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Research Article

Spatio-temporal modulation of cortical activity during motor deadaptation depends on the feedback of task-related error

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ABSTRACT

Motor adaptations are responsible for recalibrating actions and facilitating the achievement of goals in a constantly changing environment. Once consolidated, the decay of motor adaptation is a process affected by available sensory information during deadaptation. However, the cortical response to task error feedback during the deadaptation phase has received little attention. Here, we explored changes in brain cortical responses due to feedback of task-related error during deadaptation. Twelve healthy volunteers were recruited for the study. Right hand movement and EEG were recorded during repetitive trials of a hand reaching movement. A visuomotor rotation of 30° was introduced to induce motor adaptation. Volunteers participated in two experimental sessions organized in baseline, adaptation, and deadaptation blocks. In the deadaptation block, the visuomotor rotation was removed, and visual feedback was only provided in one session. Performance was quantified using angle end-point error, averaged speed, and movement onset time. A non-parametric spatiotemporal cluster-level permutation test was used to analyze the EEG recordings. During deadaptation, participants experienced a greater error reduction when feedback of the cursor was provided. The EEG responses showed larger activity in the left centro-frontal parietal areas during the deadaptation block when participants received feedback, as opposed to when they did not receive feedback. Centrally distributed clusters were found for the adaptation and deadaptation blocks in the absence of visual feedback. The results suggest that visual feedback of the task-related error activates cortical areas related to performance monitoring, depending on the accessible sensory information.

1. Introduction

Ongoing monitoring of motor actions is crucial to regulate behavioral adaptations and adjust actions to unexpected demands [23]. These motor adjustments are responsible for recalibrating actions and facilitating the achievement of goals in a changing environment, and thus they are key features for adaptation and survival. In this context, controlled perturbations are introduced to elicit motor actions, allowing the study of the development of motor adaptations. The visuomotor transformation is a consolidated paradigm used to explore the mechanisms behind these motor adaptations [18,27,36]. In this paradigm, screen-cursor transformations are performed during a reaching task. For example, the cursor represents the position of the hand, and the visual feedback of the cursor is rotated relative to the tracked hand position. The imposed visuomotor transformation promotes a motor adaptation to compensate for the associated error, that is, the discrepancy between expected and actual visual feedback. This task-relevant information across trials can be used as an indirect assessment of the motor adaptation process.

When learning a motor adaptation, an overcompensating behavior known as aftereffect is observed once the perturbation is removed [24]. This aftereffect has been described as volatile and tends to revert to baseline performance over time [43]. A possible explanation for the decay is that the fading process starts spontaneously due to the passage

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of time, even without performing any specific motor task per se. Alternatively, it could be a de-instantiation process, as a result of the brain detecting a change in the motor task parameters [42], i.e., a readaptation to new requirements.

The effect of context on the decay of motor adaptation has been extensively discussed [7]. It has been shown that different types of feedback can alter the decay process during the deadaptation phase. Specifically, in the absence of feedback, the re-adaptation towards baseline occurs at a slower rate [21]. In fact, this process has been described as highly dependent on the context [17], and can be affected by various factors, such as the way in which error feedback is presented [3] and the variations of the motor task during the learning process [45]. Furthermore, the length of time available to prepare a movement affects the aftereffects, with shorter preparation times being associated with longer aftereffects [14]. The level of complexity of the motor task also affects its retention, since more complex tasks are harder to retain [6]. Using visuomotor rotations paradigms, it has been suggested that implicit and explicit processes are coupled and competing for rapidly reducing the error during motor adaptations [1]. It can be hypothesized that deadaptation could also be influenced in a similar fashion by error during the deadaptation phase [16].

To achieve the constant adjustments, several brain regions actively participate in the motor adaptation process. Whenever the motor outcome deviates from a predicted result, central structures act to compensate for ongoing error or potential error in future actions [39]. In particular, it has been shown that sensory error feedback elicits activity in several cortical and subcortical regions, including the cerebellum, the primary motor and primary somatosensory cortex, and the basal ganglia (for more details, see [25]). However, there is scarce information about the neural response during the deadaptation, and it is unclear which cortical areas are involved in readapting to the original situation demands and whether context can influence the cortical response. Returning to baseline performance is not necessarily a short-lasting process in the absence of the task-related error feedback [46]. However, it is unclear whether the task-related errors during deadaptation would impact on the brain response, as in the adaptation phase. Thus, the aim of the present study was to describe the spatio-temporal changes in brain cortical responses due to presence/absence of task-related error during the deadaptation phase.

In this context, EEG and event-related potentials (ERPs) are frequently used to assess brain activity because they provide a detailed time course of the cognitive processing. In reaching experiments, signal morphology and specific amplitude peaks are often assessed [32]. In addition, power in specific frequency bands has also been used to describe neural processing [33,38]. When comparing conditions, there are numerous combination of EEG channels (or frequency bands) and specific points in time. This can lead to errors resulting from multiple comparisons, as controlling the family-wise error using standard statistical procedures is not feasible. Hence, non-parametric testing is necessary to evaluate spatio-temporal changes in brain activity. Among these methods, cluster-based permutations are a widely used approach due to their sensitivity and the multiple comparison correction [26,29]. Therefore, this approach is convenient for characterizing spatio-temporal changes during the deadaptation process.

2. Methods

2.1. Participants

This is an exploratory study comprising 12 healthy volunteers. Volunteers had no history of pain or neuromuscular disorders affecting the upper limb region. All volunteers received written and verbal description of the procedures and gave written informed consent, and monetary compensation for participating in the study was provided. The study was approved by the local ethics committee of Region Nordjylland (identifier: N–20130053) in accordance with the Declaration of Helsinki.

2.2. Electroencephalogram recordings

Electroencephalogram (EEG) was recorded using a 62-channel (g.tec medical engineering GmbH, Austria), using a cap with electrodes positioned according to the extended international 10–20 system. The ground electrode was situated between FPz and Fz electrodes, and a clip electrode on the left earlobe was used as reference. EEG data was sampled at 1200 Hz and stored after 24-bit A/D conversion.

2.3. Movement recordings

Right hand movements were tracked during the experiment using a KinectTM camera. A light-emitting diode (LED) marker was attached to the volunteer's index finger at the second (intermediate) phalanx pointing towards the wrist. The index finger was curled, assuming a "hook" gesture and pointing the fingertip towards the table surface, so that the LED marker pointed at the KinectTM camera placed right above the hand (Fig. 1). The rest of the fingers were clenched into a fist. Images were sampled at 30 frames per second and stored. Hand trajectories were extracted offline.



8 target directions

Fig. 1. Experimental setup. Electroencephalography (EEG) was recorded while participants performed a hand movement task. The trial started by positioning the hand (blue circle) at the center of a computer screen, with the starting area marked by a red circumference. After a 3-s countdown, the circumference turned green to cue the beginning of the trial. With a ballistic movement, volunteers had to reach one of the 8 targets that were spaced 45 degrees relative to each other on the screen. A light emitting diode (LED) marker was attached to each volunteer's index finger pointing towards the wrist, and a KinectTM camera tracked the hand position during the whole trial.

2.4. Experimental protocol

Volunteers participated in two experimental sessions separated by 96 hours. In each session, they were instructed to sit down comfortably with their hands resting on a table in front of them. Their sight of the marked right hand was blocked using a panel. A computer screen was used to display 8 visual targets, each located 45 degrees apart from one another (Fig. 1). The targets were 6 mm in diameter and located 100 mm from the center of the screen. On each trial, the target could appear at any of the 8 locations at random, and volunteers were instructed to move their hand and reach the target as fast as possible without stopping or reducing speed at the target. The position of the hand was indicated by a cursor (filled blue circle), and each trial started when volunteers guided the cursor into a starting area (red circle) in the center of the screen. The starting area had a diameter of 10 mm. After a countdown of three seconds, the circle turned green to indicate the beginning of the trial (initiation cue). The participants completed the trial by reaching the target (passing), and then manually repositioned the cursor (by moving their hand) to the start area to begin a new trial. Volunteers performed 8 familiarization trials comprising all target directions. Both sessions consisted of three blocks of trials, referred to as baseline, adaptation, and deadaptation. All target directions were equally selected in each block, and the number of trials for each block was defined following suggestions from previous studies [11]. The first block comprised 96 trials with visual feedback of the cursor and the target. After a break, the second block comprised 152 trials with a 30-degree visuomotor rotation to the visual feedback of the cursor, and volunteers had to compensate for the perturbation. Visual feedback of the cursor and target were also provided. Finally, the third block comprised 144 trials without visuomotor rotation. In the condition without feedback, the visual feedback of the cursor and the target disappeared immediately after the Go signal, whereas in the condition with feedback, they remain visible after the Go signal. Each volunteer performed both conditions in different orders between sessions, ensuring counterbalancing of potential effects caused by the presentation order (Fig. 2). When the trial was complete, participants manually placed the cursor to the starting area guided by the researcher and the color of the starting area.

2.5. Data processing and analysis

Performance was quantified using three metrics: angle end-point error [27], averaged speed (defined as the average speed between outside the starting area and the target), and movement onset time (the

length of time between cue presentation and the start of movement). The angle end-point error was calculated by assessing the angular difference between the line connecting the starting position to the center of the selected target location and the line connecting the starting position to the end point of the cursor movement at the circumference delimited by all targets. In the analysis, angle error, averaged speed, and movement onset time were averaged in groups of 8 subsequent trials that included the 8 possible task directions in random order [11,24]. Grouping all target direction facilitates the representation of the data and avoids any potential change in the task complexity between directions. EEG recordings were preprocessed using EEGLAB [9]. Continuous recordings were resampled at 500 Hz, and bandpass filtered between 0.1 and 40 Hz. The recordings were cut in 6-s epochs, starting from 3 s before the movement initiation cue. EEG epochs were visually inspected, and artifact-contaminated epochs were discarded. Eye blink and muscle activity were removed using independent component analysis (ICA), after visually inspecting time course, spectra, and scalp topography of the resulting components.

2.6. Statistics

A generalized linear mixed-effects model was adjusted in R [31,4] to test whether there was a difference on performance (error angle, averaged speed, and movement onset time) between conditions during deadaptation. The model was applied separately for error angle, averaged speed, and movement onset time data. In the model, *condition* (with or without visual feedback) and *time* (group of 8 consecutive trials) were included as fixed factors, and an interaction term (*condition* × *time*) was included to account for potential changes in the regression for feedback across trials. The participants were considered as a random factor. It was anticipated that the outcomes would exhibit an exponential relationship with time (the course of the trials). Therefore, a model with a gamma family and a log-link function was used to represent the data with negative exponential-like shapes. Histogram and Q-Q plot of residuals was used to visually check model assumptions.

A non-parametric spatio-temporal cluster-level permutation test was employed to investigate whether cortical potentials between conditions were distributed differently over time. First, we contrasted *conditions* (with or without visual feedback) within the deadaptation block. This was performed to evaluate differences in spatial activation due to feedback of the task-related error during the deadaptation phase. Second, we explored changes in cortical activity within *conditions* (with or without visual feedback) between *blocks* (adaptation-deadaptation). Spatiotemporal cluster analysis was performed using the MNE-Python



Fig. 2. Time course of the experiment. In each session, volunteers performed the motor task with visual feedback of the hand position and the target during a baseline block (96 trials). Thereafter, a visuomotor rotation of 30-degree was introduced, and 152 trials with visual feedback of the hand position and target were performed (adaptation, second block). Finally, a third block (deadaptation) consisting of 144 trials was carried out, with or without visual feedback of the hand and the target depending on the session. The order of the inclusion of the visual feedback in the third block was randomized between session for each volunteer.

toolbox [13]. Threshold-free cluster enhancement was applied (H = 2, E = 0.5) [35], and 1000 cluster permutations were used to account for multiple comparison. Cohen's *d* effect sizes were calculated in each channel and time point. Then, channels were grouped in three regions of interest located in the left, midline, and right regions of the head. For each region, the effect size was averaged inside a rectangular shape circumscribed at the outside of the significant cluster. This approach represents the lower bound effect since points outside the cluster are also included in the calculation [29]. Final effect sizes are reported as mean and standard deviation of the Cohen's *d*. Modified scripts from the MNE-Python toolbox tutorials were used to plot the cluster results.

3. Results

The evolution of the mean angle error across blocks and conditions is shown in Fig. 3. The analysis during deadaptation showed main effects for *time* ($\beta = -0.018$, [95 % CI: -0.023 to -0.12], p < 0.001) and the *condition* × *time* interaction ($\beta = -0.016$, [95 % CI: -0.023 to -0.008], p = 0.001). Participants experienced a faster reduction in angle error (linear approximation: $\beta = 0.200$, [95 % CI: -0.24 to -0.16], p < 0.001) when cursor feedback was provided. This result depicts that the difference between conditions is increasing around 0.2 degrees of angle error per trial.

The analysis of the averaged speed during the task showed differences in *condition* (with feedback = 0.23 ± 0.03 m/s vs without feedback = 0.24 ± 0.04 m/s, β = -0.15, [95 % CI: -0.23 to -0.08], p < 0.001, supplementary material A1.2). It was expected that participants would perform both tasks at the same speed. However, the statistical results showed that participants completed the task faster without feedback than with feedback. Moreover, *time* (β = -0.002, p = 0.48) and the *time* × *condition* interaction (β = -0.014, p = 0.05) did not reach statistical significance. The onset time did not present significant differences for *time* (β = -0.003, p = 0.66), *condition* (β < 0.0001, p = 0.99), or the interaction (β < 0.0001, p = 0.99).

Fig. 4 displays the grand-averaged EEG activity for conditions with and without visual feedback across the different blocks. To enhance the visibility of the temporal excursion in baseline, adaptation, and deadaptation, the signal recorded at the Cz electrode was magnified. The distribution of the grand averaged cortical activity during the motor task for deadaptation block is shown in Fig. 5. To focus on the relevant period of the motor task, only the period from -0.5 to 0.4 s is depicted. The rest of the blocks are available as supplementary material (B1).

Cluster-based nonparametric analysis showed a spatial cluster across

Cluster-based nonparametric analysis showed a spatial cluster (p < p0.008, Fig. 7) when contrasting the adaptation and deadaptation blocks for the without visual feedback condition. For the left region, Cohen's d was 0.51. \pm 0.21, calculated over the points inside the rectangle extending from -0.088 to 0.380 s from the initiation cue and over the T7, C5, FC3, FC5, FT7, F3, F5, F7, AF3, CP3 channels. For midline region, Cohen's d was 0.70 \pm 0.37, calculated over the points inside the rectangle extending from -0.096 to 0.384 s from the initiation cue and over the POZ, PZ, P2, P1, CPZ, CP1, CP2, C2, CZ, C1, FC2, FC1, FCZ, F2, F1, FZ, FP2 channels. For right region, Cohen's d was 0.66 \pm 0.28, calculated over the points inside the rectangle extending from -0.112 to 0.336 s from the initiation cue and over the T8, C6, C4, FC4, FC6 channels. Right and center regions exhibit a more pronounced effect (difference between conditions) in terms of higher values in Cohen's d when compared to the left region. No differences were found for condition within adaptation (p = 0.33), or for visual feedback between adaptation vs deadaptation (p = 0.26).

4. Discussion

The majority of studies on motor adaptation have focused on acquisition and retention of motor adaptations over time under various conditions. In other words, they have examined the extent to which motor learning is preserved when the task is repeated after a period of time. However, limited attention has been given to studying the deadaptation process, which is just as crucial as adaptation. Our results showed that the amount of angle error decreases faster when volunteers had visual feedback on the task-related error of their movement and



Fig. 3. Angle error between the cursor position and the target with (orange) and without (blue) visual feedback conditions during right ballistic hand-reach motor task. The mean value (solid line) \pm standard deviation (shaded area) across participant is shown. Angle error is shown for baseline, adaptation, and deadaptation blocks. A generalized linear mixed effects model applied to the deadaptation block showed that lower angle error is observed when participants received the task-related error feedback (green box, p < 0.001). The color of each signal denotes the entire session (with/without feedback). Visual feedback were the same for both conditions in baseline and adaptation phases, while changes in feedback between conditions was only performed in the deadaptation phase. Statistics were performed in groups of 8 consecutive repetitions as shown in supplementary material A1.1.



Fig. 4. Grand-averaged EEG activity for conditions with (orange) and without (blue) visual feedback. The mean value (solid line) \pm standard deviation (shaded areas) across participant is shown. Block of trials are depicted as baseline, adaptation, and deadaptation. Movement initiation is cued with a dotted vertical line (MOV INIT). The signal recorded at Cz electrode was magnified to enhance the visibility of the temporal excursion in baseline, adaptation, and deadaptation. The color of each signal denotes the entire session (with/without feedback), while the differentiation between feedback conditions only occurs during the deadaptation phase.

Deadaptation



Fig. 5. Topographic maps of the grand-averaged EEG in the deadaptation block. The volunteers performed the motor task with and without visual feedback of the hand position and the target during a right ballistic hand-reach motor task after performing a paradigm of visuomotor adaptation. After movement initiation cue (0 s), higher depolarization was observed in the fronto-central areas when the visual feedback was available.

were able to correct the trajectory when they could evaluate the outcome after each trial and adjusted for the subsequent trials. In parallel, the differences in cortical activity during the deadaptation between conditions were more pronounced at the mid-parietal electrodes on the left hemisphere.

4.1. Angle error and visual feedback information

The presence of visual feedback reduced the angular error compared to the condition without visual feedback during deadaptation. Visualization of the overall task error provides explicit information on how the motor task is performed, and thus it promotes readaptation to the new demands. The visual information clearly represents a strong input for adapting and deadapting from a perturbation, but also the explicit instruction on how to strategize the perturbation seems to reduce the error in the washout phase [5]. It has been proposed that the explicit component of the motor adaptation is not an independent process and thus it contributes and competes with other neural circuits in motor learning [1,37]. Then, it is not surprising that motor adaptations are more complex than simple recalibration mechanisms, and different cognitive strategies act in synergy for the enhancement of the motor performance [25].



Fig. 6. a) Spatio-temporal differences in cortical activity between conditions with and without visual feedback in the deadaptation block. Each channel group (left, midline, and right regions of the head) is shown individually, and groups are identified with a shaded area within the electrode position schematic at the upper-right corner of each plot. Points outside the cluster are masked. The red rectangles depict the area where Cohen's *d* was averaged. Effects size were $d = -0.73 \pm 0.3$ for the left region (*top*), $d = -0.78 \pm 0.30$ for the midline (*middle*), and $d = -0.58 \pm 0.19$ for the right region (*bottom*). b) Scalp representation of the distribution of the temporal extension of the clusters. Electrodes that were included in the cluster for more than 100 ms are highlighted using a black circumference, and electrodes with a duration longer than 300 ms are depicted with a black contour.

In both conditions, there was a drift towards the preadaptation motor error (baseline), and this occurs even when the motor task is performed without information about the task-related error. This decay phenomenon in the condition without feedback has been connected to a facilitating mechanism for retrieval from the long-term memory, which presumably contributes to the consolidation of the motor memory [19]. An alternative theory proposed that the decay process begins whenever a change in the motor task is detected, and as a result the brain actively disengages the motor adaptation [42]. However, there are contrasting results about the influence of context changes on the motor memory decay, suggesting that motor memory decay is an intrinsic characteristic of error-based learning that is independent of the context changes [7]. Thus, it could be hypothesized that either there is an inherent tendency to revert to pre-adaptation, or the modifications in the task (removing the visuomotor rotation and hiding the cursor) are sufficient to start this process in the condition without feedback.

4.2. Neural responses to task error feedback

We found larger cortical activity in the fronto-lateral regions when the task-related error was available during the deadaptation block. This neural activity most likely reflects an active correction or motor readaptation of the limb trajectory based on the visualization of the error, and this type of behavior is also reported for other types of feedback, such as auditory [28,39]. Specifically for speed choice reaction paradigms, an event-related potential (ERP) is observed slightly before or at the time that the subject detects a mistake [12,15]. This ERP, referred to as error-related negativity (ERN), is predominantly distributed at fronto-central cortical sites, and it peaks around 100 ms after detecting the error [47]. In our results, the recorded neural response presented a similar distribution but lasted longer than the ERN in the trials with visual feedback, suggesting that the data could be partially explained by a similar ERP response.

The distribution of the cortical activity during the motor task is concomitant with movement preparation, so it could represent a movement related cortical potential [22]. Nevertheless, the preparation period is brief in a ballistic task, and movement selection does not affect the later stages of this potential [34]. Therefore, the online correction of the motor task could likely not be attributed to this neural process. In fact, the motor system has neural mechanisms committed to monitoring motor performance [40]. In particular, the posterior medial frontal cortex (pMFC) plays a crucial role in detecting errors and interacting with other brain areas to improve motor performance [10,20,8]. The pMFC assesses whether a choice should be adjusted in accordance with recent information [10]. This suggests that motor brain areas, particularly those specialized in performance monitoring, are involved during deadaptation in the presence of task-related errors.

Different regions of the lateral anterior prefrontal cortex (aPFC) contribute to maintain and update the actions according to the contextual information [10,39]. The aPFC has been linked to self-evaluation and self-regulation of motor performance [10,44]. We found that the visualization of the task-related error presented higher activity in electrodes positioned at the left lateral cortical area. Thus, the aPFC contribution might be related to the analysis of whether corrections on the action are required. This is also supported from the structural point of view, since the aPFC presents strong interconnections with cingulate



Fig. 7. Spatio-temporal difference in cortical activity between adaptation and deadaptation blocks for the condition without feedback. Each channel group (left, midline, and right) is shown individually, and groups are identified with a shaded area within the electrode position schematic at the upper-right corner in each plot. Points outside the cluster are masked. The red rectangles represent the area where Cohen's *d* was averaged. Effects size were for $d = 0.51 \pm 0.21$ for the left region (*top*), $d = 0.70 \pm 0.37$ for the midline (*middle*), and $d = 0.66 \pm 0.28$ for the right region (*bottom*). b) Scalp representation of the distribution of the temporal extension of the clusters. Electrodes that were included in the cluster for more than 100 ms are highlighted using a black circumference, and electrodes with a duration longer than 300 ms are depicted with a black contour.

motor areas [41].

When error feedback is present, it is expected to observe increased brain activity in areas involved in performance monitoring. Our results showed that this phenomenon was found in the deadaptation, when comparing the conditions with and without visual feedback. Additionally, it was observed in the without feedback condition only when comparing between adaptation and deadaptation blocks. The brain activity was distributed in analogous regions in both conditions, although larger effects (Cohen's *d*) were observed in the right side with feedback when comparing the deadaptation block. This type of change in the brain activity has been previously observed for *Go/No go* motor tasks using functional magnetic resonance images, in which the activation of different neural circuits depends on the type of the motor task requested [2,30].

4.3. Assumptions and limitations

One of the potential limitations of the present study is that the target was removed after the *Go* signal during the without feedback condition. In experiments involving slow movements, participants might rely more on motor memory (capability to correctly remember the target location) rather than on aiming the target. In the present study, volunteers performed a ballistic motor task, so corrections of the movement are likely occurring in subsequent trials. There are experimental limitations related to establishing an appropriate control condition in this study. While it could be hypothesized that the optimal control condition would be a baseline without rotation and without feedback, there is no assurance that the angle error observe in this condition would be comparable

with the condition with feedback in the baseline. Additionally, transitioning from baseline without feedback to adaptation with feedback could induce systematic differences in the adaptation block. For instance, volunteers may inadvertently exhibit a systematic angle error during the baseline phase due to the absence of feedback. Thus, we run a control condition that was identical to the other condition, except for the difference in the deadaptation block. It is possible that a systematic error occurred due to the absence of visual feedback or increased variability resulting from motor redundancy and reduced task constraints. We are not claiming that there is a distinction between them; instead, we suggest that the return to baseline (i.e., preadaptation) could be either a passive or active process (e.g., by removing feedback). Furthermore, the Kinect[™] camera has a 30 Hz sample rate, which might be low for experiment that require correcting the aim during the movement, but it is sufficient for calculating parameters represented by the difference between the beginning and the end of the movement. In this regard, participants did not report any inconveniency in the visualization of the feedback using this framerate refresh.

5. Conclusion

This study described topographical cortical activity changes during the deadaptation phase with and without visual feedback of the taskrelated error. Results suggest that visual feedback of the task-related error activates performance monitoring areas as an active process of deadaptation. In addition, it appears that fronto-central areas are also implicated in the process of deadaptation, depending on the available sensory information. Further studies are needed to confirm the results and to generalize the findings to other types of motor perturbations.

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Declaration of Competing Interest

The authors have no conflict of interest to report.

Data availability

Data and analysis scripts are available from Open Science Framework at https://osf.io/fg26b/?view_only=9462231655c04b128472 a7892f7aa89a.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.bbr.2024.115024.

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