Neurobehavioural signatures of learning that emerge in a real-world motor skill task

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Keywords: motor learning, motor skill, real-world, full-body movement, EEG, Post-movement beta, movement variability, motor neuroscience

Declaration of Interests: The authors declare no competing financial interests.

Contributions: SH and AAF conceived and designed the study; SH and CVA acquired and analyzed the data; SH and AAF interpreted the data; SH drafted the paper; SH and AAF revised the paper

Acknowledgements: We thank our participants for taking part in the study and Marlene Gonzalez for her contribution to the data collection. We acknowledge the technical support by Alex Harston and Chaiyawan Auepanwiriyakul. We also thank Alex Harston for helpful comments on the manuscript. The study was enabled by financial support to a Royal Society-Kohn International Fellowship (NF170650) and by eNHANCE (http://www.enhance-motion.eu) under the European Union's Horizon 2020 research and innovation programme grant agreement No. 644000 (SH, AAF).

Summary

The behavioral and neural processes of real-world motor learning remain largely unknown. We demonstrate the feasibility of real-world neuroscience, using wearables for naturalistic full-body motion tracking and mobile brain imaging, to study motor learning in billiards. We highlight the similarities between motor learning in-the-wild and classic toy-tasks in well-known features, such as multiple learning rates, and the relationship between task-related variability and motor learning. However, we found that real-world motor learning affects the whole body, changing motor control from head to toe. Moreover, with a data-driven approach, based on the relationship between variability and learning, we found the arm supination to be the task relevant joint angle. Our EEG recordings highlight groups of subjects with opposing dynamics of post-movement Beta rebound (PMBR), not resolved before in toy-tasks. The first group increased PMBR over learning while the second decreased. These opposite trends were previously reported in error-based learning and skill learning tasks respectively. Behaviorally, the PMBR decreasers better controlled task-relevant variability dynamically leading to lower variability and smaller errors in the learning plateau. We speculate that these PMBR dynamics emerge because subjects must combine multi-modal mechanisms of learning in new ways when faced with the complexity of the real-world.

Introduction

Motor learning is a key feature of our development and daily lives, from a baby learning to roll, to an adult learning a new sport, or a patient undergoing rehabilitation after a stroke. The process of learning a real-world motor skill is usually long and complex, and difficult to quantify. As a result, real-world motor learning is rarely studied, and most of the motor learning literature focuses on relatively simple tasks, performed in a lab setup or an MRI scanner, such as force-field adaptations (e.g. Diedrichsen et al., 2005; Howard et al., 2015; Shadmehr and Mussa-Ivaldi, 1994; Smith et al., 2006), visuomotor perturbations (e.g. Haar et al., 2015; Krakauer et al., 2000; Mazzoni and Krakauer, 2006; Taylor et al., 2014), and sequence-learning of finger tapping or pinching tasks (Clerget et al., 2012; Ma et al., 2011; Reis et al., 2009; Yokoi et al., 2018).

These reductionistic tasks enable to isolate specific features of the motor learning and tackle them individually. While this plays an important role in our understanding of sensorimotor control and learning, it addresses a very restricted range of behaviors that do not capture the full complexity of real-world motor control and may overlook fundamental principles of motor control and learning in real-life (Ingram and Wolpert, 2011; Wolpert et al., 2011). It is only in natural behavioral settings that neuroscientific mechanisms are subject to evolutionary selection pressures and it is the operation in these contexts for which the nervous system has been designed (Hecht et al., 2014). Over the past decade there were few important efforts in this direction. One line of studies devised more complex tasks for skill learning (e.g. Abe and Sternad, 2013; Cohen and Sternad, 2009; Shmuelof et al., 2012), but those were still computer screen based toy-tasks which try to emulate real-world tasks. Another line used actual real-world tasks such as juggling (e.g. Hecht et al., 2014; Ono et al., 2015; Sampaio-Baptista et al., 2014, 2015; Scholz et al., 2009), but these studies analyzed only anatomical and functional MRI changes following learning and did not address behavior or neural activity during the learning process.

Here we are taking a novel data-driven approaches to study behavior where it matters most – in natural real-life settings. The paradigm in which we study real-world motor learning is the game of pool table billiards. Billiards is a real-world task ideally suited to neurobehavioral study as motion tracking in terms of movement in space, the natural constraints of game play, and divisibility into trials captures the style of reductionistic lab-based motor learning tasks. Billiards is also a natural task which is complex and involves many different sub-tasks (precision, alignment, ballistic movements, high-level sequential planning) which requires complex skills. To tackle the complexity of the high dimensional task space of this real-world task we applied naturalistic approaches and developed a Bioinformatics of Behavior database (Faisal et al., 2010) of real-world motor learning behavior. This includes the full body movement and EEG brain activity during the entire learning period, as well as the measurements of task performance (balls movement on the table). This enabled us to quantify the trends of changes in each of them separately, during the

entire learning process, and to look for correlations between the physiological measures and reveal neurodynamical processes behind motor learning. To the best of our knowledge, this is the first study to record both the behavior and the neural responses throughout the entire process of real-world motor learning.

The main neural signatures of voluntary movement and motor learning, that can be measured with EEG, 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 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 skill learning 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 MRS-measured GABA concentration (Cheng et al., 2017; Gaetz et al., 2011) that also decreases over skill learning tasks such as sequence learning in force tracking (Floyer-Lea et al., 2006) and serial reaction time (Kolasinski et al., 2019). These different tasks are associated with distinct learning mechanisms, model-based processes are likely to predominate in adaptation (error-based learning) tasks, and model-free processes predominate in skill tasks (Haith and Krakauer, 2013). While both mechanisms can contribute to learning in any given task, the constrains of toy-tasks induce the predominance of one over the other. Here we introduced a real-world learning task where performance errors are not driven by perturbations. Learning in this paradigm may not be predominantly mediated by a specific learning mechanism, or by the same learning mechanism for all subjects. Since there is no clear method to identify the learning mechanism used by subjects from their behavior and performance, here we explored the use of the PMBR dynamics as a signature for the dominant learning mechanism.

We structured the results as follows: We ground our results in previous work on reductionistic lab tasks, to show that our unconstrained task and its task goal (directional error of the target ball relative to the pocket it is meant to go in) displays the well-known features of human motor learning. We then characterize full-body movement structure during the task, and how learning changes the kinematics of all joints over trials. Next, we compare across subjects to map their performance, learning rates, and motor variability, and how initial variability and learning rates are linked. We then relate the EEG activity during learning which reveals two groups of learners with different PMBR dynamics and learning characteristics. We address the neural and behavioral differences between the two groups which are suggestive of differences in the learning mechanisms employed by the subjects.

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' full body movements with a 'suit' of inertial measurement units (IMUs; Figure 1B), their brain activity with wireless EEG (Figure 1C), and the balls on the pool table were tracked with a high-speed camera to assess the outcome of each trial (Figure 1D).

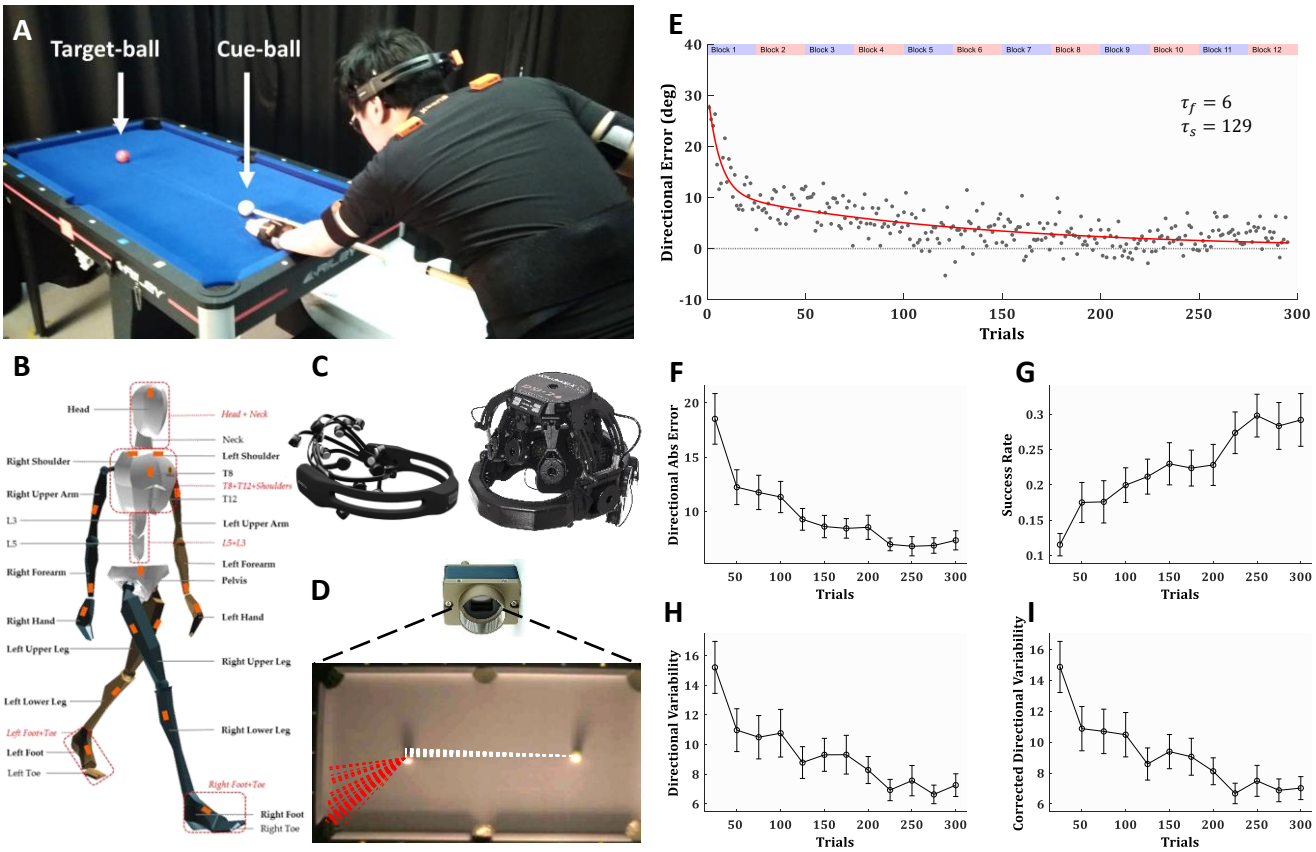

Figure 1. *Experimental setup and task performance*. (**A**) 30 right-handed healthy subjects performed 300 repeated trials of billiards shoots of the target (red) ball towards the far-left corner. (**B**) Full body movement was recorded with a 'suit' of 17 wireless IMUs (Xsens MVN Awinda). (**C**) Brain activity was recorded with wireless EEG systems: 20 subjects with eMotiv EPOC+ (left) and 10 subjects with Wearable Sensing DSI-24 (right). (**D**) 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. (**E**) The trial-by-trial directional error of the target-ball (relative to the direction from its origin to the centre of the target pocket), averaged across all subjects, with a double-exponential fit (red curve). (**F**) The mean absolute directional error of the target-ball. (**G**) The success rate. (**H**) directional variability. and (**I**) directional variability corrected for learning (see text). (**F-H**) presented over blocks of 25 trials, averaged across all subjects, error bars represent SEM.

Movement and Learning in a real-world pool task

The ball tracking data showed a double exponential learning curve for the 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 1E). The direction of the initial trials error was consistent across subject

as they tended to hit the center of the target ball and shot it forward towards the center of the table. For measuring success rates and intertrial variability 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 over blocks (Figure 1F) emphasized the reduction in the inter-subject variability during learning (decreasing error bars). The success rate over blocks (percentage of successful trials in each block; Figure 1G) showed similar learning to the directional error. The learning was also evident in the intertrial variability in the shooting direction which decayed over learning (Figure 1H). Since learning also occured within a block (especially during the first block) and the variability might be driven by the learning gradient, we corrected for it by calculating intertrial variability over the residuals from a regression line fitted to the ball direction in each block. This corrected intertrial variability showed the same pattern (Figure 1I). Overall, the task performance data suggested that subjects reached their peak performance on the fifth experimental set (blocks 9-10, trials 200-250) and are doing the same (or even slightly worse) on the last experimental set (blocks 11-12, trials 250-300). Thus, we refer to the last two experimental sets (blocks 9-12, trials 201-300) as the 'learning plateau'.

The full body movements were analyzed over the velocity profiles of all joints, and not the joint angles profiles, as those are less sensitive to potential drifts in the IMUs and have proven to be more robust and reproducible across subjects in natural behavior (Thomik, 2016). In the current data we can also see this robustness across trials (Figure 2A). The covariance of the velocity profiles, averaged across the initial ten trials of all subjects, showed that most of the variance in the movement is in the right arm, and specifically in the right shoulder (Figure 2B). This is a signature for the naivety of the subjects, as pool billiards guide books emphasize that the shooting movement should be from the elbow down while the shoulder should be kept still. The covariance of the velocity profiles averaged across the initial ten trials of the learning plateau (trials 201-210) showed similar structure with an overall decrease relative to the initial trials but an increase in the variance of right elbow rotation (Figure 2C). On the group level, the velocity profiles of all joints (including the joints of the right arm that carry most of the movement variance) showed only minor changes following learning. For example, the flexion/extension of the right elbow showed a decrease in velocity from the initial trials to the trials of the learning plateau (Figure 2A).

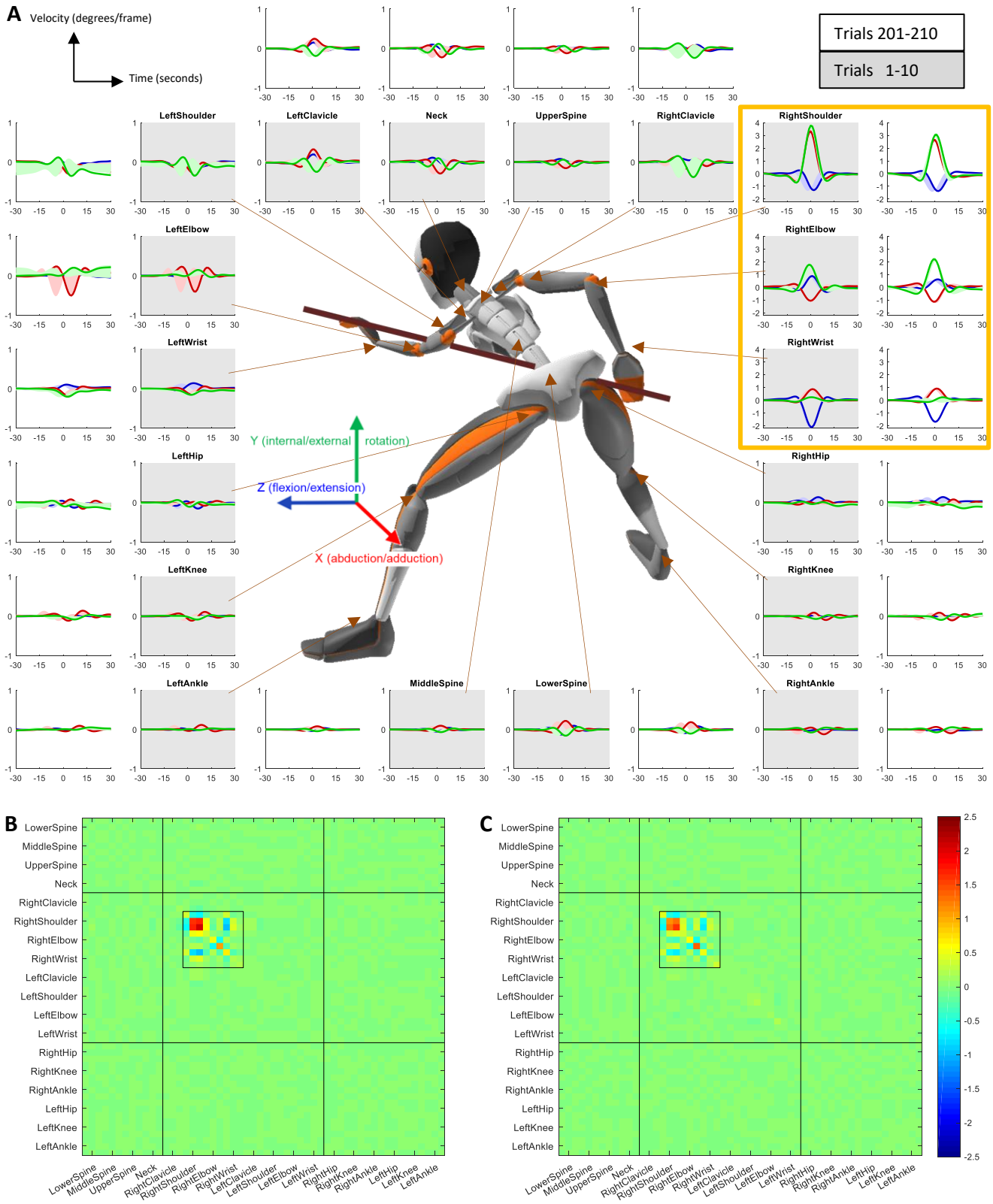

Figure 2. *Velocity profiles and covariance*. (**A**) Velocity profiles in 3 degrees of freedom (DoF) for each joint (blue: flexion/extension, red: abduction/adduction; green: internal/external rotation) averaged across subjects and trials over the initial trials (1-10) in the inner circle (grey background) and after learning plateau (201-210) in the outer circle (white background). The joints of the right arm, which do most of movement in the task, are highlighted in orange box. (**B,C**) The variance covariance matrix of the velocity profiles of all joints averaged across subjects and trials (**B**) over the initial trials (1-10) and (**C**) after learning plateau (201-210). The order of the DoF for each joint is: flexion/extension, abduction/adduction, internal/external rotation.

The generalized variance (GV; the determinant of the covariance matrix (Wilks, 1932)) over the velocity profiles of all joints increased fast over the first ~30 trials and later decreased slowly (Figure 3A), suggesting active control of the exploration-exploitation trade-off. The covariance over the initial trials, the trials over the peak GV, and trials after learning plateau (Figure 3B), showed that the changes in the GV were driven by an increase in the variance of all DoFs of the right shoulder, and the negative covariance between the abduction/adduction and internal/external rotation of the right shoulder to the flexion/extension of the right shoulder and wrist. The internal/external rotation of the right elbow showed a continuous increase in its variance, which did not follow the trend of the GV. Principal component analysis (PCA) across joints for the velocity profiles per trial for each subject, showed a slow but consistent rise in the number of PCs that explain more than 1% of the variance in the joint velocity profiles (Figure 3C). The manipulative complexity (Belić and Faisal, 2015) showed the same trend (Figure 3D), which suggests that over trials subjects use more degrees of freedom in their movement.

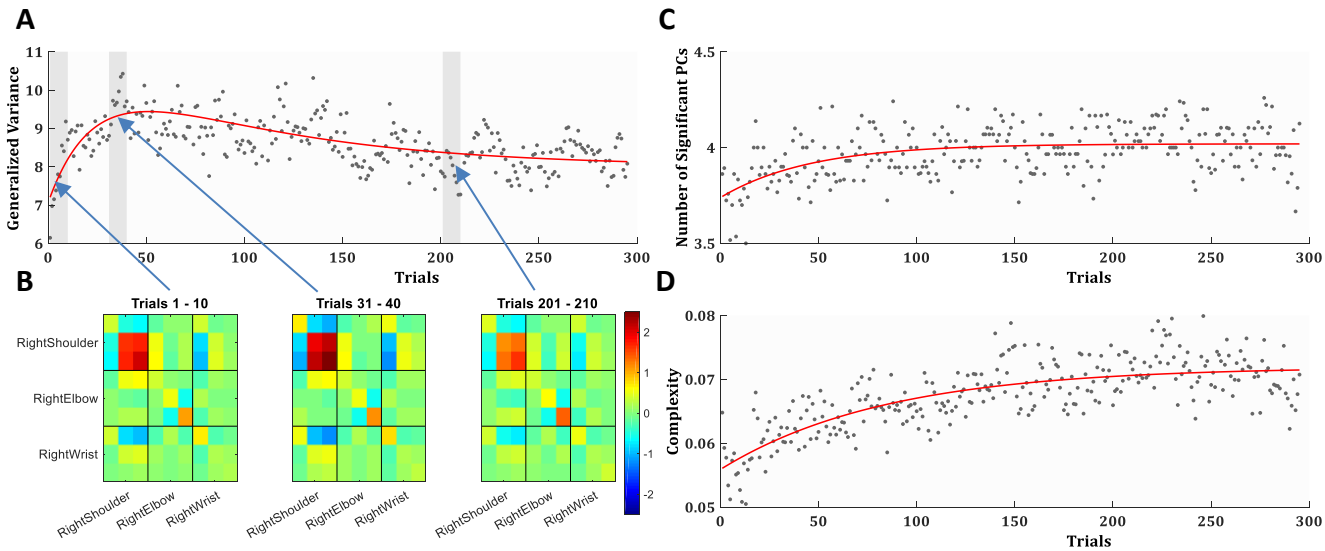

Figure 3. *Variance and Complexity*. (**A**) The trial-by-trial generalized variance (GV), with a double-exponential fit (red curve). (**B**) The variance covariance matrix of the right arm joints velocity profiles averaged across subjects and trials over the initial trials (1-10), the peak GV trials (41-50) and after learning plateau (201-210). The order of the DoF for each joint and the colorbar are the same as in Figure 2. (**C**) The number of principal components (PCs) that explain more than 1% of the variance in the velocity profiles of all joints in a single trial, with an exponential fit (red curve). (**D**) The manipulative complexity (Belić and Faisal, 2015), with an exponential fit (red curve). (**A,C,D**) Averaged across all subjects over all trials.

As a measure of task performance in body space, correlation distances were calculated between the velocity profile of each joint in each trial to the velocity profile of that joint in all successful trials. The mean over these correlation distances produced a single measure of Velocity Profile Error (VPE) for each joint in each trial.

$$VPE_i = \frac{\sum_s^{N_{scs}} corrDist(velProf_i, velProf_s)}{N_{scs}}$$

Thus, VPE in trial i was the sum of the correlation distances between the velocity profile in trial i and the velocity profile in successful trial s, divided by the number of successful trials (N_{scs}). For all joints, VPE showed a clear pattern of decay over trials in an exponential learning curve (Figure 4). A proximal-to-distal gradient in the time constant of these learning curves was observed across the right arm, from the shoulder to the elbow and the wrist rotation which showed very slow learning (the other wrist angles had very low VPE from the start, thus did not learn much). Intertrial variability in joint movement was measured over the VPEs in each block. Learning was also evident in the decay over learning of the VPE intertrial variability over most joints across the body (Fig 4 Supplement).

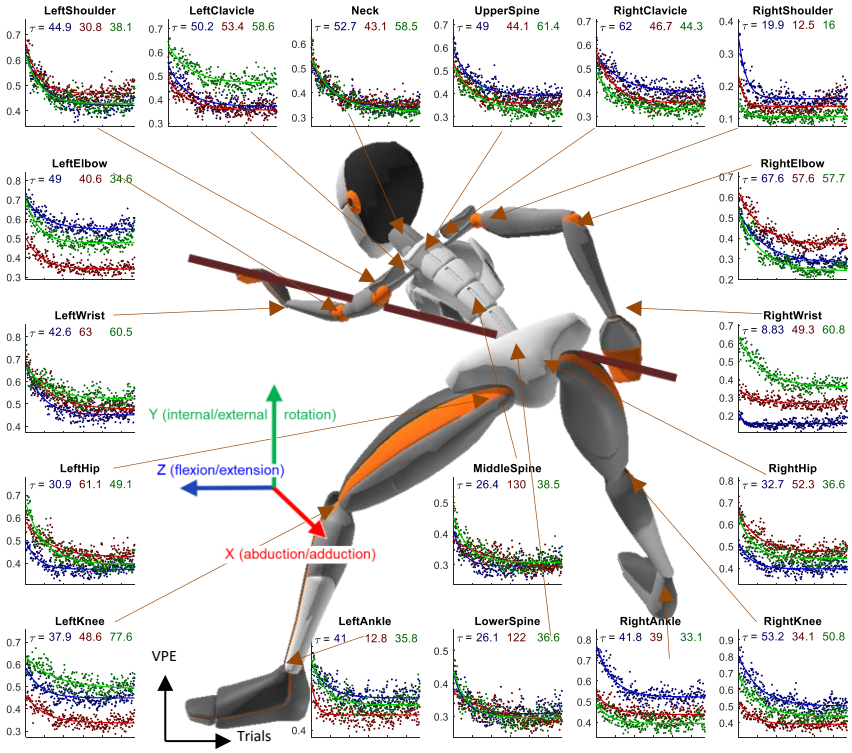

Figure 4. *Learning over Joints*. Velocity Profile Error (VPE) reduction across all joints. The trial-by-trial VPE for all 3 DoF of all joints, averaged across all subjects, with an exponential fit. The time constants of the fits are reported under the title. The color code of the DoF is the same as in figure 2 (blue: flexion/extension; red: abduction/adduction; green: internal/external rotation).

Inter-subject differences in variability and learning

We found significant differences between subjects in their initial errors, final errors, intertrial variability, and learning, which are overlooked in the group average results. One subject, who had low initial errors, showed no learning, i.e. did not reduce her error over trials from the first block (trials 1-25) to the learning plateau (trials 201-300). For all other subjects the final errors were smaller than the initial errors (Figure 5A). There was a significant correlation between the initial and the final errors, meaning subjects with higher initial errors tended to have higher final errors as well.

While over learning most subjects decreased their intertrial variability in the outcome (ball direction; Figure 1H & 5B) there was some tendency (though non-significant) for subjects who were initially more variable to be also more variable after learning (Figure 5B). The intertrial

variability of the joint velocity profiles, which also decreased over learning (Fig 4 Supplement), showed a clearer and stronger correlation between the initial and the final intertrial variability (Figure 5E & Fig 5E Supplement). While this phenomenon was observed in various joints across the body, and dominant in the abduction across the spine joints, it was most dominant in the right shoulder abduction and rotation, the two joint angles that do most of the movement and carry most of its variance (Figure 2).

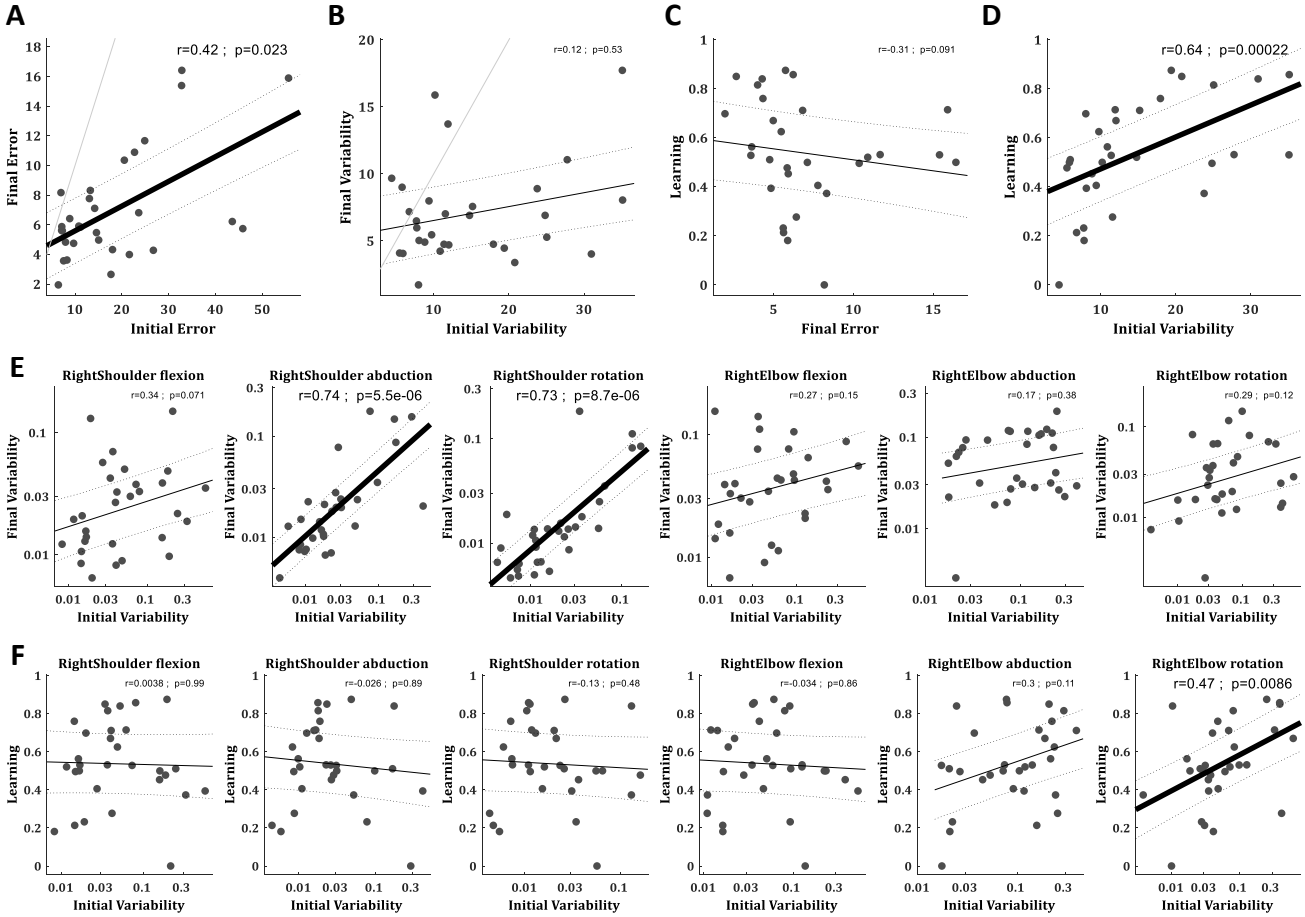

Figure 5. *Variability and learning across subjects*. (**A**) Correlation between subjects' mean absolute directional error over the first block (trials 1-25) and the learning plateau (trials 201-300). (**B**) Correlation between subjects' directional variability over first block (corrected for learning trend, see text) and over the learning plateau (**C**) Correlation between subjects' mean absolute directional error over the learning plateau and their learning (**D**) Correlation between subjects' directional variability over the first block (corrected for learning trend, see text) and their learning (**E**) Correlation between subjects' VPE variability (in logarithmic scale) over the first block and the learning plateau for the right arm joints. (**F**) Correlation between subjects' VPE variability (in logarithmic scale) over the first block and their learning for the right arm joints. (**A-F**) Correlation values are Spearman rank correlation, regression lines are linear fits with 95% confidence intervals.

Learning was defined as the difference between the initial error (over the first block: trials 1-25) and the final error (over the learning plateau: trials 201-300) normalized by the initial error. There was no significant correlation between the learning and the final error (as subjects who started worse could have learn more but still not perform better after learning), but there was a strong trend that more learning leads to smaller final errors (Figure 5C). We tested if higher levels of initial task-relevant motor variability (variability in the directional error of the target ball) in this complex real-

world task could predict faster learning across individual, as found in simple lab experiments (Wu et al., 2014). We indeed found that individuals with higher intertrial variability in the directional error of the target ball over the first block showed more learning ($r=0.64$, $p<0.001$; Figure 5D). Importantly, this is the corrected intertrial variability (as in Figure 1I) which is calculated over the residuals from a regression line fitted to the ball direction to correct for the learning that is happening within the block. Next, we tested the link between learning and initial variability over the joint velocity profiles of the right arm (Figure 5F). We found that the only joint angle where the intertrial variability showed significant correlation to learning was the right elbow rotation ($r=0.47$, $p=0.0086$), which is the arm supination. We further tested the link over the full body kinematics (Fig 5F Supplement) and found no other joint that showed this correlation. Thus, while learning leads to overall reduction in movement variability, only initial variability in specific, task-relevant, dimensions can facilitate/predict learning.

EEG activity reveals two types of learners

The most prominent feature of the EEG brain activity recorded in this study was the transient increase in beta oscillations across the sensorimotor network after the end of the movement, known as post-movement beta synchronization (Pfurtscheller et al., 1996) or post-movement beta rebound (PMBR; Figure 6A). On average across subjects there was no clear trend of PMBR (increase or decrease) over learning (Figure 6B). Testing for the subject by subject PMBR change (the difference between the final PMBR over the learning plateau: trials 201-300, and the initial PMBR over the first block: trials 1-25) revealed subjects with opposing trends.

While almost half of the subjects (N=17) showed an increase in the PMBR over learning, the other half (N=13) showed a decrease. The PMBR change was negatively correlated with the initial PMBR (Figure 6C), i.e. subjects who had higher initial PMBR had higher decrease (or lower increase) in PMBR over learning. Thus, the beta-power time courses over the first block showed a strong group effect (Figure 6D). The first group showed a clear trend of PMBR increase over learning, in consistence with adaptation studies, while the second group showed clear trend of PMBR decrease over learning, in consistence with skill learning studies (Figure 6E).

The grouping was validated using leave-one-out classification over the PMBR data (12 data points per subject, one for each block). The classifier yielded 93% accuracy. The two subjects who were miss classified were the PMBR decreasers who had the lowest negative PMBR change (>-2.5). Moving these two subjects to the other group does not change any of the reported group differences. Additionally, since the beta-power changes were calculated as percent signal change relative to the average power over the block (see methods), these group differences could potentially be driven by differences in the baseline. Importantly, this was not the case as there was no real difference in the baseline between the groups, not in the values nor in the trend over learning (Figure 6F).

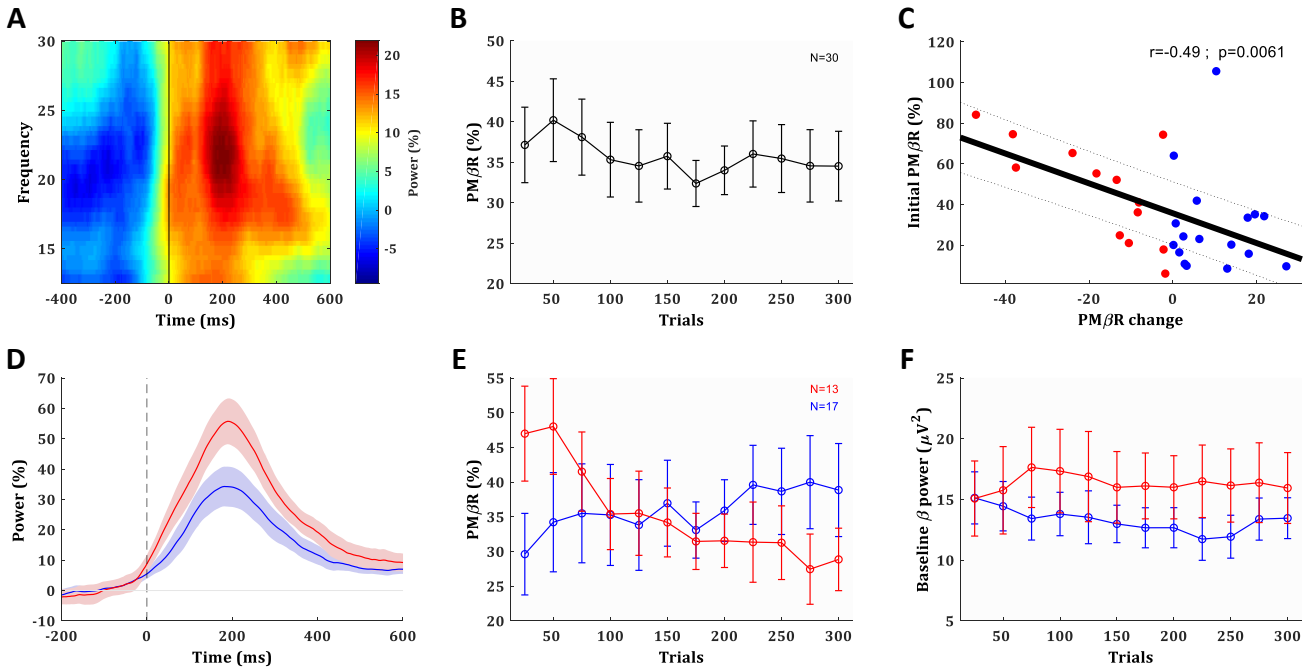

Figure 6. *Post-movement beta rebound*. (**A**) Time-frequency map of a typical subject aligned to movement offset (ball movement onset), obtained by averaging the normalized power over electrode C3. (**B**) PMBR over blocks of 25 trials, averaged across all subjects, error bars represent SEM. (**C**) Correlation between subjects' PMBR changes (from the first block (trials 1-25) to the learning plateau (trials 201-300)) and their initial PMBR (over the first block). Subjects are color coded based on their PMBR trend: subjects with a positive PMBR change are in blue (PMBR increasers) and subjects with a negative PMBR change are in red (PMBR decreasers). (**D**) Beta power profile over the first block for the PMBR increasers (blue) and decreasers (red). Line is averaged across all subjects in the group and the light background mark the SEM. (**E,F**) PMBR (E) and Baseline beta power (F) of the PMBR increasers (blue) and PMBR decreasers (red) over blocks, averaged across all subjects in each groups, error bars represent SEM.

Following the results in the EEG data, which suggest two groups of subjects who employ different learning mechanisms, we looked for group differences in the movement data. While there was no difference in the initial error between the groups, after learning plateaus the PMBR decreasers were more accurate (Figure 7A) and less variable (Figure 7B). PMBR decreasers also 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 7B). The dynamical control of the variability was even more significantly evident in their full-body movement. PMBR decreasers showed a clear decrease in their GV after learning towards the learning plateau while PMBR increasers showed no clear trend in their GV (Figure 7C). Lastly, PMBR increasers tended to have higher complexity in their movement, i.e. used more DoF (Figure 7D).

Within subject, the PMBR increasers showed significant negative correlations over blocks between the directional error and the PMBR (mean correlation: r=-0.3, t test p=0.008), while the PMBR decreasers showed significant positive correlations (mean correlation: r=0.41, t test p<0.001), leading to a very significant difference between the groups (t test p<0.001; Figure 7E). The same trend was evident for the directional variability. PMBR increasers showed negative correlations over blocks between the variability and the PMBR (mean correlation: r=-0.2, t test

p=0.03), while the PMBR decreasers showed positive correlations (mean correlation: r=0.42, t test p<0.001), leading to a very significant group difference (t test p<0.001; Figure 7F). We also looked for correlation over blocks between the PMBR and the peak head acceleration during the same time interval, as a control for head movements contamination of the PMBR effect. Here we found no significant correlations for either of the groups (mean correlation: r=0.19, t test p=0.08 and r=0.21, t test p=0.16, for the PMBR increasers and decreasers respectively; Figure 7G), and most importantly, no difference between the groups (t test p=0.91).

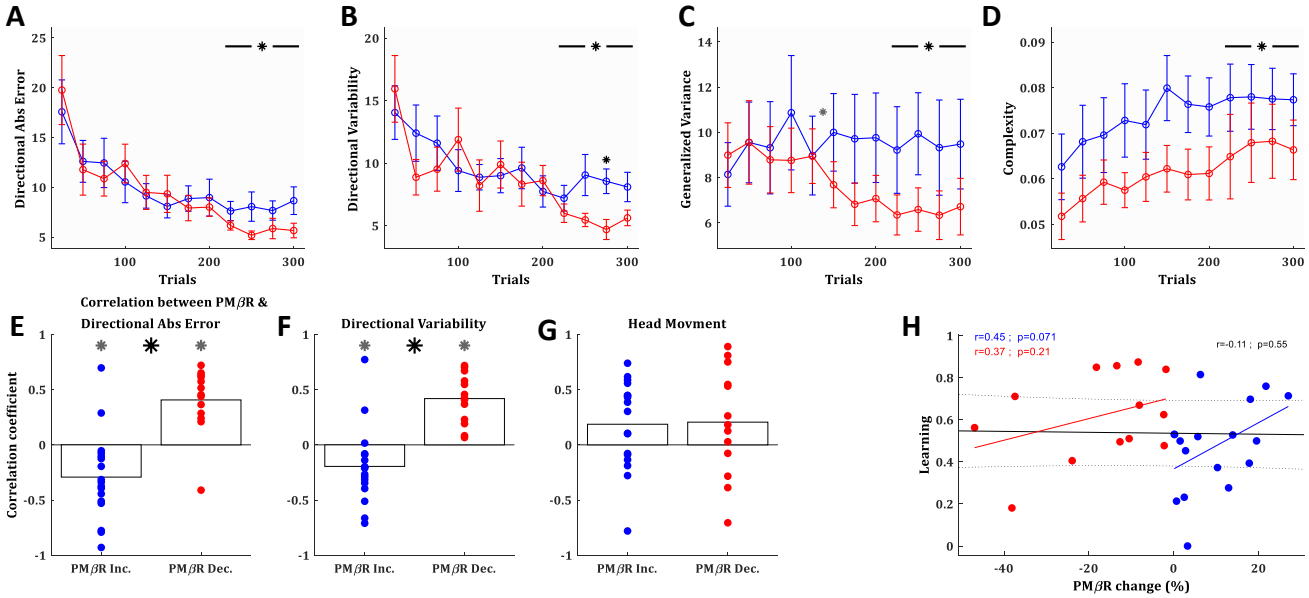

Figure 7. *Behavioural differences between the PMBR groups*. **(A-D)** Directional absolute error (**A**), directional variability (**B**), generalized variance (**C**), and manipulative complexity (**D**) of the PMBR increasers (blue) and decreasers (red) over blocks of 25 trials, averaged across all subjects in each group, error bars represent SEM. Black asterisk indicates significant difference between the groups in a block. Grey asterisk indicates significant difference between the groups in the change between blocks. Black asterisk with a line over the learning plateau indicates significant difference between the groups in the learning plateau. (**E-G**) Correlation coefficients over blocks for all individual subjects between the PMBS and the absolute directional error (**E**), the directional variability (**F**), and the head movements (**G**). Grey asterisk indicates group correlations significantly different than zero. Black asterisk indicates significant difference in the correlation coefficients between the groups. (**H**) Correlations between the PMBR change and the learning, across all subjects (black line) and within each group (blue: increases; red: decreases).

Finally, the PMBR decreasers were on average better learners (mean learning rates were 0.47 and 0.62 for the PMBR increasers and decreasers respectively) though the group difference was not significant (t test p=0.07). We explored the correlation between PMBR and learning. Across all subjects, we found no correlation between the learning rate and the initial PMBR or the PMBR change. When considering each group separately, both groups showed a clear trend (though non-significant) of positive correlation of the PMBR change with learning (Figure 7H). Meaning, for the PMBR increasers, more increase suggests more learning; for the PMBR decreasers, less decrease suggests more learning. This suggests that in the PMBR of both group there is a signature for a motor adaptation mechanism, where PMBR increase with learning, but while this is the predominant mechanism for the PMBR increasers, for the PMBR decreasers the predominant mechanism is of skill learning which have the opposing PMBR signature.

Discussion

In this paper we introduce a new paradigm for studying naturalistic motor learning during whole-body movement in a complex real-world motor skill task. Our results present new insights into motor learning in the real-world. While the learning curves in this in-the-wild paradigm are within the same range of those reported in reductionistic motor adaptation tasks (e.g. McDougle et al., 2015; Smith et al., 2006) we find that this learning is taking place not only in the task relevant joints but across the entire body. Also, we found that task relevant initial variability in the ball direction (movement outcome) can predict learning, like in toy tasks (Wu et al., 2014), and so can the initial variability in the right arm supination which is the task relevant joint angle variability. Most importantly, our neural recordings revealed two types of motor learners: PMBR increasers and PMBR decreasers. These groups were defined by their patterns of beta oscillations, which the literature link to different learning mechanism (adaptation and skill learning respectively), but also showed clear behavioral differences. PMBR decreasers were better learners, more accurate, they effectively modulated their movement variability, and they used less DoF in their movement. These is the first study to report such neurobehavioral identification of two types of learners.

Fundamentals of real-world motor learning

Across all subjects, we found that motor learning is a holistic process - the entire body is learning the task. This was evident in the decrease in the VPE and the intertrial variability over learning (Figure 4 & Fig 4 Supplement). This result should not come as a surprise considering decades of research in sport science showing this relationship. For example, baseball pitcher's torso, pelvis, and leg movements are directly associated with ball velocity (Kageyama et al., 2014; Oliver and Keeley, 2010; Stodden et al., 2006). Recently it was also demonstrated with full-body motion capture in a ball throwing task (Maselli et al., 2017). And yet, unlike baseball pitches, basketball throws, or any unconstrained overarm throw, where the whole body is moving, in a pool shot the shooting arm is doing most of the movement and there is very little body movement. Thus, the whole-body learning is not trivial and suggestive that even in arm movement toy-tasks there is a whole-body learning aspect which is overlooked.

We also found a proximal-to-distal gradient in the learning rates over the right arm joints (Figure 4). This is especially interesting in light of the well-known phenomenon of proximal-to-distal sequence in limb movements in sports science (Herring and Chapman, 1992) and in rehabilitation (Twitchell, 1951). While there are records of proximal-to-distal sequence at multiple time scales (Serrien and Baeyens, 2017), our results are the first to suggest that this gradient also occur over repetitions as part of the learning process.

Variability & learning

Intertrial variability is a fundamental characteristic of human movements and its underling neural activity (for review see Faisal et al., 2008). It was recently reported that individuals exhibit distinct magnitudes of movement variability, which are consistent across movements and effectors, suggesting an individual traits in movement variability (Haar et al., 2017). Our results show that subjects who were initially more variable tended to be also more variable after learning in many joints across the body (Figure 5E & Fig 5E Supplement) and specifically in those of right shoulder that carry most of the variance in the movement. This supports the notion that there is an individual trait in movement variability.

Intertrial kinematic variability is also thought to be critical for motor learning (e.g., Braun et al., 2009; Dhawale et al., 2017; Herzfeld and Shadmehr, 2014; Teo et al., 2011; Wilson et al., 2008). It was suggested that individuals with higher levels of task-relevant movement variability exhibit faster motor learning in both skill learning and motor adaptation error-based paradigms (Wu et al., 2014). The failures to reproduce this result in visuomotor adaptation studies (He et al., 2016; Singh et al., 2016), led to the idea that experiments with task-relevant feedback (which is common in visuomotor studies) emphasize execution noise over planning noise, whereas measurements made without feedback (as in Wu et al., 2014) may primarily reflect planning noise (Dhawale et al., 2017). This is in-line with a recent modeling work in a visuomotor adaptation study (with task-relevant feedback) in which subjects with higher planning noise showed faster learning, but the overall movement variability was dominated by execution noise that was negatively correlated with learning (van der Vliet et al., 2018). In our task there were no manipulations or perturbations, thus, task-relevant feedback was fully available to the participants. On the other hand, in real-world there is no baseline variability, and the variability was measured during early learning and therefore is probably dominated by planning noise, as subjects explore, regardless of the visual feedback. Indeed, subjects with higher variability in the target ball direction over the first block showed higher learning rates (Figure 5D). Our results straighten the link between variability and learning and are the first to show that it applies to real-world tasks. Moreover, the only joint angle that showed significant correlation between initial variability and learning was the right elbow rotation (Figure 5F & Fig 5F Supplement). Following the idea that task-relevant variability predicts learning, it would suggest that the right elbow rotation is the task-relevant joint angle to adjust during initial learning of a simple pool shoot. Indeed, guide books for pool and billiards emphasize that while shooting one should keep one's body still and move only the back (right) arm from the elbow down. While the elbow flexion movement gives the power to the shoot, the arm supination (also known as 'screwing' in billiards and measured by the elbow rotation in our IMUs setup) maintains the direction of the cue.

EEG activity predicts differences in motor learning strategy

The motor learning literature traditionally classified its toy tasks into two broad categories, motor adaptation and motor skill/sequence learning, and suggest different learning process for these categories (e.g., Doyon and Benali, 2005; Doyon et al., 2003). It was suggested that in adaptation tasks the dominant learning mechanism is model-based, guided by an internal forward model which is updated based on prediction errors; while in skill-learning tasks the dominant mechanism is model-free where the controller learns by reinforcement of successful actions (Haith and Krakauer, 2013). PMBR was reported to increase over error-based adaptation tasks (e.g. Tan et al., 2014, 2016; Torrecillos et al., 2015), and decrease (itself or its MRS correlate) over skill-learning tasks (e.g. Floyer-Lea et al., 2006; Kolasinski et al., 2019; Kranczioch et al., 2008). Since Beta oscillations are related to GABAergic activity (Hall et al., 2010, 2011; Roopun et al., 2006; Yamawaki et al., 2008) and PMBR is positively correlated with MRS-measured GABA concentration (Cheng et al., 2017; Gaetz et al., 2011), the opposing PMBR (and MRS-measured GABA) trends suggest that there might be different GABAergic mechanisms related to the different learning mechanisms. Those might be GABAergic inputs from different subcortical regions: cerebellum for the model-based adaptation and basal ganglia for the model-free skill learning (Doyon and Benali, 2005; Doyon et al., 2003). Presumably, the dominance ratio between the learning mechanisms is revealed by the trend of the PMBR over learning.

Accordingly, we looked at the PMBR as a signature of learning mechanism. In the EEG data recorded during real-world motor learning in the current study, we found two groups of subjects: PMBR increasers and decreasers. While future studies will need to capture the PMBR dynamics during learning of the same paradigm with different dominant mechanism (using feedback manipulations and constrains for example) to farther validate this approach, the behavioral differences between the groups support the notion of different predominant learning mechanism. The first group, that had low initial PMBR amplitudes and showed an increase over learning, presumably used model-based adaptation as its dominant learning mechanism. The second group, that had high initial PMBR amplitudes and showed a decrease over learning, presumably used model-free skill learning as its dominant learning mechanism. While there were no significant differences between the groups in their initial errors or in the total learning, there were clear group difference in the learning process and the learning plateau. PMBR decreasers (model-free skill learners) were more accurate at the end of learning in terms of directional error and directional variability of the target ball (Figure 7A&B). This is inline with previous studies showing that adding reward feedback can enhance motor learning in an error-based learning paradigm (e.g. Nikooyan and Ahmed, 2015). PMBR decreasers also used less degrees of freedom in their body movement (Figure 7D) and were less variable in their body movement following learning, as they decrease the overall variability of their movement (GV; Figure 7C). They also showed higher initial variability in the direction of the target ball which was quickly and drastically

suppressed in the second block (Figure 7B). This last two points suggest an active control of the exploration-exploitation trade-off, which is another support that those subjects used model-free learning (Phillips et al., 2011).

Lab-based paradigms 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 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 model-based adaptation as they learned from the directional error of the target ball in each trial, but they also performed model-free skill-learning as they learned to use the cue and their body joints while making a shot. We speculate that the PMBR increasers, who showed the neural pattern reported in motor adaptation paradigms, mostly learned from their error in a model-based motor adaptation approach, while the PMBR decreasers, who showed the neural pattern reported in skill learning tasks, used more model-free skill learning mechanism.

Conclusions

In this study we demonstrate the feasibility and importance of studying human neuroscience in-the-wild, and specifically in naturalistic real-world skill tasks. While finding similarities in learning structure between our real-world paradigm and lab-based motor learning studies, we highlight crucial differences: namely, real-world motor learning is a holistic full-body process which involves multi-modal learning mechanisms which subjects have to combine in new ways when faced with the complexity of learning in the real world, and different subjects will emphasize one 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. The volunteers, who had little to no 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. 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' full body movements with a motion tracking ‘suit’ of 17 wireless inertial measurement units (IMUs; Figure 1B), and their brain activity with a wireless EEG headset (Figure 1C). 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 1D).

Full-Body Motion Tracking. Kinematic data were recorded at 60 Hz using a wearable motion tracking 'suit' of 17 wireless IMUs (Xsens MVN Awinda, Xsens Technologies BV, Enschede, The Netherlands). Data acquisition was done via a graphical interface (MVN Analyze, Xsens technologies BV, Ensched, The Netherlands). The Xsens joint angles and position data were exported as XML files and analyzed using a custom software written in MATLAB (R2017a, The MathWorks, Inc., MA, USA). The Xsens full body kinematics were extracted in joint angles in 3 degrees of freedom for each joint that followed the International Society of Biomechanics (ISB) recommendations for Euler angle extractions of Z (flexion/extension), X (abduction/adduction) Y (internal/external rotation).

Movement Velocity Profile Analysis. From the joint angles we extracted the velocity profiles of all joints in all trials. We defined the peak of the trial as the peak of the average absolute velocity across the DoFs of the right shoulder and the right elbow. We aligned all trials around the peak of the trial and cropped a window of 1 sec around the peak for the analysis of joint angles and velocity profiles.

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 farther 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), 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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Supplementary Figures

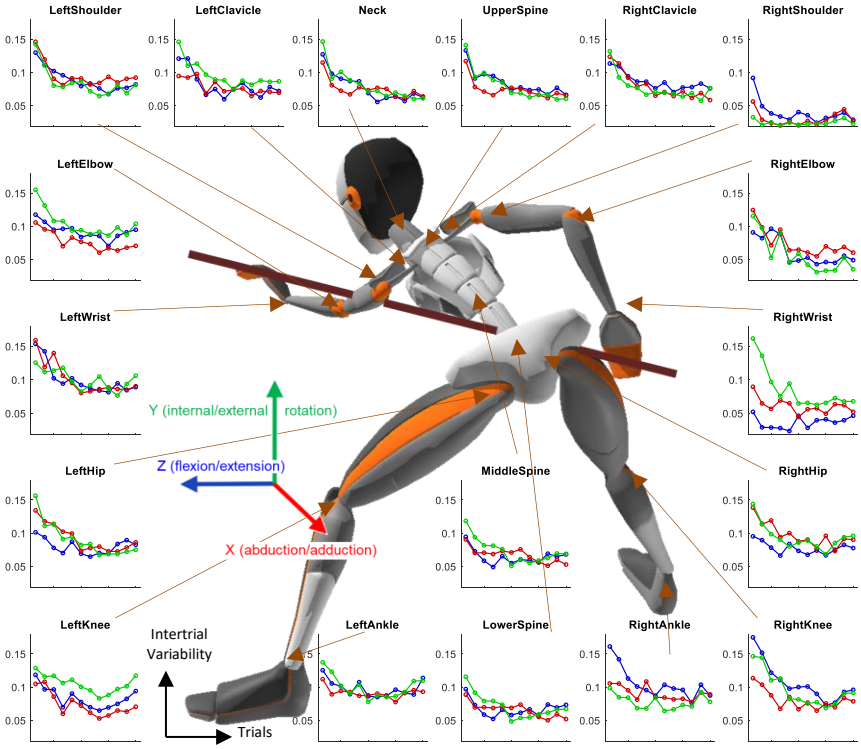

Figure 4 supp. *Learning over Joints*. Velocity Profile Error (VPE) intertrial variability over blocks of 25 trials, averaged across all subjects.

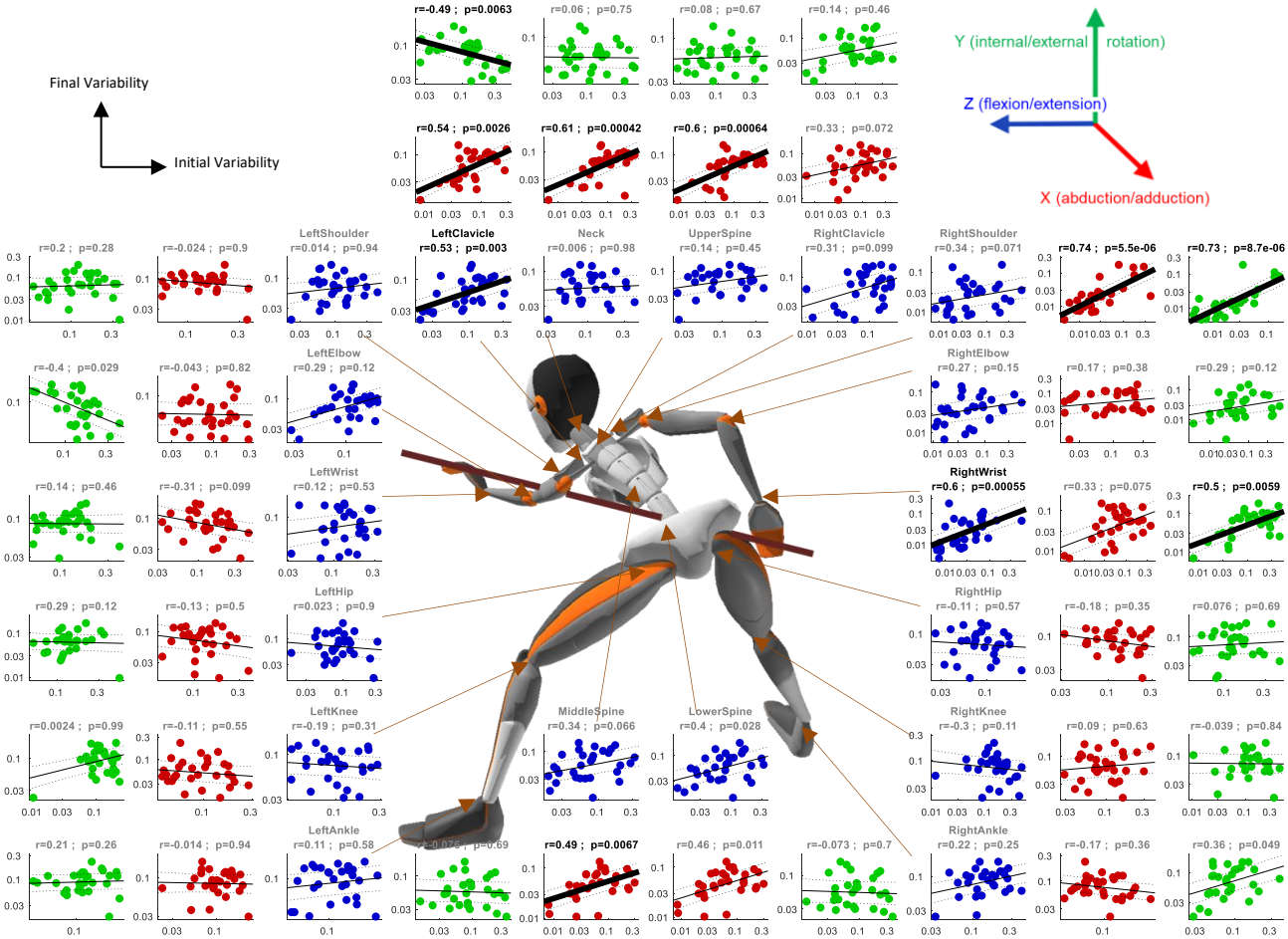

Figure 5E supp. Correlation between subjects' VPE variability over the first block and over the learning plateau, for all joints.

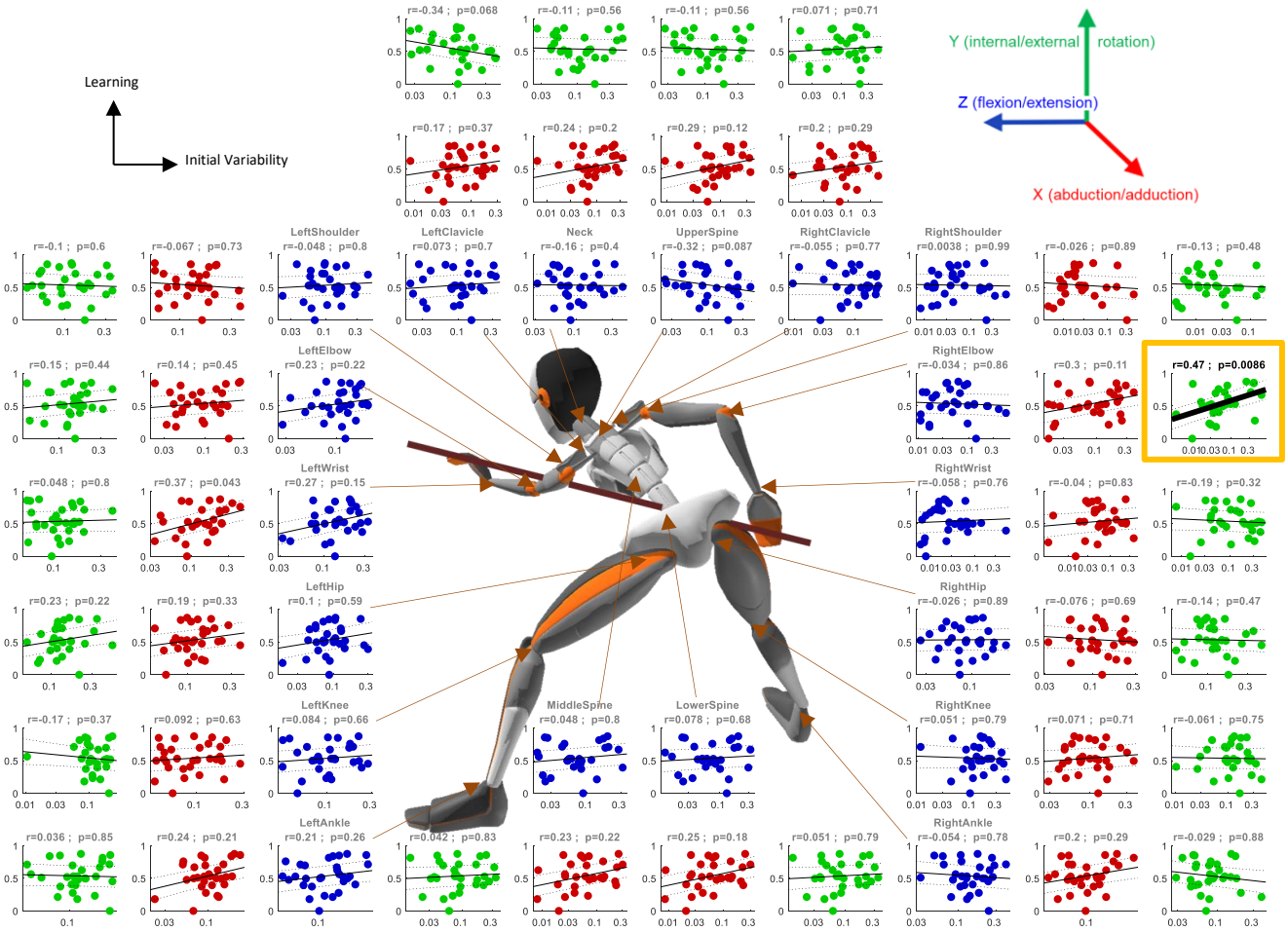

Figure 5F supp. Correlation between subjects' VPE variability over first block and their learning, for all joints.

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