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

Shlomi Haar[1,3*], Camille M. van Assel[1] & A. Aldo Faisal[1,2,3,4,5*]

1. Brain and Behaviour Lab: Dept. of Bioengineering, Imperial College London, London, UK
2. Dept. of Computing, Imperial College London, London, UK
3. Behaviour Analytics Lab, Data Science Institute, Imperial College London, London, UK
4. UKRI CDT in AI for Healthcare, Imperial College London, London, UK
5. MRC London Institute of Medical Sciences, London, UK

*** Corresponding authors:** aldo.faisal@imperial.ac.uk (AAF) and s.haar@imperial.ac.uk (SH)

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Abstract

The neurobehavioral mechanisms of human motor-control and learning evolved in free behaving, real-life settings, yet to date is studied in simplified lab-based settings. 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. Studying in-the-wild learning enable looking at global observables of motor learning, as well as relating learning to mechanisms deduced from reductionist models. The analysis of the velocity profiles of all joints enabled in depth understanding of the structure of learning across the body. First, while most of the movement was done by the right arm, the entire body learned the task, as evident by the decrease in both inter- and intra- trial variabilities of various joints across the body over learning. Second, while over learning all subjects decreased their movement variability and the variability in the outcome (ball direction), subjects who were initially more variable were also more variable after learning, supporting the notion that movement variability is an individual trait. Lastly, when exploring the link between variability and learning over joints we found that only the variability in the right elbow supination shows significant correlation to learning. This demonstrates the relation between learning and variability: while learning leads to overall reduction in movement variability, only initial variability in specific task relevant dimensions can facilitate faster learning.

Author Summary

This study addresses a foundational problem in the neuroscience: studying the mechanisms of motor control and learning in free behaving, real-life tasks, where our brains and bodies operate in on a daily basis and which contains the richness of stimuli and responses for what our nervous system evolved. We used the competitive sports of pool billiard to frame an unconstrained real-world skill learning experiment which is amenable to predictive modelling and understanding. Our data-driven approach unfolds the structure and complexity of movement, variability, and motor-learning, highlighting that real-world motor-learning affects the whole body, changing motor-control from head to toe. Crucially, we are enabling novel hypothesis driven experimental approaches to study behavior where it matters most - in real life settings.

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 (e.g. 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 (Faisal et al., 2010; 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 research 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 based toy-tasks which try to emulate real-world tasks. The other line used actual real-world tasks such as juggling (e.g. van Beers et al., 2013; 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 approach 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 playing, 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 neurobehavioral database of real-world motor learning behavior. This includes the full body movement 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 changes in the body movement and the performance in the task.

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.

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), and the balls on the pool table were tracked with a high-speed camera to assess the outcome of each trial (Figure 1C).

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 1D). The direction of the initial trials error was consistent across subjects 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 1E) 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 1F) 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 1G). Since learning also occurred 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 (while the learning curve is exponential, within the small blocks of 25 trials it is almost linear). This corrected intertrial variability showed the same pattern (Figure 1H). 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'.

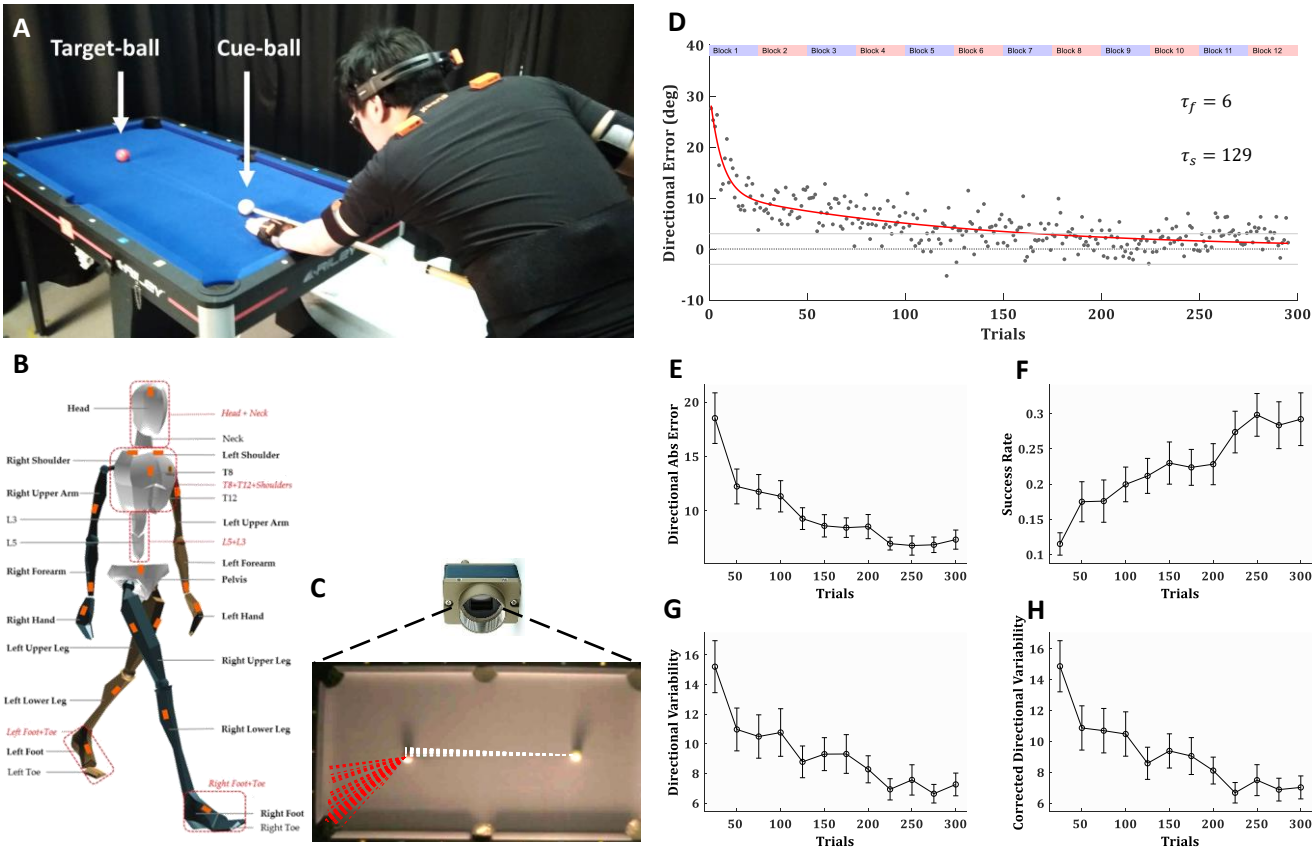

Figure 1. *Experimental setup and task performance*. (**A**) 30 right-handed healthy subjects performed 300 repeated trials of billiards shoots of the target (red) ball towards the far-left corner. (**B**) Full body movement was recorded with a 'suit' of 17 wireless IMUs (Xsens MVN Awinda). (**C**) The 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 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). Grey lines mark the range of successful trials. (**E**) The mean absolute directional error of the target-ball. (**F**) The success rates. (**G**) directional variability. and (**H**) directional variability corrected for learning (see text). (**E-H**) presented over blocks of 25 trials, averaged across all subjects, error bars represent SEM.

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 matrix over the velocity profiles of the different joints, averaged across the initial block 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 block of the learning plateau (trials 201-225) showed similar structure with an overall decrease relative to the initial trials but an increase in the variance of right elbow rotation (Figure 2C).

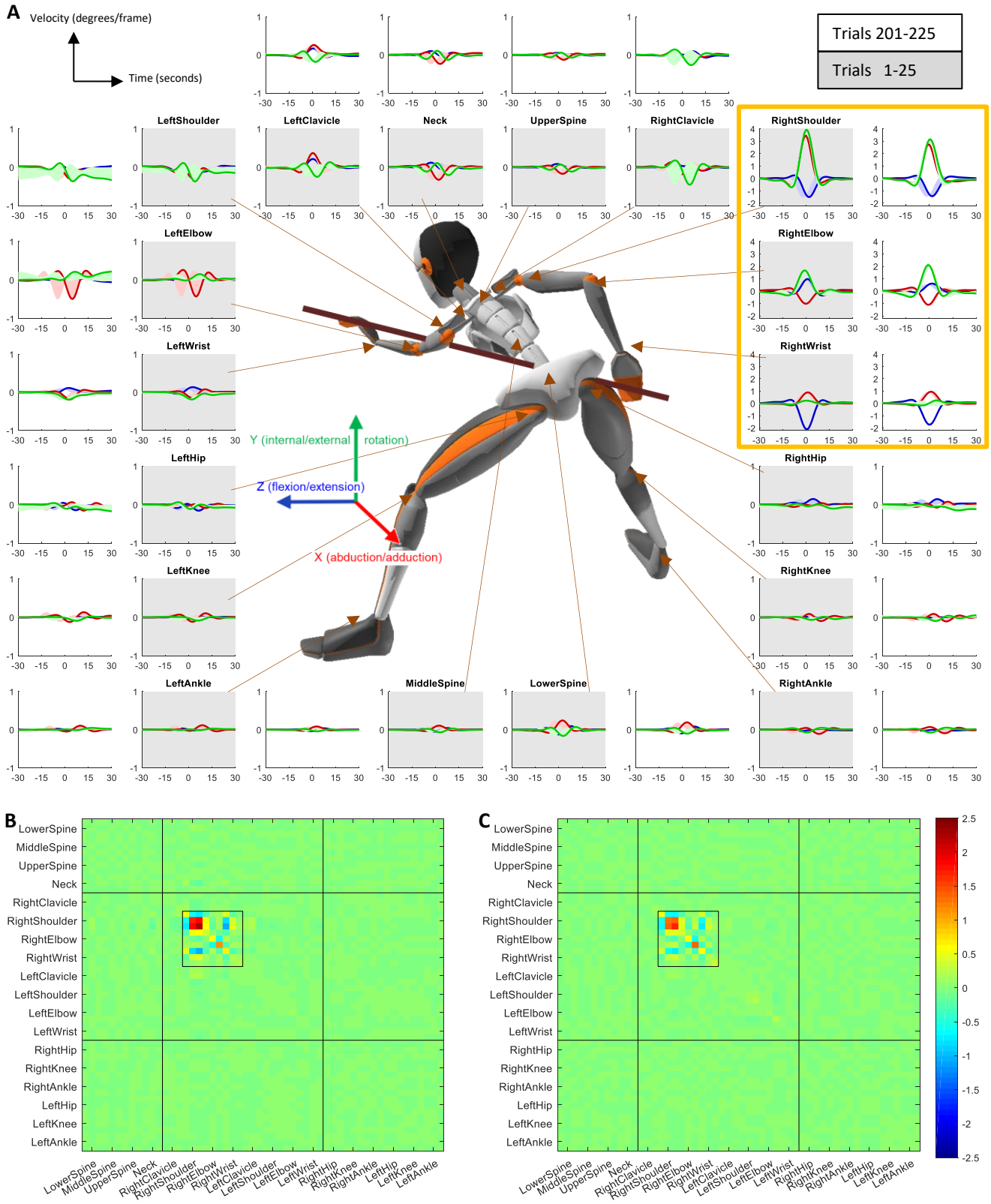

Figure 2. *Velocity profiles and covariance*. (**A**) Velocity profiles in 3 degrees of freedom (DoF) for each joint (blue: flexion/extension, red: abduction/adduction; green: internal/external rotation) averaged across subjects and trials over the first block of trials (1-25) in the inner circle (grey background) and the first block after learning plateau (201-225) 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 block (1-25) and (**C**) first block after learning plateau (201-225). The order of the DoF for each joint is: flexion/extension, abduction/adduction, internal/external rotation.

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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).

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 block, the block over the peak GV, and first block after learning plateau (Figure 3B), shows 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 that while in all trials ~90% of the variance can be explained by the first PC, there is 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, suggested by Belić and Faisal (2015) as way to quantify complexity for a given number of PCs on a fixed scale (C = 1 implies that all PCs contribute equally, and C = 0 if one PC explains all data variability), showed cleaner trajectory with the same trend (Figure 3D). This suggests that over trials subjects use more degrees of freedom in their movement.

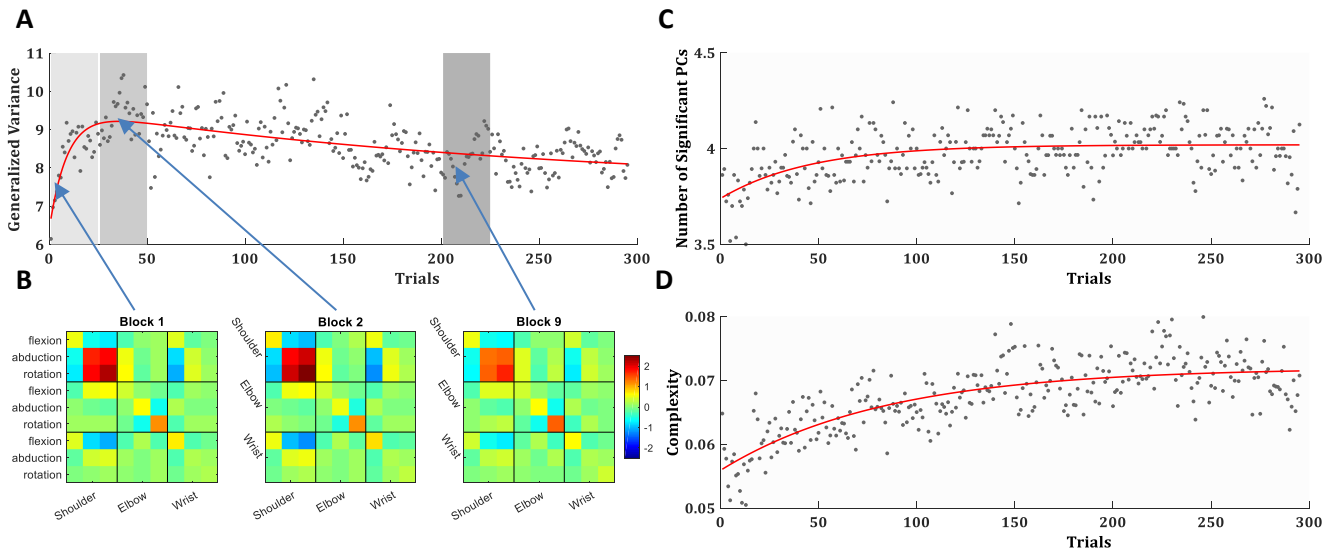

Figure 3. *Variance and Complexity*. (**A**) The trial-by-trial generalized variance (GV), with a double-exponential fit (red curve). (**B**) The variance covariance matrix of the right arm joints velocity profiles averaged across subjects and trials over the initial block (trials 1-25), the second block (trials 26-50), in which the GV peaks, and first block after learning plateau (block 9, trials 201-225). 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, we defined a measure of Velocity Profile Error (VPE) for each joint in each trial (see methods). For all joints, VPE showed a clear pattern of decay over trials in an exponential learning curve (Figure 4A). 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 (Figure 4B).

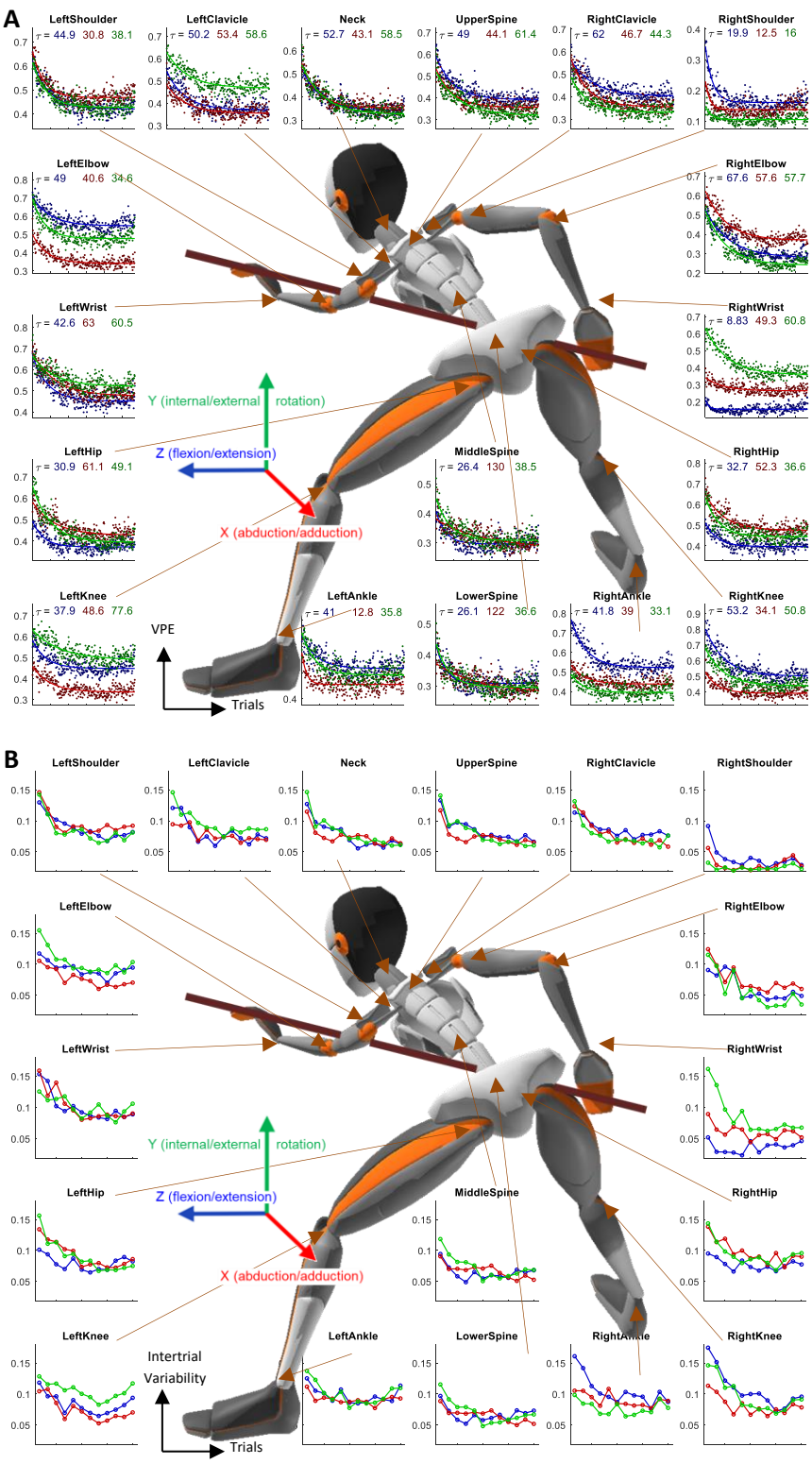

Figure 4. *Learning over Joints*. (**A**) Velocity Profile Error (VPE) reduction across all joints. The trial-by-trial VPE for all 3 DoF of all joints, averaged across all subjects, with an exponential fit. The time constants of the fits are reported under the title. The color code of the DoF is the same as in figure 2 (blue: flexion/extension; red: abduction/adduction; green: internal/external rotation). (**B**) Velocity Profile Error (VPE) intertrial variability over blocks of 25 trials, averaged across all subjects.

Inter-subject differences in variability and learning

We found substantial 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.

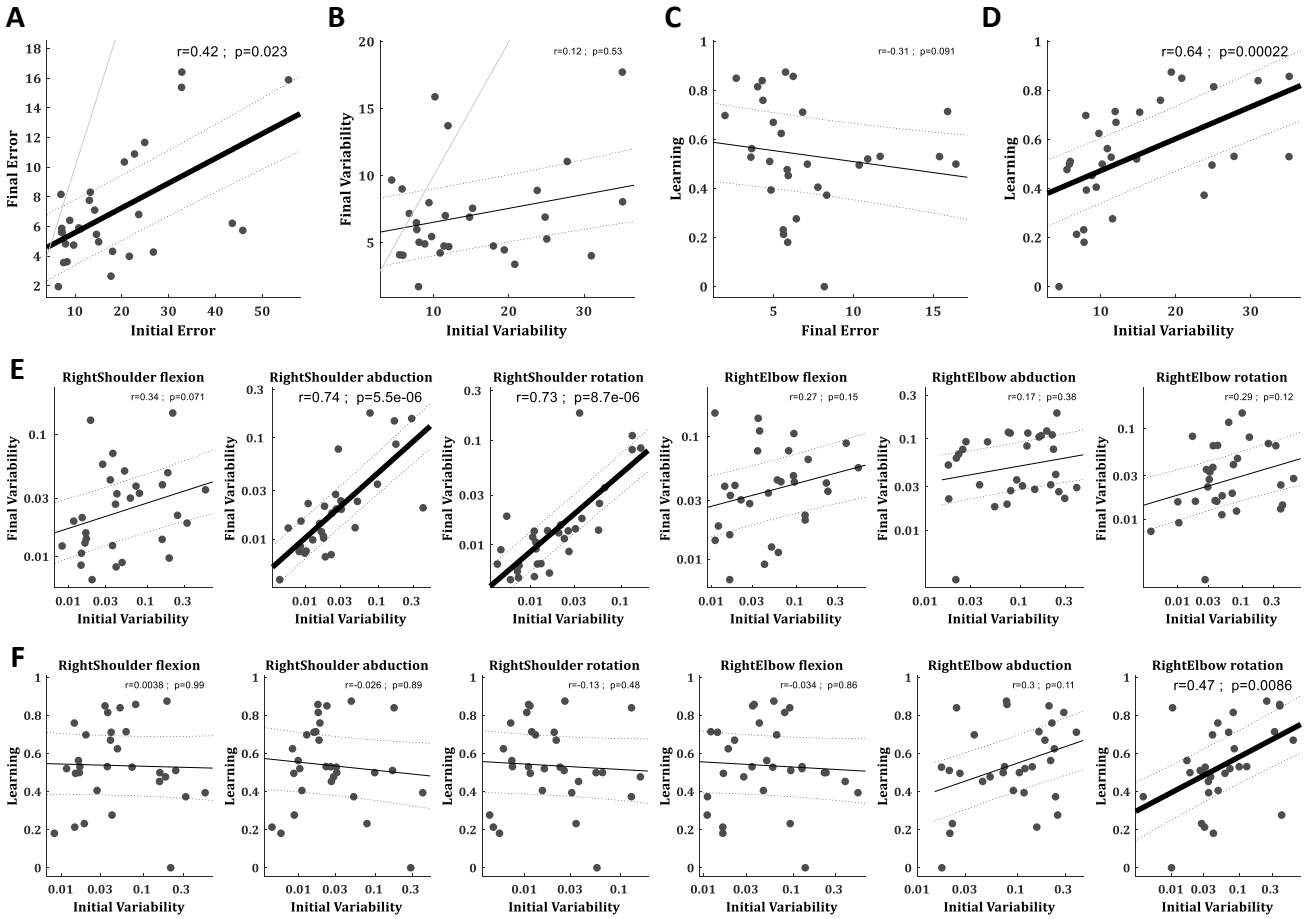

Figure 5. *Variability and learning across subjects*. (**A**) Correlation between subjects' mean absolute directional error over the first block (trials 1-25) and the learning plateau (trials 201-300). (**B**) Correlation between subjects' directional variability over first block (corrected for learning 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.

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 (Figure 4B), showed a clearer and stronger correlation between the initial and the final intertrial variability (Figure 5E & S1 Fig). 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).

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 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 (Spearman rank correlation $r=0.64$, $p<0.001$; 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. As a control we also tested for correlation with the initial variability in the target ball velocity, task-irrelevant motor variability, and found no correlation (Spearman rank correlation $r=0.06$, $p=0.77$). 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 (Spearman rank correlation $r=0.47$, $p=0.0086$), which is the arm supination. We further tested the link over the full body kinematics (S2 Fig) 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.

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.

While pushing towards real-world neuroscience, we started here with a relatively constrained version of the real-world task, asking subjects to perform repeated trials of the same pool shot. This was to enable analysis using well developed methods of laboratory studies in toy-tasks. Nonetheless, it is a major step in the direction of a naturalistic study. First, we allow full-

body unconstrained movement. Second, we do not use any artificial go cue and allow self-paced movement and as many preparatory movements as the subject needs for each shoot. Third, subjects receive natural somatosensory feedback. And last, we do not perturb the feedback to induce learning.

Fundamentals of real-world motor learning

Across all subjects, we found that motor learning is a holistic process - the body is affected as a whole from learning the task. This was evident in the decrease in the VPE and the intertrial variability over learning (Figure 4). 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 4A). 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 & S1 Fig) 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 & S2 Fig). 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.

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. Looking at the motor behavior over learning across the entire body enabled us to explore the relationship between variability and learning and define task relevant variability that can facilitate learning.

Methods

Ethics statement. All experimental procedures were approved by Imperial College Research Ethics Committee and performed in accordance with the declaration of Helsinki. All subjects gave informed consent prior participating to the study.

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). Brain activity was recorded with wireless EEG, neural findings reported elsewhere (Haar and Faisal, 2020). 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).

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.

Statistical Analysis. Trial by trial learning curves were fitted with a single or a double exponential learning curve using matlab fit function.

As a measure of task performance in body space, correlation distances (one minus Pearson correlation coefficient) were calculated between the velocity profile of each joint in each trial to the velocity profiles 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 ($velProf_i$) and the velocity profiles in successful trials s ($velProf_s$), divided by the number of successful trials (N_{scs}).

For measuring success rates and intertrial variability we divided the trials into blocks of 25 trials by dividing each experimental set of 50 trials to two blocks. This was done to increase the resolution in time from calculating those on the full sets. To improve robustness and account for outliers, we fitted the errors in each block with a t-distribution and used the location and scale parameters (μ and σ) as the blocks' center and variability measures. Similarly, all correlations between error, variability, and learning are Spearman's rank correlation coefficients. Regression lines are based on linear regression fits (in logarithmic scale for VPE variability) and are presented with 95% confidence intervals.

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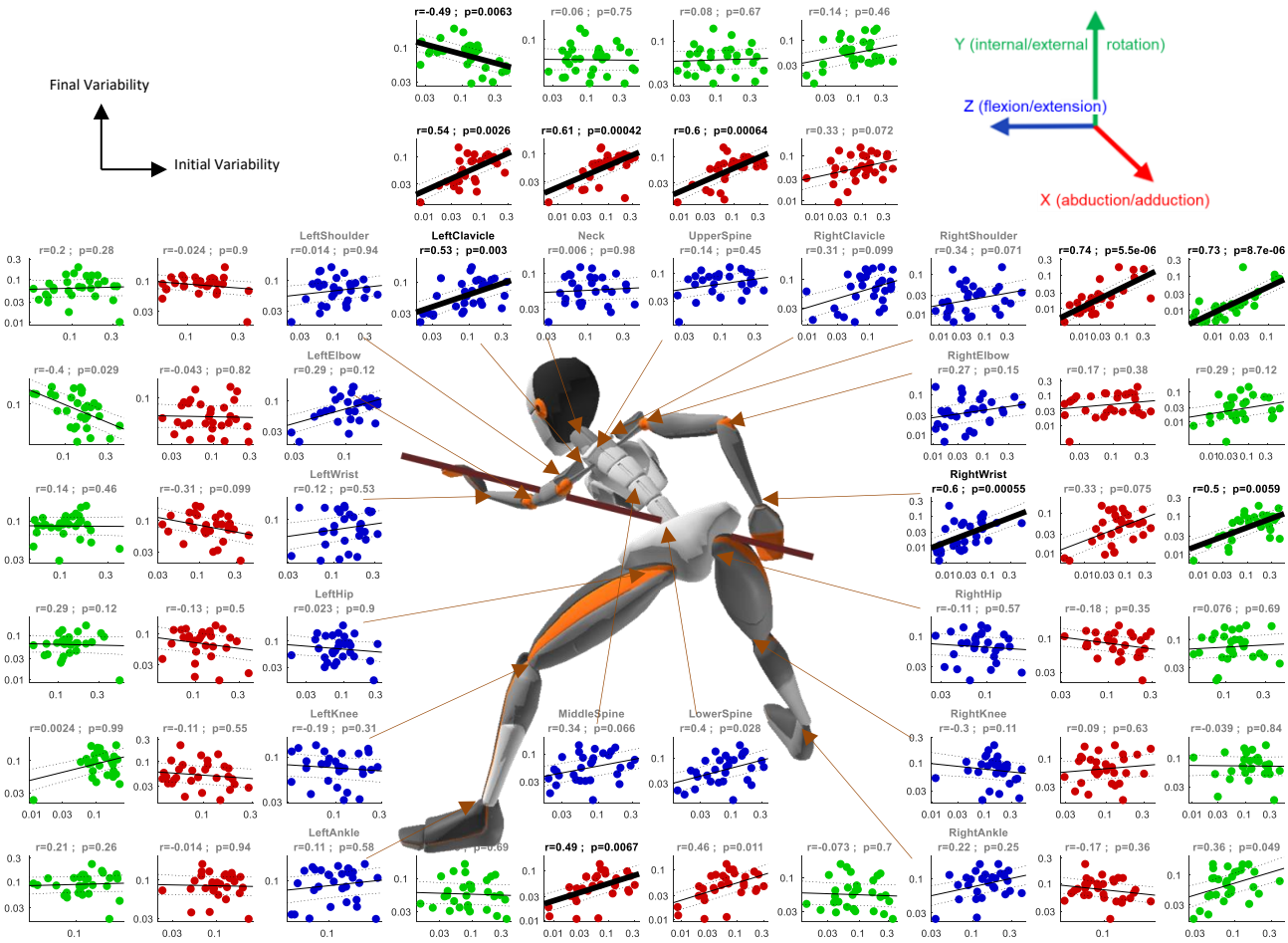
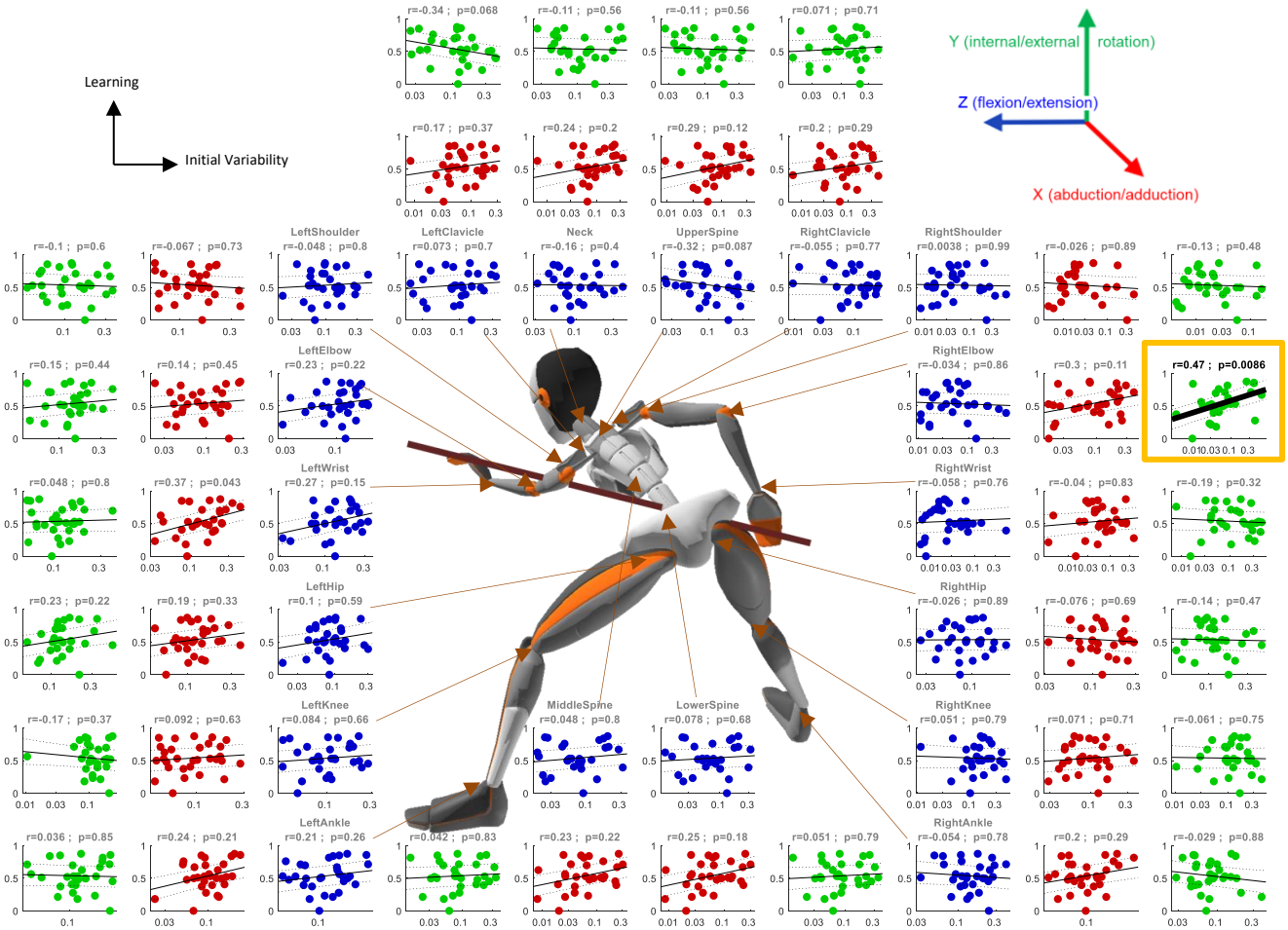
Supporting Information



S1 Fig. *Correlation between subjects' VPE variability over the first block and over the learning plateau*. Presented for all joints in 3 degrees of freedom (DoF) for each joint (blue: flexion/extension, red: abduction/adduction; green: internal/external rotation). Subjects' VPE variability is in logarithmic scale. Correlation values are Spearman rank correlation, regression lines are linear.



S2 Fig. *Correlation between subjects' VPE variability over first block and their learning*. Presented for all joints in 3 degrees of freedom (DoF) for each joint (blue: flexion/extension, red: abduction/adduction; green: internal/external rotation). Subjects' VPE variability is in logarithmic scale. Correlation values are Spearman rank correlation, regression lines are linear.

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