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Neural biomarkers of multiple motor-learning mechanisms in a real-world task

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Abstract

Many recent studies found signatures of motor learning in neural beta oscillations (13–30Hz), and specifically in the post-movement beta rebound (PMBR). All these studies were in simplified laboratory-tasks in which learning was either error-based or reward-based. Interestingly, these studies reported opposing dynamics of the PMBR magnitude over learning for the error-based and reward-based tasks (increase verses decrease, respectively). Here we explored the PMBR dynamics during real-world motor-skill-learning in a billiards task using mobile-brain-imaging. Our EEG recordings highlight opposing dynamics of PMBR magnitudes between different subjects performing the same task. The groups of subjects, defined by their neural-dynamics, also showed behavioral differences expected for error-based verses reward-based learning. Our results suggest that when faced with the complexity of the real-world different subjects might use different learning mechanisms for the same complex task. We speculate that all subjects combine multi-modal mechanisms of learning, but different subjects have different predominant learning mechanisms.

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Introduction

While many different forms of motor learning were described and studied using various laboratory-tasks over the past decades (for review see Krakauer et al., 2019), two main learning mechanisms are considered to account for most of our motor learning capabilities: error-based adaptation and reward-based reinforcement learning. Error-based adaptation is driven by sensory-prediction errors, while reward-based learning is driven by reinforcement of successful actions (Haith and Krakauer, 2013; Krakauer and Mazzoni, 2011). While both mechanisms can contribute to learning in any given task, the constrains of the highly controlled laboratory-tasks common in the field induce the predominance of one mechanism over the other, and show different neural dynamics associated with the different learning mechanisms (Palidis et al., 2019; Uehara et al., 2018).

A main neural signatures of voluntary movement and motor learning are the beta oscillations (13–30 Hz), which are related to GABAergic activity (Hall et al., 2010, 2011; Roopun et al., 2006; Yamawaki et al., 2008). More specifically, there is transient and prominent increase in beta oscillations magnitude across the sensorimotor network after cessation of voluntary movement known as post-movement beta rebound (PMBR) or post-movement beta synchronization (Pfurtscheller et al., 1996). In motor adaptation studies PMBR was reported to negatively correlate with movement errors, lower errors induced higher PMBR (e.g. Tan et al., 2014, 2016; Torrecillos et al., 2015) and therefore PMBR increases over learning. In reward-based tasks the PMBR shows the opposite trend; e.g., in a force tracking task PMBR decreased with learning (Kranczioch et al., 2008). Additionally, PMBR is positively correlated with GABA concentration as measured by magnetic resonance spectroscopy (Cheng et al., 2017; Gaetz et al., 2011) which also decreases over reward-based learning tasks such as sequence learning in force tracking (Floyer-Lea et al., 2006) and serial reaction time (Kolasinski et al., 2019).

Here, we set to study the neurobehavioral dynamics of real-world motor learning, asking to what extent previous findings in laboratory-tasks can be validated in a complex, fully-body task people choose to experience in daily life. We recently introduced a real-world motor-skill learning paradigm in a pool table billiards (Haar et al., 2019). Subjects had to do a pool shot in order to put the ball in the pocket using full body, self-paced movement, with as many preparatory movements as the subject needs for each shoot. We implemented this as a real-world task, basically only adding sensors to a pool table setting, i.e. subjects use the natural tools and setups they normally would, carry out the natural motor commands, receive the natural somatosensory feedback and experience the same satisfaction rewards when they put the ball in pocket. In this paradigm, as in most everyday motor learning experiences, performance errors were not driven by perturbations but by the complexity of learning the task (which takes years to master) and noise in the nervous system (Faisal et al., 2008). Due to the lack of constrains and feedback manipulations, learning in this

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paradigm may not be predominantly mediated by a specific learning mechanism, or by the same learning mechanism for all subjects. We explored the use of the PMBR dynamics as a signature for a dominant learning mechanism, and validated it using task-performance metrices.

Results

30 right-handed volunteers, with little to no previous experience playing billiards, performed 300 repeated trials (6 sets of 50 trials each with short breaks in-between) where the cue ball and target ball were placed in the same locations, and subjects were asked to shoot the target ball towards the far-left corner pocket (Figure 1A). During the entire learning process, we recorded the subjects' brain activity with wireless EEG (Figure 1B), and the balls on the pool table were tracked with a high-speed camera to assess the outcome of each trial (Figure 1C). We divided the trials into blocks of 25 trials (each experimental set of 50 trials was divided to two blocks to increase the resolution in time). The learning curve showed a decay in the directional error of the target ball (relative to the direction from its origin to the center of the target pocket) over trials (Figure 1D).

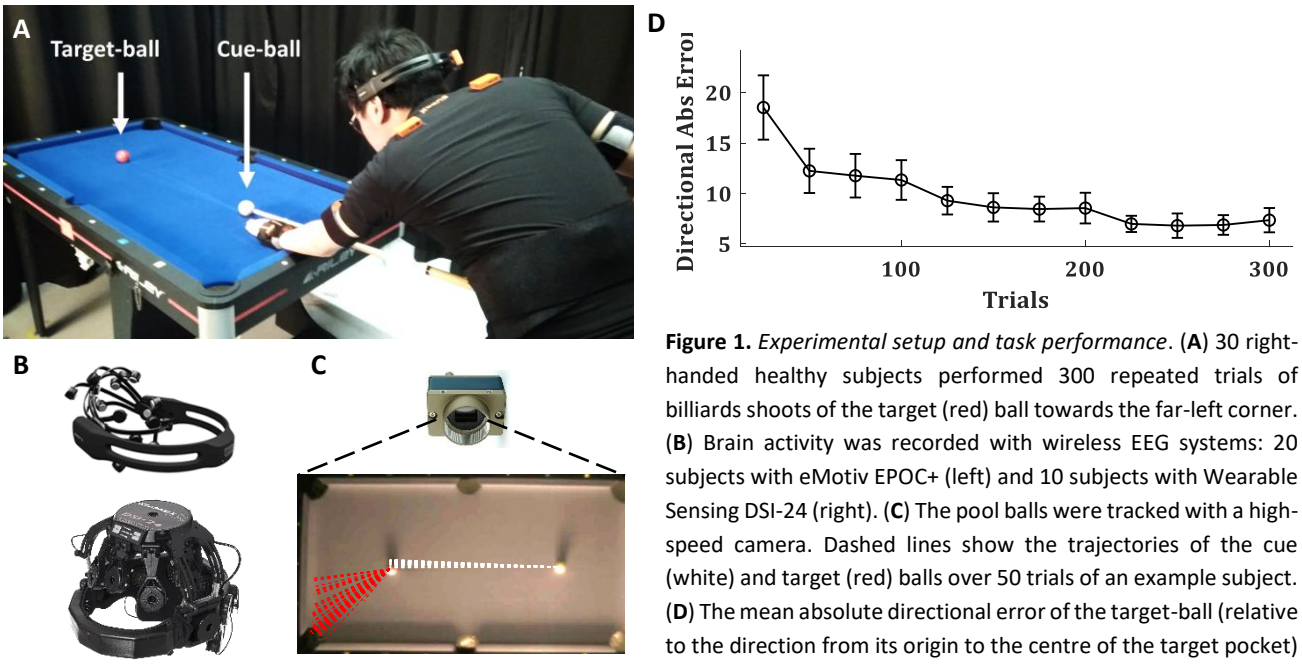

Figure 1. *Experimental setup and task performance*. (**A**) 30 right-handed healthy subjects performed 300 repeated trials of billiards shoots of the target (red) ball towards the far-left corner. (**B**) Brain activity was recorded with wireless EEG systems: 20 subjects with eMotiv EPOC+ (left) and 10 subjects with Wearable Sensing DSI-24 (right). (**C**) The pool balls were tracked with a high-speed camera. Dashed lines show the trajectories of the cue (white) and target (red) balls over 50 trials of an example subject. (**D**) The mean absolute directional error of the target-ball (relative to the direction from its origin to the centre of the target pocket) over blocks of 25 trials, averaged across all subjects, error bars represent SEM across subjects.

The PMBR, a transient increase in beta oscillations across the sensorimotor network after the end of the movement, was clearly evident in the data (Figure 2A). On average across subjects there was no clear trend of PMBR (increase or decrease) over learning (Figure 2B). With a data driven approach, we assessed if there may be multiple groups with different PMBR trends that averaging blends away. We used generative Bayesian modelling and fitted the PMBR data (a 12-dimensional matrix, one data point per run for each subject) with Gaussian mixture models of one

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to five components. The Akaike information criterion (AIC) and its corrected version for small sample size (AICc) both yield that there are two groups in the data (Figure 2C).

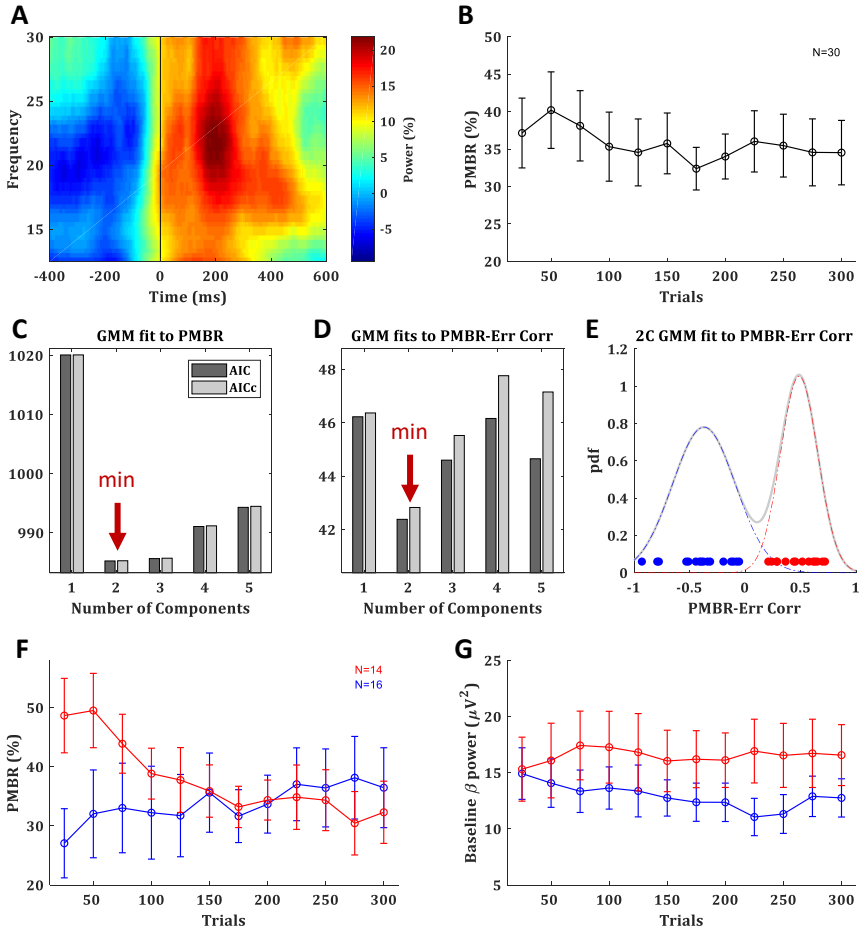

Figure 2. *Post-movement beta rebound*. (**A**) Time-frequency map of a typical subject aligned to movement offset (ball movement onset), obtained by averaging the normalized power over electrode C3. (**B**) PMBR over blocks (of 25 trials), averaged across all subjects, error bars represent SEM. (**C**) The information criterions (AIC & AICc) of Gaussian mixture model (GMM) fits with 1 to 5 components to the PMBR data. (**D**) The information criterions of GMM fits to the PMBR-Error correlations (**E**) The distribution of subject-by-subject PMBR-Error correlations fitted with two-component GMM. Subjects are color coded based on the two-component model: subjects with negative correlations are in blue (*PMBR Increasers*) and subjects with positive correlations are in red (*PMBR Decreasers*). The grouping was also validated by unsupervised clustering (see main text). (**F,G**) PMBR (F) and Baseline beta power (G) of the *PMBR Increasers* (blue) and *PMBR Decreasers* (red) over blocks, averaged across all subjects in each groups, error bars represent SEM.

The most meaningful measure for learning is the PMBR correlation with the performance error, as it actually accounts for the dependency between this brain signal and the behavior, and it was reported to show negative correlations in classic adaptation task consistently across individuals (e.g. Tan et al., 2016). The subject-by-subject correlation over blocks between the PMBR and the directional error showed a clear bimodal grouping. While 16 of the 30 subjects showed negative PMBR-Error correlations (as reported in adaptation studies), the other 14 subjects showed positive correlations. Again, we used generative Bayesian modelling and fitted the PMBR-Error correlations distribution with Gaussian mixture models of one to five components, the information criterions (AIC & AICc) yield a bimodal distribution (Figure 2D), clearly grouping the subjects with the positive and the negative correlation coefficients (Figure 2E). The opposite signs of the correlations reflect opposite dynamics, further justifying a grouping into two distinct groups. This validated our findings with the purely data driven approach on the multidimensional PMBR data. Since errors decay over learning, the PMBR-Error correlation was negatively correlated with the

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PMBR dynamic (increase/decrease). Thus, the first group showed a clear trend of PMBR increase over learning ($p<0.001$), while the second group showed clear trend of PMBR decrease over learning ($p<0.0001$) (Figure 2F). Thus, for simplicity, we named the groups *PMBR Increasers* and *PMBR Decreasers*.

While we pursued a probabilistic analysis Bayesian framework of data science, to further validate this grouping we also tried a completely different method. We used unsupervised fuzzy c-means (FCM) clustering, tested for two to ten clusters using a cluster validity index based on the ratio between within cluster variation and between clusters separation (Zhang et al., 2008). The validity index strictly suggested two clusters in the data, which were the same groups found by the Gaussian mixture model: the subjects with the positive and the negative PMBR-Error correlation coefficients. Additionally, since we calculated beta-power changes as percent signal change relative to the average power over the block (see methods), the observed group differences might be driven by differences in their baselines. However, we found that this was not the case: there was no real difference in the beta-power baseline between the groups, in terms of their values nor in their trend over learning (Figure 2G). There was no significant difference between the groups' beta-power baseline in any of the blocks ($p>0.07$) and not in the change of the beta-power baseline between blocks ($p>0.58$). Lastly, we ensured that these grouping were evident with both EEG systems used in the study. The brain activity of 20 subjects was recorded with EPOC+ while the other 10 were recorded with DSI-24 (see methods). From the subjects recorded with the EPOC+ system 10 subjects were *PMBR Increasers* and the other 10 were *PMBR Decreasers*. From the subjects recorded with the DSI-24 there were 6 *PMBR Increasers* and 4 *PMBR Decreasers*. Correspondingly, there was no correlation between the system and the PMBR-Error correlation (Spearman rank correlation $r=0.01$, $p=0.97$).

Based on the EEG data, which suggests two groups of subjects with different PMBR dynamics, we looked for behavioral signatures in the task performance of different learning between these groups. The lag-1 autocorrelation (ACF(1)) of the performance measure (in our case, the directional error of the target-ball relative to the pocket) was suggested as an index of performance in motor-skill learning, where close to zero values corresponds to high skill (van Beers et al., 2013). We calculated for each subject the ACF(1) in the first and the second half of the training session (blocks 1-6 and 7-12, respectively). The ACF(1) values of both groups were significantly greater than zero during both halves of the session (t test $p<0.01$), as expected for naïve participance (Figure 3A). But, the decay in the ACF(1) from the first half of the training session to the second was significantly higher for the *PMBR Decreasers* (t test $p<0.01$, Figure 3B). Additionally, the decay in the intertrial variability (measured from the first block (trials 1-25) to the learning plateau (trials 201-300)) was also significantly larger in the *PMBR Decreasers* (t test $p<0.05$, Figure 3C).

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Within subject, the *PMBR Increasers* showed negative correlations over blocks between the PMBR and the directional variability, while the *PMBR Decreasers* showed positive correlations, leading to a very significant difference between the groups (t test p<0.0001, Figure 3D left). The same trend was evident for the trial-to-trial directional changes (t test p<0.0001, Figure 3D middle). As a control for head movements contamination of the PMBR dynamics we looked for correlation over blocks between the PMBR and the peak head acceleration during the same time interval. Here we found no significant correlations for either of the groups (Figure 3D right), and most importantly, no difference between the groups (t test p=0.99).

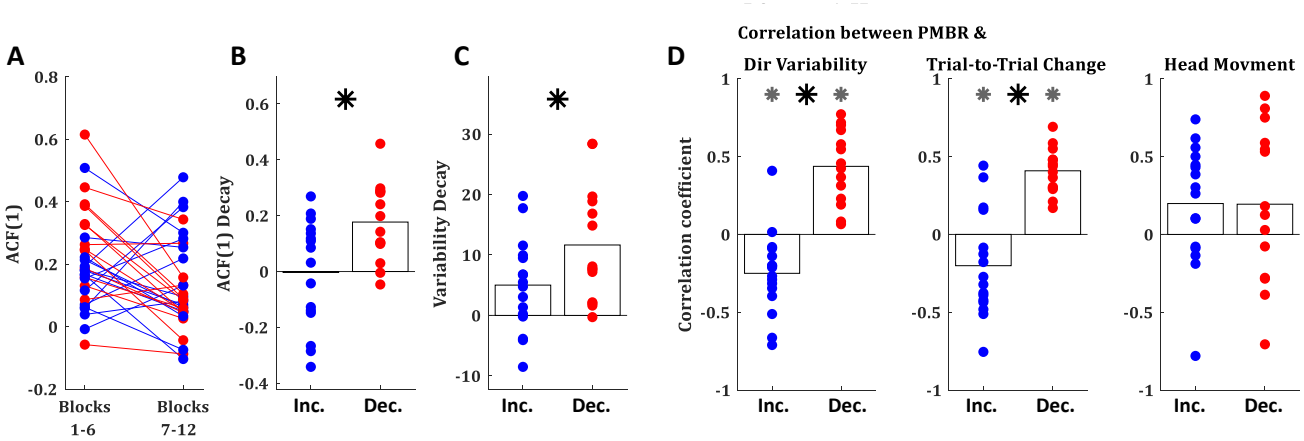

Figure 3. *Behavioural differences between the groups*. (**A**) Lag-1 autocorrelation of the target ball direction over the first and the second half of the training session (blue: *PMBR Increasers*; red: *PMBR Decreasers*). (**B**) Decay of the lag-1 autocorrelation from the first to the second half of the training session (Inc: *PMBR Increasers*; Dec: *PMBR Decreasers*). (**C**) Directional variability decay from the first block (trials 1-25) to the learning plateau (trials 201-300). (**D**) Correlation coefficients over blocks for all individual subjects between the PMBR and the directional variability (left), trial-to-trial directional change (middle), and head movements (right). Grey asterisk indicates group correlations significantly different than zero. Black asterisk indicates significant difference in the correlation coefficients between the groups.

After learning plateaus, the *PMBR Decreasers* were slightly more accurate (Figure 4A) and less variable (Figure 4B). More importantly, *PMBR Decreasers* seemed to modify their variability (actively control of the exploration-exploitation trade-off, explicitly or implicitly) to improve learning, as evidenced by their high variability in the first block and the very steep decrease towards the second (Figure 4B). The dynamical control of the variability was even more strongly evident in the trial-to-trail directional changes, where the *PMBR Decreasers* showed much bigger changes over the first 4 blocks (100 trials), therefore using more exploration then the *PMBR Increasers* who made smaller changes from one trial to the next (t test p<0.05, Figure 4C). Also, *PMBR Increasers* tended to have higher complexity in their movement, i.e. use more DoF, throughout the training session (t test p<0.05, Figure 4D).

Finally, the *PMBR Decreasers* were on average better learners (mean learning rates were 0.48 and 0.6 for the *PMBR Increasers* and *PMBR Decreasers* respectively) though the group difference was not significant (t test p=0.17). We explored the correlation between learning and the

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PMBR change over blocks (the difference between the final PMBR over the learning plateau: trials 201-300, and the initial PMBR over the first block: trials 1-25). Across all subjects, we found no correlation between the learning rate and the initial PMBR or the PMBR change. When considering each group separately, for the *PMBR Decreasers* there was no clear trend, but the *PMBR Increasers* showed a clear trend (though non-significant) of positive correlation of the PMBR change with learning (Figure 4E). Meaning, in the *PMBR Increasers* group subjects who had more PMBR increase showed more learning.

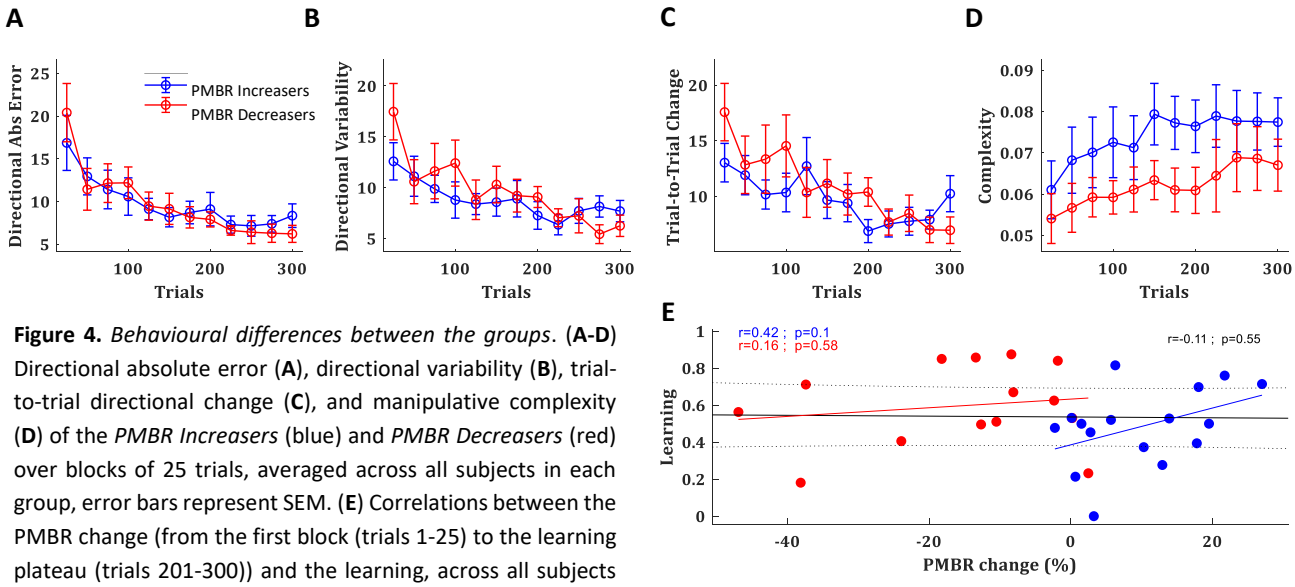

Figure 4. *Behavioural differences between the groups*. (**A-D**) Directional absolute error (**A**), directional variability (**B**), trial-to-trial directional change (**C**), and manipulative complexity (**D**) of the *PMBR Increasers* (blue) and *PMBR Decreasers* (red) over blocks of 25 trials, averaged across all subjects in each group, error bars represent SEM. (**E**) Correlations between the PMBR change (from the first block (trials 1-25) to the learning plateau (trials 201-300)) and the learning, across all subjects (black line) and within each group (blue: *PMBR Increasers*; red: *PMBR Decreasers*).

Discussion

In this paper we detected brain activity signatures for motor learning in complex real-world task. Our results produce new insights into motor learning by revealing two types of motor learners with different EEG dynamics in their PMBR over learning: *PMBR Increasers* and *PMBR Decreasers*. These groups were defined by the correlation between the dynamics of their PMBR and their performance errors, but also showed clear task-level differences which suggest differences in the underlying learning mechanisms.

The two known main mechanisms that drive motor learning – error-based learning and reward-based reinforcement learning – are engaging different neural processes (e.g. Doyon and Benali, 2005; Doyon et al., 2003; Uehara et al., 2018). While both mechanisms can contribute to learning in any given task, the constrains of the highly controlled laboratory-tasks common in the field induce the predominance of one mechanism over the other. In motor adaptation tasks the dominant mechanism is error-based learning, guided by an internal forward model which is updated

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based on sensory-prediction errors; while in tasks often addressed as skill-learning (such as sequence-learning, curve-tracking, and force-tracking) the dominant mechanism is reward-based learning where the controller learns form reinforcement of successful actions (Haith and Krakauer, 2013; Krakauer and Mazzoni, 2011). PMBR was reported to increase over learning in adaptation tasks (e.g. Tan et al., 2014, 2016; Torrecillos et al., 2015), showing negative correlations with the decreasing errors, and decrease (itself or its magnetic resonance spectroscopy correlate) over skill-learning tasks (e.g. Floyer-Lea et al., 2006; Kolasinski et al., 2019; Kranczioch et al., 2008). PMBR is positively correlated with magnetic resonance spectroscopy-measured GABA concentration (Cheng et al., 2017; Gaetz et al., 2011). This may be due to the general correlation of Beta activity with GABAergic activity (Hall et al., 2010, 2011; Roopun et al., 2006; Yamawaki et al., 2008). We raise the possibility of a more nuanced link of GABA to motor learning: namely that the two diverging PMBR dynamics (increase vs decrease) reflect that GABA activity is a distinguishing feature of different motor learning mechanisms. These may be reflections of GABAergic projections from different subcortical regions, cerebellum for error-based adaptation and basal ganglia for reward-based reinforcement learning (Doyon and Benali, 2005; Doyon et al., 2003).

In summary, we find the PMBR-Error correlation to be a signature of motor learning mechanisms. In the data recorded during real-world motor learning in the current study, we found two groups of subjects: *PMBR Increasers* and *PMBR Decreasers*. The *PMBR Increasers* had low initial PMBR amplitudes and showed an increase over learning negatively correlated with the decreasing directional errors, presumably used error-based adaptation as its dominant learning mechanism. The *PMBR Decreasers* had higher initial PMBR amplitudes and showed a decrease over learning positively correlated with the decreasing directional errors, presumably used reward-based learning as its dominant learning mechanism. Importantly, on a subject-by-subject basis, previous works in laboratory adaptation tasks showed only one category of learners, all have negative PMBR-Error correlations (e.g. Tan et al., 2016). Thus, our findings here reveal that real-world learning is more complex, in terms of learning mechanism, and involve more inter-subject differences.

The behavioral differences between the groups support the notion of a different predominant learning mechanism. While there were no significant differences between the groups in their initial errors or their total learning, there were clear group difference in the learning process. First, the lag-1 autocorrelation (ACF(1)) was suggested as an index of performance in motor-skill learning, measuring the optimality of trial-by-trial motor planning (van Beers et al., 2013). ACF(1) of zero indicates optimal performance. Here we used the decay in the ACF(1) as a measure for skill learning: during skill learning ACF(1) should decay towards zero. Since the estimation of autocorrelations from short time series is fundamentally biased (van Beers, 2009; Kendall, 1954; Marriott and Pope, 1954), we calculated the ACF(1) over the first and the second halves of the learning session (150 trials) and not in each block of 25 trials. As expected for naïve participance,

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the ACF(1) values of both groups during both halves of the session were significantly greater than zero (Figure 3A). More importantly, while the *PMBR Increasers* showed no significant difference in the ACF(1) between the two halves of the session, the *PMBR Decreasers* showed a significant decay (Figure 3B). This decay is a behavioral indication for learning mechanism differences between the groups. Second, the intertrial variability patterns were in line with the suggested learning mechanisms. The *PMBR Decreasers* (reward-based learners) showed more decay in their intertrial variability over learning (Figure 3C & Figure 4B), a known feature of skill learning (Krakauer et al., 2019; Shmuelof et al., 2012). Additionally, the trial-to-trail directional changes over the first 4 blocks (100 trials) were much higher for the *PMBR Decreasers* (reward-based learners) than the *PMBR Increasers* (error-based learners), suggesting that the first group used more exploration while the second made smaller changes from trial-to-trial, as expected in error-based adaptation (Figure 4C).

Laboratory-tasks tend to emphasize a specific learning mechanism for all subjects based on the types of feedback and perturbation (e.g. Galea et al., 2015; Huang et al., 2011; Kim et al., 2019). In contrast, real-world motor learning probably involves multiple high- and low-level learning mechanisms, where different subjects might emphasize one learning modality over the other. In our real-world learning paradigm, subjects performed error-based adaptation as they learned from the directional error of the target ball in each trial, but they also performed reward-based learning as they learned to use the cue and their body joints while making a shot by reinforcement of successful actions. We speculate that the *PMBR Increasers*, who showed the neural and behavioral patterns reported in motor adaptation paradigms, mostly learned via error-based learning approach, while the *PMBR Decreasers*, who showed the neural and behavioral patterns reported in skill learning tasks, used more reinforcement of successful actions.

Recent studies suggest that event-related desynchronizations and synchronizations, such as PMBR, are driven by beta bursts (Little et al., 2019; Seedat et al., 2020; Wessel, 2020) which carry more information than the trail-averaged band oscillation. At the same time, a recent study suggested spatial differences between beta oscillations that reflect implicit and explicit learning (Jahani et al., 2020). These recent developments highlight the potential for capturing neural signatures of learning in EEG beta. To further validate the current findings, future studies will need to compare the PMBR dynamics during learning of the same paradigm with different dominant mechanism, forced by experimental trickery (i.e. using feedback manipulations and constrains).

Conclusions

In this study we demonstrate the feasibility and importance of studying human neuroscience in-the-wild, and specifically in naturalistic real-world motor learning. We highlight that real-world motor learning involves different neural dynamics for different subjects, which were previously associated different learning mechanisms in different tasks. Presumably, the individual

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subject's proportion of applying the two learning mechanisms could be revealed by the overall trend of the PMBR over learning. It suggests that real-world motor learning involves multi-modal learning mechanisms which subjects combine in new ways when faced with the complexity of learning in the real-world, and different subjects emphasize one mechanism over the other.

Methods

Experimental Setup and Design. 30 right-handed healthy human volunteers with normal or corrected-to-normal visual acuity (12 women and 18 men, aged 24±3) participated in the study. All volunteers gave informed consent prior participating to the study, and all experimental procedures were approved by Imperial College Research Ethics Committee and performed in accordance with the declaration of Helsinki. The volunteers, who had little to none previous experience with playing billiards, performed 300 repeated trials where the cue ball (white) and the target ball (red) were placed in the same locations and the subject was asked to shoot the target ball towards the pocket of the far-left corner (Figure 1A). The trials were split into 6 sets of 50 trials with a short break in-between to allow the subjects to reset a bit and reduce potential fatigue. Each experimental set (of 50 trials) took 8 to 12 minutes. For the data analysis we further split each set into two blocks of 25 trials each, resulting in 12 blocks. During the entire learning process, we recorded the subjects' brain activity with a wireless EEG headset (Figure 1B). The balls on the pool table were tracked with a high-speed camera (Dalsa Genie Nano) to assess the subjects' success in the game and to analyze the changes throughout learning, not only in the body movement and brain activity but also in its outcome – the ball movement (Figure 1C).

EEG acquisition and preprocessing. For 20 subjects, EEG was recorded at 256Hz using a wireless 14 channel EEG system (Emotiv EPOC+, Emotiv Inc., CA, USA). For the other 10 subjects, EEG was recorded at 300Hz using a wireless 21 channel EEG system (DSI-24, Wearable Sensing Inc., CA, USA) and down sampled to 256Hz to be analyzed with the same pipeline as the other subjects. EEG signals were preprocessed in EEGLAB (https://sccn.ucsd.edu/eeglab; Delorme and Makeig, 2004). EEG signals were first band-pass filtered at 5-35 Hz using a basic FIR filter, and then decomposed into independent component (IC) and artifacted ICs were removed with ADJUST, an EEGLAB plug-in for automatic artifact detection (Mognon et al., 2011). All further analysis was performed on the C3 channel. For the Emotiv subjects it was interpolated from the recorded channels with spherical splines using EEGLAB 'eeg_interp' function.

EEG time-frequency analysis. Each block was transformed in the time-frequency domain by convolution with the complex Morlet wavelets in 1 Hz steps. Event-related EEG power change was subsequently calculated as the percentage change by log-transforming the raw power data and then normalizing relative to the average power calculated over the block, as no clear baseline could be defined during the task (Alayrangues et al., 2019; Tan et al., 2014, 2016; Torrecillos et al., 2015),

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and then subtracting one from the normalized value and multiplying by 100. Event-related power changes in the beta band (13–30 Hz) were investigated. Since it is a free behavior study there was no go cue and the subject shoot when they wanted. As a result, the best-defined time point during a trial was the end of the movement, defined by the beginning of the cue ball movement. Thus, the post-movement beta rebound (PMBR) was defined as the average normalized power over a 200ms window centered on the peak of the power after movement termination (Tan et al., 2016). The PMBR was calculated for each individual trial before averaging over blocks for further analysis. The time frequency analysis was performed with custom software written in MATLAB (R2017a, The MathWorks, Inc., MA, USA).

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