these trials was higher for the practice trials than for the main experiment (8/30 versus 100/900). In total, completion of both the practice trials and the main experiment took about one hour.

EEG acquisition and preprocessing

A 64-channel active electrode EEG system was used to record brain activity throughout the experiment (Brain Products, Gilching, Germany). Horizontal and vertical electro-oculograms (EOGs) were recorded by placing electrodes at the supraorbital and infraorbital ridges of the left eye and the outer canthi of the left and right eye. Impedance values were kept below 20 kΩ and the signal of all electrodes was referenced to the signal on left mastoid electrode TP9. The data was filtered online with a low cutoff value of 0.016 Hz and a high cutoff value of 200 Hz and digitized with a sampling frequency of 500 Hz and a resolution of 0.1 μV. To avoid excessive eye movements during the experiment, the participants were instructed to look at the gaze fixation cross throughout the experiment. However, to enable the participants to accurately touch the target, the participants were free to move their eyes during the presentation of the target.

The FieldTrip toolbox was used to process the EEG data off-line in MATLAB (Oostenveld, Fries, Maris, & Schoffelen, 2011). The data was re-referenced to the average signal of all EEG electrodes. Slow drifts in the signal and noise originating from the power lines were eliminated by applying a high-pass filter of 1 Hz and a band-stop filter at frequencies of 50 Hz, 100 Hz, and 150 Hz, respectively. Trials were time-locked to the onset of the cue as recorded by the photodiode. Trials with blinks around the onset of the cue were removed from the dataset because the blinks could have altered the timing of movement preparation. Blinks were automatically identified with Fieldtrip toolbox. To do so, first, the difference between the signal of the vertical EOG electrodes was computed, after which a fourth order Butterworth band-pass filter with a frequency range of 1 to 15 Hz was applied to the signal. The band-pass filtered data was transformed by applying a Hilbert transformation, after which the data was z-transformed. If z-transformed values exceeded the cutoff value of 3, this indicated the detection of a blink. Trials in which participants blinked around the onset of the cue, in the time window from 75 ms prior to cue onset to 25 ms after cue onset, were removed from further analyses. On average, this resulted in removal of 21 trials per participant (*SE* = 4.85).

Ocular artifacts not centered around the onset of the cue were removed from the data by running an independent component analysis (ICA). Rejection of components with an evident ocular origin was done according to the criteria described by McMenamin et al. (2010). After removal of these components, trials with excessive muscle activity during and preceding the cue period were automatically identified and removed by looking into high-frequency components of the data. To do so, the data was band-pass filtered by means of a ninth-order Butterworth band-pass filter with a frequency range of 110 to 140 Hz. The band-pass filtered data was transformed by applying a Hilbert transformation, after which the data was z-transformed. Trials in which z-transformed values exceeded the cutoff value of 13 in the time window from the start of the baseline period (0.3 s prior to cue onset) to target onset were considered trials with excessive muscle activity. These trials were removed from further analyses. On average, this resulted in removal of 103 trials per participant (*SE* = 12.30).

After identification and removal of trials containing artifacts, as well as removal of ocular components in the data, the data was low-pass filtered with a frequency threshold of 90 Hz and down-sampled from 500 Hz to 200 Hz to reduce the size of the data set and lower the processing capacity needed for further analyses. Excessively noisy or *dead* electrodes were identified by visually inspecting the preprocessed data for continuous high frequency noise or a lack of signal, respectively, and were replaced through interpolation of the EEG signal of electrodes adjacent to the respective electrode. Adjacent electrodes were identified based on a two-dimensional projection of the position of the electrodes and data of four participants contained such a noisy or irresponsive electrode (FC1, TP7, PO3, or Oz).

Analysis of natural choice behavior

Hand choice was determined for each trial as the hand that released the touch screen after the onset of the target. Trials during which the participant released both hands were not taken into account in further analyses. First, each participant's natural choice behavior was described by focusing on correctly cued choice trials. The preference to use the hand ipsilateral to the target position was tested with a non-parametric Wilcoxon signed-rank test comparing the proportion of right hand reaches for targets presented in the left-hemifield and targets presented in the right-hemifield. The general preference to use the dominant hand was tested with a non-parametric Wilcoxon rank-sum test comparing the overall proportion of right hand reaches with 0.5.

Next, the proportion of right hand choices for each target position during correctly cued choice trials was described by fitting a cumulative Gaussian distribution. The cumulative Gaussian distribution is described as follows:

$$P\,(x) = \lambda + (1 - 2\lambda)\,\frac{1}{\sigma\sqrt{(2\pi)}}\int_{-\infty}^{x} e^{-\frac{(t-\mu)^2}{2\sigma^2}}\,dt \quad (1)$$

P (x) represents the proportion of right hand reaches for target position x. The mean of the fitted curve, μ, represents the participant's PSE. The standard deviation of the curve is represented by σ and is related to the steepness of the curve, whereas λ represents the lapse or error rate. This error rate was controlled to improve the fit of the curve and was limited to values smaller than 0.1. The value of t ranged from $-\infty$ to x. Fitting the cumulative Gaussian distribution to the experimental data was done according to a maximum Likelihood approach and was carried out with MATLAB functions 'normcdf' and 'fmincon'.

The preference to use the dominant hand to reach towards targets presented close to the body midline was tested with a two-tailed independent t-test comparing PSE values with 0°. Based on the cumulative Gaussian distribution fit for each individual participant, the target was determined for which the competition between movement plans for each of the two hands was greatest. This high competition target was defined as the target closest to the participant's PSE and will be referred to as the PSE target. Two low competition targets were defined as the leftmost target (-40°) and the rightmost target (40°). Participants were expected to show a clear preference to reach for these targets with the left hand or the right hand, respectively, and these targets will be referred to as the extreme targets. Analyses of reaching movements to these extreme targets will focus only on the extreme target ipsilateral to the hand used (left extreme target for left hand reaches and right extreme target for right hand reaches).

Three participants showed such a strong preference to reach with their dominant right hand for the correctly cued choice trials that it was not possible to determine a low competition extreme target at which reaches with the left hand were evidently preferred. Their overall proportion of right hand reaches for correctly cued choice trials was 0.868, 0.833, and 0.993, and the proportion of right hand reaches towards the leftmost target was 0.663, 0.413, and 0.988, respectively. These three participants were excluded from further analyses.

Analysis of cue and target-based choice behavior

As mentioned earlier, incorrectly cued choice trials were introduced to verify that the participants used the cue to prepare the reaching movement. If the participants did indeed prepare a reaching movement towards the cue, hand choice should be biased based on cue position. Such a bias in hand choice would also indicate that the competition between movement plans for reaching movements with one of the two hands is, at least partially, resolved prior to target onset. Main effects of cue and target position on hand choice, as well as an interaction effect, were tested with a factorial repeated-measures ANOVA. If the results of Mauchly's test indicated that the assumption of sphericity was violated, the degrees of freedom were corrected according to the Greenhouse-Geisser estimates of sphericity. The outcome of particular cue x target combinations was assessed post-hoc.

Analysis of reaction times

Reaction times were defined as the first moment after target onset at which one of the hands released the screen as registered by the touch monitor. Trials with reaction times exceeding 1 s were not taken into account in any of the following analyses (similar to Tzagarakis et al., 2010). The effect of competition on reaction time was assessed with a factorial repeated-measures ANOVA. To additionally assess the effect of the length of the cue period on reaction times, cue period was added as an independent variable. The design was thus trial type (hand predetermined or choice) x target (extreme or PSE) x cue period (1.00, 1.25, or 1.50 s). If the results of Mauchly's test indicated that the assumption of sphericity was violated, the degrees of freedom were corrected according to the Greenhouse-Geisser estimates of sphericity.

Analysis of beta-band ERD

Beta-band ERD was determined by performing a time-frequency analysis of the EEG data. The time-frequency analysis was based on multiplication in the frequency domain and made use of a single Hanning taper with variable window length. The window length was dependent on the frequency of interest and was set to 5 divided by the frequency of interest, resulting in five cycles per time window.

Frequencies of interest initially ranged from 13 to 30 Hz ($M_{\text{frequency resolution}} = 4.30$ Hz, $M_{\text{window length}} = 0.25$ s). Power values were computed every 10 ms starting from 0.3 s prior to cue onset up to 1.0 s after cue onset in steps of 0.5 Hz. Computed power values were corrected relative to baseline power in the period of 300 to 1000 ms prior to cue onset.

The beta-band frequency range appropriate in this study was determined by calculating the mean power relative to baseline over the entire frequency range (13 to 30 Hz) and for all electrodes in the time period of 0.8 to 1.0 s after cue onset. Power values for each frequency were averaged across participants, resulting in a two-dimensional dataset (electrode x frequency). This analysis focused on predetermined trials only, and separate averages were computed for left and right hand reaches. By subtracting the mean power preceding right hand reaches from the mean power preceding left hand reaches for each electrode, the frequency range that showed the clearest lateralization in activity across the two hands could be determined. In a similar way, the electrodes that showed where this lateralization was greatest were identified. Mean power was computed only across the frequency range that showed the clearest lateralization in activity across the two hands. The topographic distribution of the contrast was plotted and electrodes that showed the greatest lateralization in activity were selected for further analyses.

Beta-band power over time was calculated by averaging power values across the appropriate frequency range. This analysis resulted in a three-dimensional dataset with power values for each participant (trial x electrode x time). For the choice trials, this analysis focused on correctly cued trials only. We assumed that, for these trials, participants did not deviate from the movement plan that was dominant during the cue period after the onset of the target and thus eventually reached with the hand that *won the competition*. After the time-frequency analysis, trials were grouped based on the following criteria: trial type (hand predetermined or choice), target (extreme or PSE), and the hand used for the reaching movement (left or right).

The effect of movement plan competition on beta-band ERD was assessed with a nonparametric cluster-based permutation test (Maris & Oostenveld, 2007). This statistical analysis is based on the calculation of cluster-level statistics, connecting samples based on temporal adjacency, and circumvents the multiple comparisons problem often encountered during the analysis of large multidimensional neuroimaging datasets. To compute the cluster-based permutation test statistic all samples were first compared across conditions using multiple dependent t-tests. After this, samples with a t-value greater than a certain threshold were connected based on temporal adjacency and cluster-level statistics were computed. Differences between conditions were then evaluated by using the cluster-level statistic with the largest absolute value as a test statistic and determining the p-value under a permutation distribution. Here, the cluster-based permutation test was performed with the function 'ft_freqstatistics' of the FieldTrip toolbox and the permutation distribution was constructed with the maximum number of random partitions. Samples for which cluster-level statistics were computed ranged from 0.1 to 1 s after cue onset. Both the initial threshold for forming the clusters and the ultimate critical alpha-level to assess differences between conditions were set to 0.05.

First, to assess the effect of competition on beta-band ERD based on the ability to choose the hand to use, beta-band ERD was compared for predetermined and choice trials, both for reaching movements to the PSE target and the extreme targets. Second, to assess the effect of competition on beta-band ERD based on reaching movements towards target locations that evoke high competition between the left and the right hand to those associated with low competition between the hands, beta-band ERD was compared for reaching movements to the PSE target and the extreme targets, both for predetermined and choice trials.

Results

Natural choice behavior

When participants were free to choose which hand to use, they showed an overall preference to reach with the hand ipsilateral to the target position for the correctly cued choice trials. The proportion of right hand reaches was significantly smaller for the two targets presented at -40° and -10° (median = 0.28) than for the two targets presented at 10° and 40° (median = 0.98), $z = -3.62$, $p < 0.001$. Overall, however, the participants preferred to use their dominant right hand. The proportion of right hand reaches across all targets was significantly greater than 0.5 (median = 0.67), $z = -3.48$, $p < 0.001$. These results are in line with previous observations (Bryden, Pryde, & Roy, 2000; Gabbard & Rabb, 2000).

Figure 2 shows the Cumulative Gaussian distribution fits to the natural choice behavior of three participants who demonstrated different preferences in hand choice. Fit parameters for all participants are described in Supplementary Table 1. Overall, the PSE was significantly smaller than 0° (*M* = -9.97, *SE* = 2.16), *t*(16) = -4.61, $p < 0.001$ (Fig. 2D), indicating that the PSE was usually left of the body midline. On average, participants used their left and right hand with approximately equal amounts to reach for the -10° target. The target closest to, or with the minimum absolute distance from, each individual participant's PSE was selected as the high competition target for that particular participant. Thirteen out of seventeen participants had the -10° target as PSE target, and three participants the 0° target. One participant showed a preference to reach with the left hand: the 10° target was the PSE target.

Cue and target-based choice behavior

To verify that participants prepared the reaching movement during the cue period and did not delay movement preparation until target presentation, we examined whether the position of the cue-biased hand choice using a factorial repeated-measures ANOVA which showed that both cue *F*(1.70, 27.20) = 27.66, $p < 0.001$, and target *F*(1.70, 27.12) = 104.28, $p < 0.001$, affected the proportion of right hand reaches. Additionally, there was an interaction effect between cue and target, *F*(7.01, 112.13) = 7.02, $p < 0.001$. The effects are shown in Figure 3. Modulations of target position on hand choice are reflected by a shift in the proportion of right hand reaches along the x-axis. Modulations of cue position on hand choice are reflected by a shift in the proportion of right hand reaches between the cue positions (different colored lines). Main effects showed that the proportion of right hand reaches increased for both cues and targets presented more to the right on the semicircle. Bonferroni corrected post-hoc tests confirmed significant interactions and indicated that the effect of the cue was largest for targets presented in line with or left of the body midline. In general, these results confirm that participants used the cue to prepare the reaching movement prior to target onset.

Reaction times

Effects of decision uncertainty and the length of the cue period on reaction times were tested with a factorial repeated-measures ANOVA. No significant interactions or main effects of trial type or target position were found (Fig. 4). The length of the cue period, however, significantly affected reaction times, *F*(2, 32) = 9.00, $p < 0.001$. Post-hoc tests revealed that reaction times were significantly longer following the shortest cue period of 1.00 s (*M*= 349 ms, *SE* = 6.74) compared to the intermediate cue period of 1.25 s (*M* = 336 ms, *SE* = 7.02), *t*(16)= 3.38, *p* = 0.003, and the longest cue period of 1.50 s (*M* = 336 ms, *SE* = 8.09), *t*(16) = 3.20, *p* = 0.006. Reaction times did not significantly differ across the intermediate and the longest cue periods of 1.25 and 1.50 s, respectively. These results suggest that longer cue periods resulted in greater response preparation, but that this response preparation did not differ when the cue period was lengthened from 1.25 to 1.50 s.

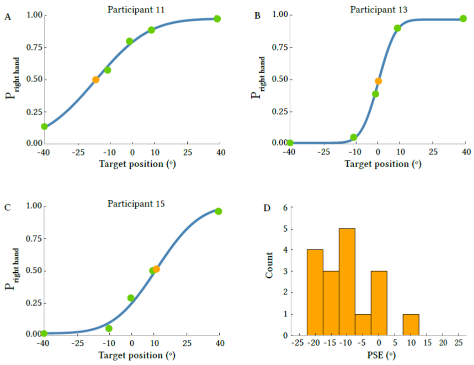

Figure 2. Cumulative Gaussian distribution fit for three participants showing different hand choice preferences and the distribution of PSE values. (A, B, C) Proportion of right hand reaches for each target position for three individual participants (green dots). Note that these data only comprise the correctly cued choice trials. The Cumulative Gaussian distribution fit is shown in blue and the mean of this distribution, i.e., the PSE, is indicated with an orange dot. (D) Histogram shows the distribution of PSE values for all participants.

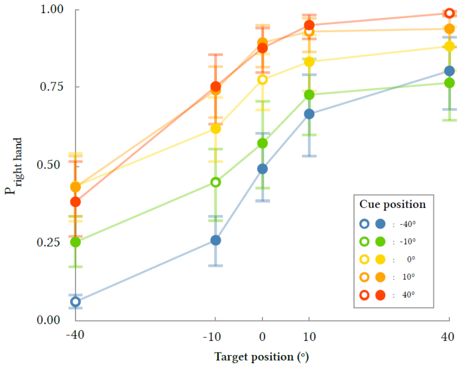

Figure 3. Effect of cue and target position on hand choice for each target position for incorrectly cued (filled dots) and correctly cued (open dots) choice trials. Mean proportion of right hand reaches over participants (± SE) is shown as a function of cue and target position.

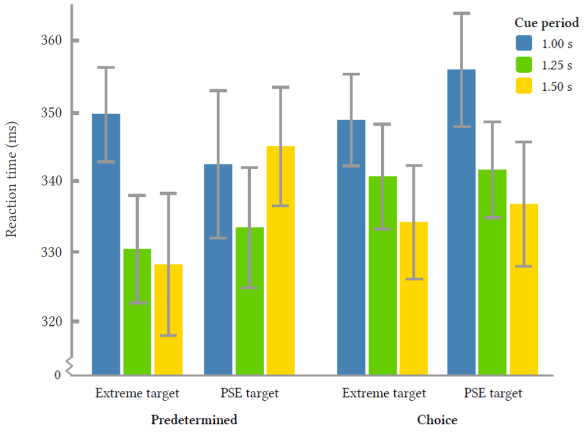

Figure 4. Mean reaction times over participants (± inter-participant SE).

Beta-band ERD

The frequency range that showed the greatest lateralization in activity preceding left and right hand reaches ranged from 16 to 23 Hz. For the sake of clarity, this frequency range will be referred to as beta-band. Figure 5A shows the topographic distribution of beta-band power preceding the reaching movement for left and right hand trials separately. Computing the contrast between these beta-band power distributions showed that the greatest lateralization could be found at central electrodes C3 and C4 (Fig. 5B). Further analyses therefore focus on these two electrodes; C3 for right hand reaches, and C4 for left hand reaches.

Modulations of beta-band ERD due to movement plan competition were tested by comparing predetermined and correctly cued choice trials for reaching movements to the PSE target (Fig. 6). Reaches to the PSE target were thought to involve high movement plan competition for choice trials because left and right hand choices were close to equiprobable. For predetermined trials, on the other hand, movement plan competition was expected to be low, or even absent, because the hand to use was already specified. If beta-band ERD preceding the reaching movement reflects movement plan competition, beta-band ERD is expected to be smaller with greater movement plan competition (Tzagarakis et al., 2010). We found that beta-band ERD was indeed significantly smaller for choice trials than for predetermined trials. This effect was found preceding both left ($p = 0.044$) and right hand reaches ($p < 0.001$) and was found approximately 0.6s after cue onset (mean onset of the effect across hands). These results are in line with our hypothesis and indicate that movement plan competition is reflected in the level of beta-band ERD, with greater movement plan competition resulting in less beta-band ERD.

Next, we investigated whether the modulation of beta-band ERD described above could be due to movement plan competition induced by having to decide which hand to use instead of making a predetermined reaching movement. Figure 7 illustrates the level of beta-band ERD preceding reaching movements for predetermined and correctly cued choice trials to the extreme targets. As participants showed a clear preference to reach with the left and right hand to the left and right extreme targets respectively, we expect movement plan competition to be low for both choice and predetermined trials.

Indeed, for left hand reaches, there was no significant difference in beta-band ERD between predetermined and choice trials. For right hand reaches, however, beta-band ERD was significantly smaller for choice trials than for predetermined trials, $p = 0.020$. This effect was found late in the cue period, approximately 0.8 s after cue onset.

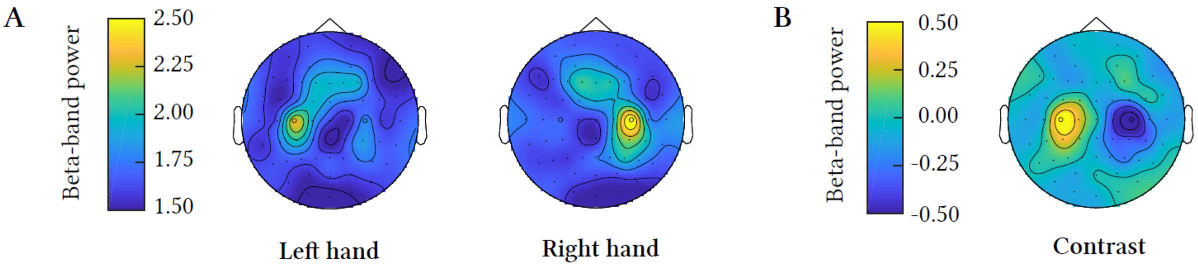

Figure 5. Localization of beta-band ERD. Topographic distribution of beta-band ERD preceding the reaching movement in the predetermined trials. Shown is the mean power as a ratio of baseline power in the frequency range from 16-23 Hz in the time period between 0.8 and 1.0 s after cue presentation. (A) Beta-band ERD preceding left and right hand reaches separately. (B) Difference in beta-band ERD preceding left and right hand reaches shown in panel A (left hand – right hand). Electrodes at which the contrast was greatest are C3 (left hemisphere) and C4 (right hemisphere).

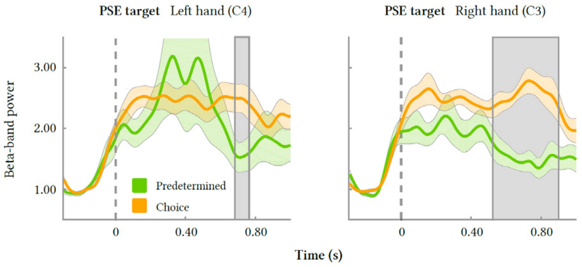

Figure 6. Beta-band ERD over time for the PSE target: predetermined versus choice. Shaded areas represent the SE over participants. Time point 0 indicates the onset of the cue. Grey areas indicate significant differences between the two conditions based on a nonparametric cluster-based permutation test ($p < 0.05$). Note that the line representing choice trials is based on more data than the line representing predetermined trials.

These results suggest that, at least for right hand reaches, having to choose the hand to use increases movement plan competition relative to making a reaching movement with a predetermined hand.

Based on the finding that movement plan competition modulates beta-band ERD when comparing predetermined and choice trials, we further examined the effect of movement plan competition within trials of the same condition. To do so, we compared beta-band ERD preceding correctly cued reaches to an extreme target versus the PSE target (Fig. 8). Reaches to the PSE target are thought to involve maximum movement plan competition, whereas movement plan competition is thought to be low for reaches to extreme targets. If movement plan competition based on target position is reflected in beta-band ERD, it is expected to be smaller preceding reaches to the PSE target. However, no significant differences in beta-band ERD were observed across the two target positions.

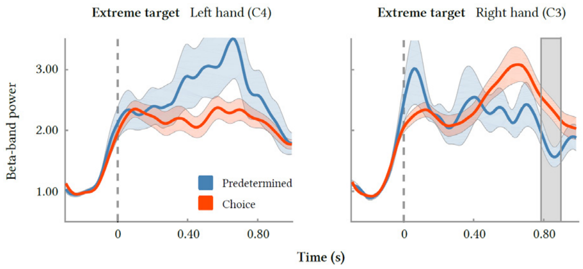

Figure 7. Beta-band ERD over time for the extreme targets: predetermined versus choice. Shaded areas represent the SE over participants. Time point 0 indicates the onset of the cue. Grey areas indicate significant differences between the two conditions based on a nonparametric cluster-based permutation test ($p < 0.05$).

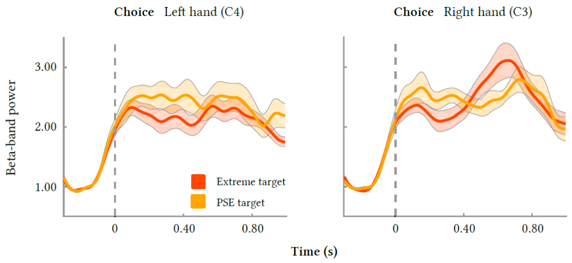

Figure 8. Beta-band ERD over time for choice trials: extreme target versus PSE target. Shaded areas represent the SE over participants. Time point 0 indicates the onset of the cue.

To investigate whether target position did not modulate beta-band ERD for predetermined reaches either, we compared beta-band ERD preceding predetermined reaches to an extreme target versus the PSE target (Fig. 9). Movement plan competition is expected to be low for all predetermined reaches, as the hand to use was already specified. We found, however, that beta-band ERD was significantly greater for reaches to the PSE target than for an extreme target. This effect was found for both left ($p = 0.024$) and right hand reaches ($p = 0.002$) and was found approximately 0.6 s after cue onset (mean onset of the effect across hands). This result suggests that beta-band ERD is modulated by target position. However, the modulation is opposite from the expected modulation, but not observed, for choice reaches. The difference in modulation patterns between the latter two comparisons suggests that the beta-band ERD modulation for predetermined reaches based on target position is not merely an effect of the position of the target in space, as this would have resulted in a similar modulation pattern of beta-band ERD for choice reaches. More likely, modulations based on target position involve processes other than movement plan competition.

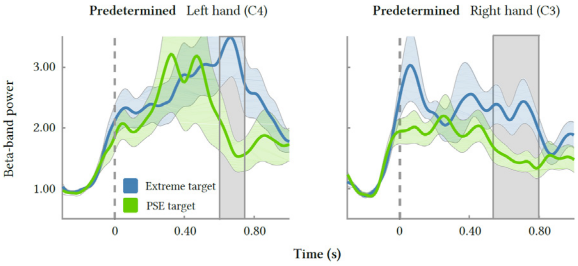

Figure 9. Beta-band ERD over time for predetermined trials: extreme target versus PSE target. Shaded areas represent the SE over participants. Time point 0 indicates the onset of the cue. Grey areas indicate significant differences between the two conditions based on a nonparametric cluster-based permutation test ($p<0.05$).

Discussion

In this study, we sought to find neural evidence for parallel processing of movement plans for hand choice. We hypothesized that beta-band ERD preceding a reaching movement is modulated by movement plan competition and tested this by recording brain activity during a speeded hand-selection reaching task. More specifically, greater movement plan competition was expected to be associated with greater decision uncertainty and less beta-band ERD preceding the reaching movement. The results indicate that beta-band ERD is indeed modulated by the level of movement plan competition: when reaching to a target close to the PSE, beta-band ERD was significantly smaller when participants freely selected the hand to use compared to when the hand to use was predetermined. Movement plan competition is thought to be maximal for reaches to the PSE when freely selecting the hand to use, as participants are equally likely to reach with their left hand or their right hand. For predetermined reaches, on the other hand, movement plan competition is expected to be low, independent of the target position. The observed modulation of beta-band ERD is therefore consistent with contemporary theories that suggest parallel processing of movement plans; ambiguity causes the internal representations of simultaneously prepared movement plans to compete (Cisek, 2007; Cisek & Kalaska, 2010).

It is noteworthy that shortly after cue onset, we observed an increase in power in the beta-band frequency range relative to baseline, instead of a decrease as the term beta-band ERD implies. This initial increase in power is thought to be due to the short inter-trial interval of the experimental paradigm, during which beta-band power has not fully recovered to true baseline values. While the short inter-trial interval is a shortcoming of the present study, the initial increase in power relative to baseline was observed in all comparisons and occurred at a time period outside the interval of interest in the cluster-based permutation test. We therefore do not think that this observation has an effect on the interpretation of the results discussed.

The interpretation of the modulation of beta-band ERD being based on ambiguity in hand choice is underlined by the finding that, for reaches to low competition targets, the ability to choose the hand to use was also associated with significantly smaller beta-band ERD compared to predetermined reaches. Both for choice and predetermined reaches, the decision uncertainty for reaches to these extreme targets is low. However, movement plan competition appears to be greater for choice reaches due to the fact that participants have to select the hand to use. The fact that no significant differences in beta-band ERD were observed within these choice reaches, when comparing reaches to the PSE target with reaches to an extreme target, is therefore surprising. This finding either suggests that movement plan competition does not differ for reaches to the PSE target and reaches to an extreme target, or that this difference in movement plan competition is not reflected in the level of beta-band ERD. However, based on the finding that beta-band ERD was modulated based on target position within predetermined trials, we would like to propose a third alternative explanation: movement plan competition does differ across target positions and does modulate the level of beta-band ERD, but this modulation is not observed for choice reaches due to an attentional benefit for reaches to the PSE target, additionally reflected in the level of beta-band ERD.

This explanation is based on the finding that, for predetermined reaches, beta-band ERD was significantly greater for reaches to the PSE target than for reaches to an extreme target. This unexpected finding is comparable to reaction time results reported by Oliveira et al. (2010), who studied behavioral correlates of movement plan competition for hand choice with a similar experimental paradigm, except for the fact that the target position was not cued. For predetermined trials, they found that reaction times for reaches to the PSE target were shorter than for reaches to extreme targets. The authors argued that this unanticipated result might be due to the possibility that participants focus their attention on the center of the experimental set-up, detecting central targets more readily than extreme targets. The idea of an attentional benefit for targets presented in the center of the screen could also explain the differences in beta-band ERD found for predetermined reaches in the present study. Beta-band activity in the frontal eye fields, located close to the premotor cortex, is known to be suppressed in a spatial selective fashion with attention (Siegel, Donner, Oostenveld, Fries, & Engel, 2008). Given the smeared spatial resolution of EEG signals, this attentional suppression might underlie the greater beta-band ERD for predetermined reaches to the PSE target compared to an extreme target. For choice trials, the attentional benefit for reaches to the PSE target and the accompanying enhancement of beta-band ERD might overpower the effect of movement plan competition on beta-band ERD, resulting in a net difference of zero between reaches to the PSE target and reaches to the extreme targets.

Next to the attentional benefit reflected in reaction times for predetermined reaches to the PSE target, Oliveira et al. (2010) found that reaction times for choice reaches to the PSE target were longer than for reaches to extreme targets. Though these patterns in reaction times are roughly in line with our findings on beta-band ERD modulation, we did not find similar differences in reaction times. This is perhaps due to experimental differences, as the experimental paradigm of Oliveira et al. (2010) did not include the presentation of a cue prior to target onset. Here, on the other hand, participants were instructed to prepare the reaching movement based on the position of the cue during the cue period (ranging from 1.00 to 1.50 s). Reaction time differences, similar to the ones that Oliveira et al. (2010), observed might not hold with this adapted experimental paradigm: based on the bias in hand choice due to incorrect cueing, movement plan competition is thought to be, at least partially, resolved prior to target onset. This suggests that the movement has been prepared during the cue period, underlined by the finding that reaction times appeared to be shorter with longer cue periods in this study. These ideas are corroborated by general differences in reaction times across the two studies: mean reaction times reported here were approximately 340 ms, whereas Oliveira et al. (2010) reported reaction times of approximately 410 ms.

Here, all observed differences in beta-band ERD were found rather late in the cue period, from approximately 0.6 or 0.8 s after cue onset. If participants started preparing the movement immediately after cue onset, differences in beta-band ERD due to movement plan competition were expected to be exhibited in the beginning of the cue period. However, it appears that participants delayed movement preparation until later in the cue period. This idea is supported by the finding that reaction times did not differ between cue periods with a duration of 1.25 and 1.50 s, but were significantly longer for cue periods with a duration of 1.00 s. Perhaps participants considered the average duration of the cue period, 1.25 s, as the standard time period within which the movement had to be prepared: with a longer cue period of 1.50 s the movement had already been prepared when the target appeared, but with a shorter cue period of 1.00 s movement preparation was still in progress at target onset. As movement preparation is generally thought to take less than 1.00 s, participants might have efficiently delayed the onset of movement preparation in time. This delay could explain the late onset of differences in the level of beta-band ERD. Even though it is known that the onset of beta-band ERD is related to the onset of movement preparation (Kaiser, Birbaumer, & Lutzenberger, 2001), to the best of our knowledge the human ability to intentionally delay movement preparation has not been studied.

A shortcoming of the present study is the large spread of PSE values. Even though for most participants the target at -10° was picked as being the PSE target, the variability in the distance between the PSE target and the extreme targets might have complicated the interpretation of the results. To avoid this asymmetry in the experimental set-up, future studies could assess the PSE value prior to the experiment and align the target in the middle of the experimental set-up with this PSE value.

In conclusion, this study focused on competition between movement plans for the left and right hand by investigating neural synchronization during a speeded hand-selection reaching task. Beta-band ERD was shown to decrease with greater competition between the two hands: for reaches to the PSE target, beta-band ERD was smaller for choice trials than for predetermined trials. These results support the idea that hand choice is based on a competitive process between movement plans for the left and right hand and therefore provide us with valuable information about the way the brain processes sensory information to prepare goal-directed movements and enables us to interact within complex environments.

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