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Motor Variability Prior to Learning does not Facilitate the Ability to Adopt new Movement Solutions

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Abstract—Many contexts in motor learning require a learner to change from an existing movement solution to a novel movement solution to perform the same task. Recent evidence has pointed to motor variability prior to learning as a potential marker for predicting individual differences in motor learning. However, it is not known if this variability is predictive of the ability to adopt a new movement solution for the same task. Here, we examined this question in the context of a redundant precision task requiring control of motor variability. Fifty young adults learned a precision task that involved throwing a virtual puck toward a target using both hands. Because the speed of the puck depended on the sum of speeds of both hands, this task could be achieved using multiple solutions. Participants initially performed a baseline task where there was no constraint on the movement solution, and then performed a novel task where they were constrained to adopt a specific movement solution requiring asymmetric left and right hand speeds. Results showed that participants were able to learn the new solution, and this change was associated with changes in both the amount and structure of variability. However, increased baseline motor variability did not facilitate initial or final task performance when using the new solution – in fact, greater variability was associated with higher errors. These results suggest that motor variability is not necessarily indicative of flexibility and highlight the role of the task context in determining the relation between motor variability and learning.

Key words: coordination, synergy, bimanual, reorganization, redundancy, flexibility.

INTRODUCTION

The presence of motor redundancy at several levels in the human body and the task gives rise to the phenomenon that a given task goal can be achieved using multiple movement solutions. Although the evidence for how participants exploit this redundancy in the body and the task has been well described (Scholz and Schöner, 1999; Todorov and Jordan, 2002; Cusumano and Cesari, 2006; Cohen and Sternad, 2009; Ranganathan et al., 2013), the question of how 'flexible' participants are in changing from one movement solution to another is less well understood. In the current context, we define flexibility as the ability of participants to perform the task using a different movement solution from the one that they typically use. Understanding individual differences in such flexibility is critical since several contexts such as coaching and neurorehabilitation require participants to learn a new movement solution to perform the same task.

One potential feature that is relevant to predicting how flexible an individual is in adopting a new movement solution is motor variability. In task with redundancy, variability can be split into two components (Scholz and Schöner, 1999; Mosier et al., 2005; Cusumano and Cesari, 2006) – (i) 'task space' variability, i.e., the component of movement variability that affects task outcome, and (ii) 'null space' variability, i.e., the component of movement variability that does not affect the task outcome. Because flexibility is a measure of how well participants can move from one point in the null space to another, the null space variability has been hypothesized as a measure of how flexible participants are, with greater null space variability (relative to the task space variability) indicative of stronger synergies (Latash et al., 2002). More recently, motor variability has also been shown to predict individual differences in motor learning – when participants have greater variability, they can engage in more efficient exploration strategies to facilitate learning (Wu et al., 2014). Although the generality of this finding has been questioned (He et al., 2016; Singh et al., 2016), there has been support for this result in real-world tasks like pool billiards (Haar et al., 2020) and overall these results support the view that motor variability is

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not simply noise (Newell and Corcos, 1993), and can be a potential signature for predicting future motor learning (Dhawale et al., 2017).

However, in understanding the role of motor variability in predicting individual differences in learning, two issues remain unaddressed. First, the issue of flexibility (i.e., how well participants can move from one solution to another) has received little attention. A critical component for understanding this question is the use of tasks that have redundancy. Second, prior studies on using variability to predict individual differences in motor learning have primarily focused on adaptation tasks (Wu et al. 2014; He et al. 2016; Singh et al. 2016). Although adaptation is one form of motor learning, a more common form of motor learning relevant to real-world contexts is skill learning, where there is a relatively permanent change in the underlying movement capacity (Krakauer and Mazzoni, 2011; Schmidt and Lee, 2011; Sternad, 2018). One such class of skill learning tasks are precision tasks that require learning to produce a consistent outcome over multiple trials (Muller and Sternad, 2004; Cohen and Sternad, 2009; Ranganathan and Newell, 2010a; Shmuelof et al., 2012). In contrast to motor adaptation which require reduction in constant error, learning these precision tasks require a reduction in variable error, which require a fundamental change in the quality of execution of the movement (Shmuelof et al., 2012). Here, we address both these issues using a precision task that has redundancy.

The goals of this study were to (i) characterize changes in task performance and movement variability when learning a new solution to perform a task, and (ii) examine if motor variability prior to learning is predictive of motor performance when learning a new solution to a redundant motor task. Participants learned a bimanual throwing task which required participants to slide a virtual puck to a specified target. The motion of the puck depended on the sum of the speeds of the two hands, making the task redundant. We exploited the fact that participants in bimanual tasks tend to typically use symmetric (or near-symmetric) contributions from both hands (Kelso et al., 1979; MacKenzie and Marteniuk, 1985), and designed a task that required them to switch to a novel asymmetric solution to this task. We anticipated that if motor variability is predictive of individual differences in learning new solutions, then the motor variability observed at baseline (i.e., prior to the learning of the new solution) should be predictive of performance using the new solution, with higher variability being associated with better task performance (i.e. lower errors).

EXPERIMENTAL PROCEDURES

Participants

Participants were college-aged adults with no history of movement impairments in the upper extremity ($N = 50$, age 18–25 years, 40 women) and were naive to the purpose of the experiment. All participants provided written consent and the experimental protocol was approved by the Michigan State University Institutional Review Board.

Apparatus

The participants performed all the tasks on a two joint bimanual end-point robot (KINARM technologies, Kingston, ON, USA) (Fig. 1a). The position data from the two robot handles were sampled at 1000 Hz. The visual display was set up through a semi-silvered screen so that images were shown in the plane of the hands and direct vision of the hands was obstructed.

Task

The task used was a virtual shuffleboard task where the goal of the participant was to slide a virtual puck toward a target shown on the screen (Cardis et al., 2018) (Fig. 1a). At the start of each throw, participants were instructed to position both hands in a respective 'home' position. At this point, the individual hand cursors disappeared and were replaced by a circular puck at the average position of the hands. They were then asked to slide the puck toward a slot positioned straight ahead. Once participants crossed the slot, the puck was 'released' and a second screen was shown where the puck traveled towards a target in a uniformly decelerated motion. The speed of the puck at release was dependent on the sum of the speeds of the left and right hands at release (i.e., $V_{puck} = V_L + V_R$) and perfect task performance (i.e., landing on the center of the target) was achieved when $V_{puck} = 1.5$ m/s. Because the speed is dependent on both hands, multiple solutions can be used to achieve perfect task performance.

There were two versions of the task (Fig. 1b). In the 'baseline' version of the task, participants were not constrained to use any specific solutions for the task. Visual feedback of the puck was provided as a horizontal line stretching across the screen. After each throw, participants saw the position of the horizontal line and were provided a numerical score depending on the error (with a max of 100 points). In the 'novel' version of the task, participants were constrained to use a specific set of solutions. Visual feedback was provided as a circular puck. The vertical motion of the puck was identical to the motion of the line in the baseline blocks, and the horizontal dimension was controlled by the difference in the hand velocities so that a higher velocity on the right (left) hand would move the puck further to the right (left). We then constrained the solution adopted by adding a wall with a hole in a specific region. The hole was placed on the right-hand side of the screen so that participants now had to produce a higher velocity on the right hand by 0.3 ± 0.15 m/s to make the puck pass through the hole. Therefore, for the puck to pass through the center of the hole and land perfectly on the target, the combination would be $(V_R, V_L) = (0.9, 0.6)$ m/s – i.e., the $V_L + V_R$ needs to be 1.5 m/s and V_R would have to be 60% of the total speed. The scoring system was the same as the baseline blocks with the addition that if the puck collided against the wall, that trial was scored as zero points. The solution space in terms of the two-hand speeds for both the baseline and novel blocks is shown (Fig. 1c). Note that even though the 'hole' in the target was shifted to the right, the first

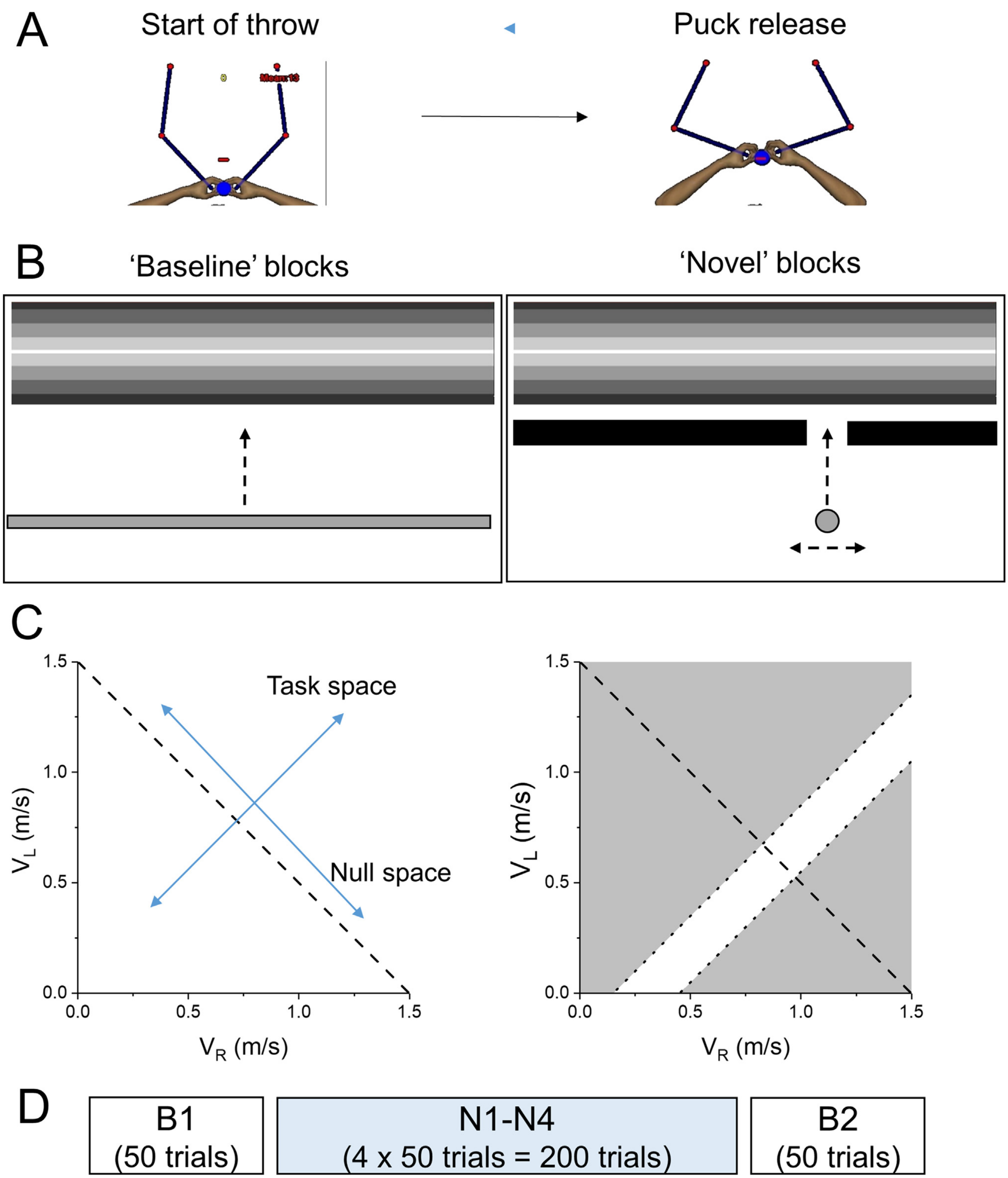

Fig. 1. Schematic of task and experiment. **(A)** Virtual shuffleboard task – participants grasped a bimanual robot and performed a throwing motion toward a slot located 10 cm away. When the puck crossed this slot, the puck was 'released' and participants saw visual feedback indicating their task performance. Note that the two arms of the robot could be moved independently (i.e., they were not mechanically coupled) **(B)** Visual feedback of task performance. During the baseline blocks, participants saw the puck as a 'horizontal' bar and a puck speed of 1.5 m/s would land the bar right on the middle of the target (indicated in white). During the novel blocks, participants saw the puck as a circle. The vertical motion of the puck was exactly the same as the horizontal bar in the baseline blocks, but the horizontal motion of the puck was determined by the difference in the right and left hand speeds. Participants had to select specific solutions to make sure that the ball passed through the hole in the wall. **(C)** Solution space in terms of left and right hand speeds. In the baseline blocks (left), the solution manifold is represented by the dotted line, which indicates the speed combination that lead to a total of 1.5 m/s. In the novel blocks (right), the presence of the hole in the wall reduces the solution manifold to a much smaller area (all areas shaded in grey would lead to a collision with the wall). **(D)** Experimental protocol. After an initial familiarization, all participants completed a baseline block **(B1)**, followed by four novel blocks (N1-N4) and a return to baseline **(B2)**.

screen that the participants saw prior to the throw had the 'slot' still straight ahead – so participants were aware that they still had to make movements in the forward direction, but adjust the relative speeds of the two hands to get the puck to move right or left on the second screen.

Procedure

Participants were first given 10 familiarization trials in both the baseline and the novel condition to make sure they understood the goal of the task, including the fact that they had to modulate the speeds of the two hands to move the puck horizontally in the novel condition. This was followed by 6 blocks of practice – a baseline block (B1), 4 novel blocks (N1–N4), and a baseline block (B2) (Fig. 1d). Each block consisted of 50 throws and the entire experiment was done in a single session that lasted about 45 min.

DATA ANALYSIS

Task performance

Absolute error. Because perfect task performance was achieved when the puck release speed was 1.5 m/s, we computed the absolute error as the absolute difference between the actual puck speed at release and the desired release speed of 1.5 m/s.

Collisions. To indicate how well participants adapted to the novel condition, we computed the frequency of trials in which the ball collided with the wall in each block (relative to the total number of trials in the block). A higher number of collisions indicated greater difficulty with changing to the novel condition. Because there was no wall in the baseline conditions, the number of collisions in the baseline blocks is zero by definition.

Coordination

Speed ratio. The coordination in this task was measured as the contribution of the right hand to the puck speed – i.e., $V_R/(V_R + V_L)$. As mentioned earlier, in the baseline blocks, there was no constraint on the coordination, but a symmetric contribution from both hands would result in a ratio of close to 0.5. During the novel blocks, given the position of the obstacle, this ratio had to be close to 0.6 for the puck to pass through the center of the hole.

Variability measures

Movement variability. In each block, we split the movement variability along two orthogonal dimensions- the task space and the null space (as shown in Fig. 1c). Each trial was represented as a point in this 2D space and projected to the task and null space. The variability along each of these dimensions was calculated using the variance (in m^2/s^2) and is referred to as the task and null space variability (Cardis et al., 2018).

Autocorrelation. In addition to the amount of variability, we also computed the lag-1 autocorrelation in the task and null spaces as a measure of the structure of variability (Abe and Sternad, 2013; Dingwell et al., 2013; van Beers et al., 2013; Cardis et al., 2018). Each trial, represented by a point in the (V_L, V_R) space was projected on to the task space and the null space and the time series of these two projections was used for the autocorrelation analyses. A positive lag-1 autocorrelation indicates that deviations tend to persist over time, whereas a negative lag-1 autocorrelation indicates that a positive deviation is more likely to be followed by a negative deviation on the next trial.

In addition, we also computed a 'detrended' autocorrelation after removing the linear trend in the data. Because this was a learning task, where changes in mean performance are to be expected within each block, this analysis allowed us to evaluate the trial-to-trial fluctuations while minimizing the effects of any overall shift.

Statistical analysis

Learning a new solution. We first quantified the learning in the task by observing changes over the practice blocks. For all dependent variables except collisions, this was analyzed by a one-way repeated-measures analysis of variance (ANOVA) with block as the fixed effect (6 levels- B1, N1, N2, N3, N4 and B2). We performed three a priori comparisons related to this ANOVA by comparing the following blocks: (i) B1 and N1 (i.e., what happens when participants initially switch to the new solution), (ii) N1 and N4 (i.e., what happens when they learn the new solution), and (iii) N4 and B2 (i.e., what happens when they change from new solution back to baseline). Corrections for violation of sphericity were performed using the Greenhouse-Geisser correction when appropriate. The level of significance was set at 0.017 (corrected for the three comparisons). For the analysis of collisions, which only occurred in the novel blocks, we used a paired *t*-test to compare the collisions in N1 and N4. All analyses were run in JASP version 0.9 (JASP Team, 2018).

Predicting individual differences. The primary focus was to examine if the initial and final performance on the novel task could be predicted by motor variability at baseline. Here, we use the term 'prediction' in the context of whether performance in the novel task is correlated with prior performance in the baseline task (which was performed earlier in time). So we examined Pearson's correlations between: (i) absolute error in N1 with task space and null space variability in B1, and (ii) absolute error in N4 with task and null space variability in B1. Given that there is prior evidence that higher variability facilitates learning (Wu et al., 2014), we used a Bayes factor (using a default stretched beta prior width of 1) to quantify the strength of the hypothesis that this correlation was negative (i.e., increased variability was associated with smaller errors).

In addition, we also computed if the final performance on the novel task could be predicted using the variability on the first block of the novel task and computed the correlation between absolute error in N4 with the task and null space variability in N1. Since we examined a total of six correlations, we chose a Bonferroni correction so that the significance threshold was set at 0.0083. Since there was a pair of correlation coefficients (one correlation with the task space variability and one with the null space variability), we also compared these two correlation coefficients using the cocor package (Diedenhofen and Musch, 2015) to examine if the correlation in one space was bigger than the other. Finally, we noticed that the correlations did not satisfy the assumption bivariate normality (as measured by a Shaipro-Wilk's test) – so we performed a bootstrap analysis and generated 95% CIs for these six correlations. The bootstrap analyses were performed in SPSS for Windows (version 26).

RESULTS

Based on Tukey's boxplots of the absolute error in B1, data from two participants was excluded from analysis. Both individuals had higher error in B1 than the Tukey's criterion.

Learning a new solution

The mean score that participants received generally increased with practice, except when they first switched to the new solution (Fig. 2a). Even though the absolute error is technically only one component of task performance when learning the new solution (the score that participants received also depended on whether they successfully avoided the barrier), we found that the mean absolute error was highly negatively correlated to the mean score that the participants received, both in N1 ($r = -0.884$) and N4 ($r = -0.922$). Therefore, we focus our analysis on the absolute error as it is more easily interpretable (being in units of m/s) than the score.

Participants showed an increase in absolute error when using the new solution. This error decreased with continued practice and was retained in the second baseline (Fig. 2b). There was a significant main effect of block ($F_{3.15,148.21} = 23.07$, $p < 0.001$). Comparisons indicated that absolute error in B1 was not significantly different from N1 ($p = 0.068$), absolute error in N4 was lower than N1 ($p < 0.001$) and there was no difference between N4 and B2 ($p = 0.227$). To examine if the increase in error from B1 to N1 was due to averaging over the entire block of 50 trials, we performed a secondary analysis where we examined the change in error from the last 10 trials of B1 to the first 10 trials of N1, and found that there was a significant increase in error going from B1 to N1 ($t_{47} = 4.446$, $p < 0.001$). The improvements in task performance using the new solution (from N1 to N4) were also reflected in a decrease in the number of collisions ($t_{47} = 6.30$, $p < 0.001$) (Fig. 2c).

In terms of the coordination, participants showed a change in the speed ratio during the novel blocks but this returned to the original coordination pattern in the second baseline (Fig. 2d). There was a significant main effect of block $F_{3.03,\ 142.44} = 377.7$, $p < 0.001$). Comparisons indicated that the right hand ratio increased between B1 and N1 ($p < 0.001$), decreased from N1 to N4 ($p < 0.001$), and then decreased again from N4 to B2 ($p < 0.001$).

In terms of task space variability, there was a general decrease in variability across practice (Fig. 3a–d). There was a significant main effect of block ($F_{2.83,133.10} = 8.70$, $p < 0.001$). Comparisons indicated that task space variability (i) was not significantly different between B1 and N1 ($p = 0.835$), (ii) decreased from N1 to N4 ($p < 0.001$), and (iii) was not significantly different between N4 and B2 ($p = 0.592$) (Fig. 3e).

In terms of null space variability, there was an increase in null space variability at the start of novel task, followed by a general decrease until the end of the last novel block, and a sudden decrease when going back to the baseline (Fig. 3e). There was a significant main effect of block ($F_{2.70,126.88} = 47.31$, $p < 0.001$). Comparisons indicated that null space variability (i) increased from B1 to N1 ($p < 0.001$), (ii) decreased from N1 to N4 ($p < 0.001$), and (iii) decreased from N4 to B2 ($p < 0.001$).

In terms of the task space autocorrelation, there was an increase in the lag-1 autocorrelation at the start of the novel task, followed by a general decrease until the end of practice (Fig. 3f). There was a significant main effect of block ($F_{5,\ 235} = 8.18$, $p < 0.001$). Comparisons indicated that the autocorrelation (i) increased from B1 to N1 ($p < 0.001$), (ii) decreased from N1 to N4 ($p = 0.004$), and (iii) was not significantly different between N4 and B2 ($p = 0.599$).

In terms of the null space autocorrelation, there was no significant change in the structure during practice ($F_{5,\ 235} = 0.272$, $p = 0.928$) (Fig. 3f).

Predicting individual differences

Initial learning on the task. Task space variability at baseline was weakly and positively correlated to the initial error at the novel task, indicating that higher variability at baseline was associated with worse initial task performance (Fig. 4a). Absolute error at N1 was significantly positively correlated with task space variability at B1 ($r = 0.398$, 95% bootstrap CI [0.083, 0.645], $p = 0.005$) but the correlation with null space variability at B1 ($r = 0.324$, 95% bootstrap CI [0.078, 0.625], $p = 0.025$) did not meet the Bonferroni corrected level of significance (Fig. 4b). The difference between these two correlation coefficients was not significant. Bayes factors for these correlations (task space: BF = 20.33, null space: BF = 17.30) indicated very strong support against the hypothesis that the correlation was negative (i.e., the hypothesis that higher baseline variability resulted in lower initial errors in the novel task).

Final learning on the task. Task space and null space variabilities at baseline were not correlated with final

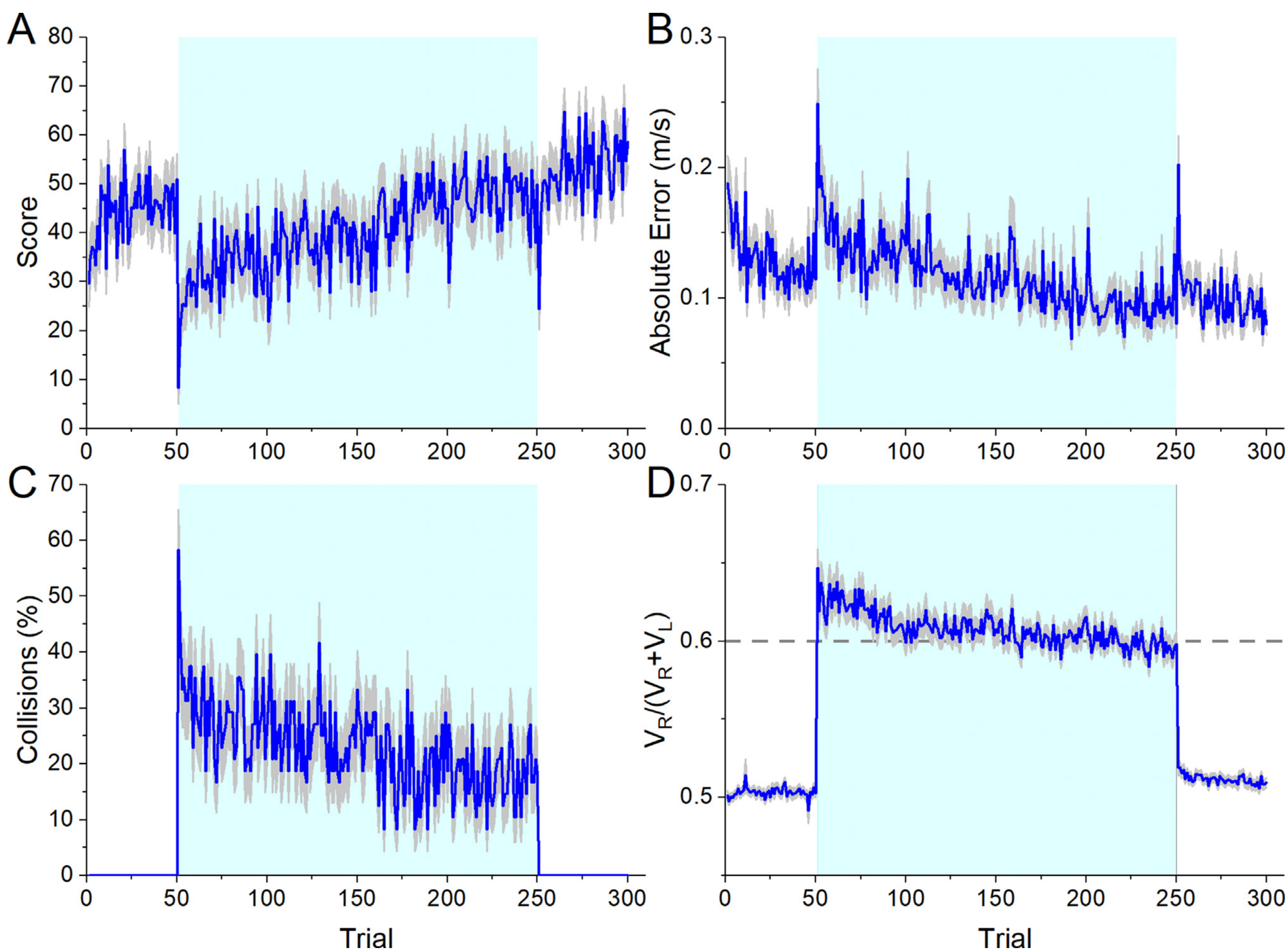

Fig. 2. Task performance and coordination during practice. **(A)** Score, **(B)** absolute error, **(C)** number of collisions, and **(D)** contribution of the right hand to the total puck speed are shown as a function of practice. Trials in the novel condition (trials 51–250) are highlighted in blue. Participants were able to adapt to the new solution as indicated by an increase in the score, reduction in absolute error, decrease in the number of collisions, and adjusting the right hand contribution to the ideal level of 0.6. Error bars indicate one standard error (between-participant).

performance on the novel task (Fig. 4c, d). The correlation of final errors at N4 with task space variability at B1 (r = 0.326, 95% bootstrap CI [0.037, 0.566], p = 0.024) and with null space variability at B1 (r = 0.249, 95% bootstrap CI [−0.053 0.583], p = 0.088) did not meet the Bonferroni corrected level of significance. Once again, the difference between these two correlation coefficients was not statistically significant. Bayes factors for these correlations (task space: BF = 17.37, null space: BF = 14.29) indicated very strong support against the hypothesis that the correlation was negative (i.e., the hypothesis that higher baseline variability resulted in lower final errors in the novel task).

When we examined if the final performance at the novel task could be predicted by task and null space variabilities during the first block of the novel task (instead of the baseline), we found strong positive correlations, indicating that higher variability in the initial block were associated with higher errors (Fig. 4e, f). The correlations of final errors at N4 with task space variability at N1 (r = 0.751, 95% bootstrap CI [0.554, 0.868], p < 0.001) and null space variability at N1 (r = 0.447, 95% bootstrap CI [0.238, 0.663], p = 0.001) were significant. The difference between these two correlation coefficients was also significant with a higher correlation for the task space variability (p = 0.01).

Exploratory analysis. We also performed some exploratory analysis on the data. Given that these analyses were not the predicted effects of interest, these analyses are reported as is, with no corrections to the significance values.

Comparing normalized values of the null space variability. Given that the amount of null space variability is correlated to the total variability, we examined if the 'normalized' null space variability would have a positive correlation to initial or final performance. So, we computed a normalized null space variability metric $Var_{null,norm} = Var_{null}/(Var_{task} + Var_{null})$. However, the correlation of the normalized null space variability at baseline was not significant either with the absolute error at N1 (r = 0.080, p = 0.589) or N4 (r = −0.026, p = 0.862).

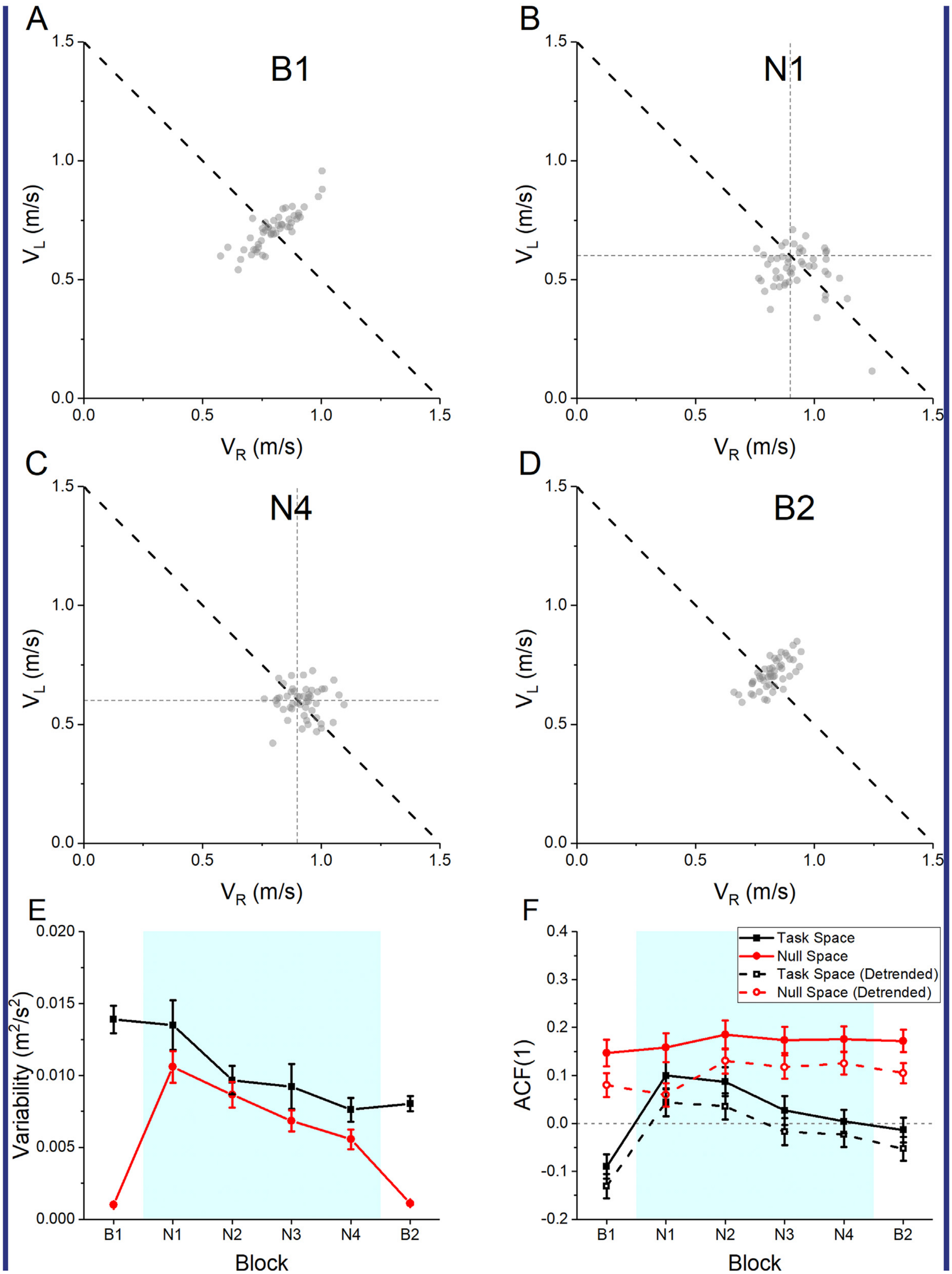

Fig. 3. Magnitude and structure of variability with practice. **(A–D)** Sample trials from one participant in block B1, N1, N4 and B2. The solution manifold is represented by the dotted line, which indicates the speed combination that lead to a total of 1.5 m/s. The horizontal and vertical reference lines from the axes in **(B, C)** indicate the solution in the novel task. **(E)** Task and null space variability with practice. Task space variability showed a general reduction with practice. On the other hand, null space variability showed a marked increase in the novel conditions. **(F)** Autocorrelation. The structure of variability was computed using a lag-1 autocorrelation, both with the actual time series (solid lines), and a detrended time series (dashed lines). In the task space, there was a marked increase in the autocorrelation in the novel conditions, but the null space showed no specific trend across practice. Error bars indicate one standard error (between-participant).

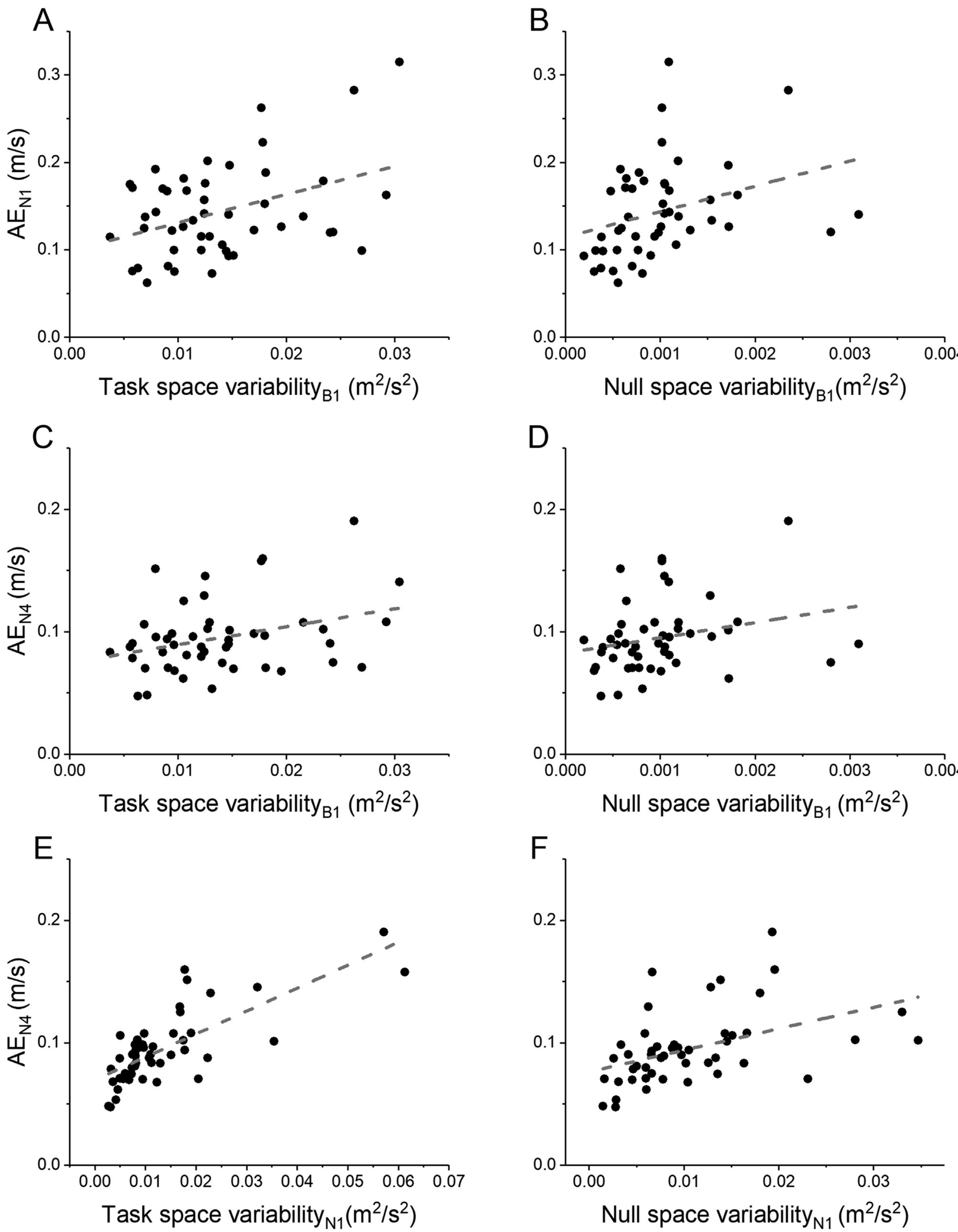

Fig. 4. Predicting individual differences in initial and final error from movement variability. **(A)** Task space variability at baseline was weakly positively correlated with initial error on the novel task (block N1), indicating that individuals showing higher variability had higher initial errors. **(B)** Null space variability had a non-significant correlation with the initial error at N1. When predicting the final error on the novel task (block N4), these correlations were not significant either for movement variability at baseline in either **(C)** task space or **(D)** null space. However, a strong positive correlation was observed when correlating the final errors (block N4) to the movement variability in the novel task (block N1) for both the **(E)** task space and **(F)** the null space. Once again, these correlations were positive, indicating that individuals with higher variability at the start tended to have higher errors on the task at the end.

Comparing B2 with B1. We examined if the performance in the second baseline block relative to B1using paired t-tests. We found that although the speed ratio in B2 was significantly higher than the speed ratio in B1 (0.512 vs. 0.503, $t_{47} = 5.368$, $p < 0.001$). In terms of absolute error, the error in B2 was significantly lower than B1 (0.1 m/s vs. 0.13 m/s, $t_{47} = 7.050$, $p < 0.001$). This indicates that during the second baseline block, there was a tendency to return to the symmetric coordination pattern, but this reversion in the coordination was incomplete. However, in spite of this change in the coordination pattern used, participants were able to maintain the improved level of task performance (when combined with the result that the absolute error in B2 was comparable to that in N4). This indicates that there was a transfer of learning from the novel asymmetric solution to the symmetric solution. Given the exploratory nature of these results, these are not mentioned further in the Discussion.

Correlations with other variables. Since our main variable was absolute error (which measures how well they could 'use' the new solution after moving to the new solution), we also performed exploratory analyses to examine if the baseline variability was correlated with the ability to move to the new solution (i.e., the number of collisions or the speed ratio). None of these correlations were significant (Table 1).

Another factor that could have potentially influenced the results is whether the number of trials we used to perform the analysis in block N1 could have failed to capture any short-term changes when they first moved to the new solution. So we examined the correlations between the baseline variability and the absolute error/score when we considered only the first 10 or 25 trials of N1 (instead of all 50). In all cases, we found that correlations were of the same sign and got stronger with more trials being included in N1, indicating that there was no evidence of any short-term behavior that was not captured with using all 50 trials (Table 2).

DISCUSSION

The goals of this study were – (i) to characterize changes in task performance and movement variability when moving to a new solution to perform the task, and (ii) to examine if movement variability at baseline could predict the ability to perform the task using a new solution. Overall, we found that (i) moving to a new solution resulted in changes in task performance and also in the amount and structure of movement variability, (ii) increased movement variability at baseline did not facilitate either initial or final performance levels when performing the task using a new solution.

Table 1. Exploratory correlations between the baseline variability (block B1) and the collisions and speed ratio variables during the first block (block N1) and last block (block N4) of the novel task

			Pearson's *r*	*p*
Task space variability_B1	-	Collisions_N1	0.237	0.104
	-	Collisions_N4	0.265	0.068
	-	Speed Ratio_N1	0.054	0.717
	-	Speed Ratio_N4	−0.037	0.804
Null space variability_B1	-	Collisions_N1	0.199	0.175
	-	Collisions_N4	0.111	0.453
	-	Speed Ratio_N1	0.028	0.848
	-	Speed Ratio_N4	−0.159	0.282

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Table 2. Exploratory correlations between the baseline variability (block B1) and the Absolute Error and Score in the first block (block N1), when varying the number of trials considered in N1

			Pearson's *r*		*p*
Task space variability_B1	-	Absolute Error_N1_Trials1to10	0.271		0.063
	-	Absolute Error_N1_Trials1to25	0.323	*	0.025
	-	Absolute Error_N1_All trials	0.398	**	0.005
	-	Score_N1_Trials1to10	−0.197		0.180
	-	Score_N1_Trials1to25	−0.291	*	0.045
	-	Score_N1_All trials	−0.291	*	0.044
Null space variability _B1	-	Absolute Error_N1_Trials1to10	0.180		0.220
	-	Absolute Error_N1_Trials1to25	0.273		0.061
	-	Absolute Error_N1_All trials	0.324	*	0.025
	-	Score_N1_Trials1to10	−0.100		0.500
	-	Score_N1_Trials1to25	−0.278		0.056
	-	Score_N1_All trials	−0.300	*	0.038

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Changes in movement variability when learning a new solution

We found that learning a new solution was associated with several features. From a task performance standpoint, there was an increase in absolute error which was then gradually reduced with practice. This was also associated with an increase in the null space variability (not only in absolute terms but also in relative terms to the task space variability) indicating that participants were exploring the null space to find the new solution. This null space variability decreased with additional practice but was still much higher than what was observed in both the first and second baseline blocks. This effect is particularly surprising because in the novel blocks, the solution space was restricted and therefore the null space variability was at least partially relevant to task performance (since excessive deviations along the null space could lead to collisions with the obstacle). These suggest that the presence of higher null space variability, by itself, is not always "good" and may potentially reflect the difficulty the task (Scholz et al., 2001; Latash, 2010) or the use of a solution that is not particularly stable (Ranganathan and Newell, 2013).

In addition to the amount of variability, there were also changes in the structure of the variability as measured by the lag-1 autocorrelation function in the task space. The lag-1 autocorrelation in the task space is an index of how errors on the previous trial are being used to correct the next trial, and this was negative in the baseline condition, which is typical for novice performance. However, when moving to the new solution, this lag-1 autocorrelation became positive, indicating that participants likely placed less emphasis on immediately correcting task errors when they were trying to learn the new solution. However, with practice, the lag-1 autocorrelation once again became closer to zero, likely indicating that participants might be using a learning rate that minimizes the overall variance (van Beers et al., 2013). Surprisingly, we found no effect of the novel task on the autocorrelation in the null space (even though participants had feedback in the null space during the novel task from the left/right motion of the puck), suggesting that the sudden increase in the task space autocorrelation was not due to changes in how participants corrected deviations in the null space. The same pattern of results in the lag-1 autocorrelation was also seen when we analyzed the detrended data (i.e. after removing any linear trend in the data) – so these changes likely reflect actual trial-to-trial dynamics and are not driven by the overall mean shift during learning.

Predicting individual differences

Given that a prior study (Wu et al., 2014) had shown that rates of learning were positively correlated with variability, we had expected that correlations would be negative – i.e., initial errors would be smaller for individuals with higher null space variability at baseline (note that in our study, the null space variability is the 'task relevant' dimension in the terminology of Wu et al. because this is the intended direction along which exploration should occur to find the new solution). However, we found that the opposite was true – higher null space variability (as well as task space variability) was associated with higher errors, indicating that individuals with greater variability showed lesser ability to produce a consistent outcome using the new solution. This was also seen in the correlations for final performance using the new solution. Exploratory analyses revealed that when the null space variability in the baseline task was normalized to total variability, there was no significant correlation with performance, indicating that the total amount of variability was more critical in predicting performance when using the new solution.

We did find a strong 'specificity' effect when predicting the final performance at the novel task – movement variability when initially learning the task was highly predictive of final performance using the new solution. But these correlations were once again positive, indicating a detrimental role for variability in learning a new solution. Overall, these results highlight that in the current context, motor variability (both at baseline and the initial learning of the new solution) was more indicative of 'noise' in the nervous system – individuals with higher variability showed slower exploration to the new solution and continued to have higher errors in the task. On the other hand, individuals with lower movement variability at baseline were actually 'more flexible' – i.e., not only did they perform the task better at baseline, they could also adapt to the new movement solution more easily.

We wish to clarify two issues about the learning and exploration in the current context. Given that focus of the current work was on understanding flexibility, our experimental paradigm focused on two aspects – (i) moving to a different solution (i.e., a different point in the null space), and (ii) controlling the variability around this new solution. Therefore, the learning and exploration observed in this task reflected both components. For example, participants not only had to produce a sufficient difference between the hand speeds to avoid the puck hitting the wall but also had to simultaneously control the sum of the speeds so that the puck landed on the target. This exploration was long-lasting throughout the experiment as seen by the gradual reduction in absolute error and collisions, and also a sustained increase in the null space variability. A second issue is that given our interest was in the flexibility to adopt 'novel solutions', we made the novel solution relatively 'far away' from the baseline solution (relative to the baseline variability). In other words, because the new solution was significantly far away from the baseline solution, participants in our task could not accidentally 'stumble upon' the new solution but instead had to actively direct their search toward a new solution that was different from their current solution. Therefore, the exploration seen here is likely distinct from reinforcement paradigms where the new solution is typically very 'close' to the original solution in terms of the variability.

Three issues are critical when considering these findings in the context of prior work – the measurement of variability, the measure of learning, and the role of the task. From the viewpoint of measurement of variability, a central problem in understanding the role of motor variability is to distinguish 'noise' from 'exploration' (Therrien et al., 2016). Dhawale and colleagues (Dhawale et al., 2017) attempted to reconcile the somewhat contradictory findings of a meta-analysis on variability (He et al., 2016) by hypothesizing that one critical difference may be related to measuring variability in the presence or absence of feedback. Specifically, measuring variability with task relevant feedback could reflect the 'noise' component whereas variability measured without feedback yielded the true 'exploratory' component. Our experiment provided a unique test of this hypothesis because the task space variability had feedback, whereas the null space variability in the baseline conditions did not. However, both components of variability showed positive correlations with errors in the task, suggesting that this difference cannot fully account for such discrepancies in the results. Other approaches have highlighted the importance of the temporal structure of variability in predicting motor learning - for example, by using measures of statistical persistence (Barbado Murillo et al., 2017; Beaton et al., 2017). With the very short time series in our baseline data, we were unable to test this hypothesis, but could be explored in future work.

The second issue relates to the measure of learning – given our definition of flexibility as the "ability" to perform using a different movement solution, the focus of the current study was on correlating the baseline variability to the 'level' of performance (i.e., the mean error in the initial and final blocks) whereas prior studies have focused on the 'rate' of learning. We had two justifications for this choice: (i) estimating true rates of learning (for e.g. through exponential fits) in precision tasks is extremely challenging because there is not a steady decrease in error over trials (i.e., because the focus of such tasks is on reducing variability, a trial with low error may immediately be followed by a trial with high error and vice versa), (ii) using proxy measures for rates of learning (for e.g. using a change score) can be problematic because they can create spurious correlations with the baseline score due to mathematical coupling and ceiling effects (Hawe et al., 2019). For example, in our data, the correlation between the performance at the start of the novel task (i.e., the absolute error in N1) and the 'gain score' (i.e., the difference in absolute error between N1 and N4) was extremely high ($r = 0.85$), indicating that individuals with higher absolute error had more gains than individuals with lower absolute errors (since they had greater room to improve). However, despite this difference in dependent variable from prior work, we examined if rates of learning reflected in the average level of performance 'early in learning' (i.e., the first block of the novel task) (Wu et al., 2014). In this regard, we found no evidence of increased variability in the baseline block (B1) facilitating the rate of learning. Although we used an average of 50 trials to estimate the early learning (which was a relatively long period), the results still showed the same trends when examining 10 or 25 trials. In summary, while it is possible that there are effects of variability on the rate of learning, the current results suggest that individuals with low baseline variability can still be flexible in using a new solution to perform the task.

Finally, from a task viewpoint, the design of the task and the knowledge of the task goal is an important context modulating the importance of variability in learning. Prior work examining the role of variability have generally focused on adaptation tasks (Wu et al., 2014; He et al., 2016; Singh et al., 2016) or reinforcement-based paradigms using simple tasks (Wu et al., 2014). Adaptation tasks are characterized by adjustments to systematic errors (i.e. changes in constant error or 'bias') and several have argued that adaptations to force fields or visuomotor rotations are distinct from tasks where there is an underlying change in the skill (Krakauer and Mazzoni, 2011; Sternad, 2018). Similarly, in reinforcement learning paradigms, the role of motor variability can be over-estimated because the learning in these tasks is primarily the learning of the task goal, and does not necessarily involve a change in skill. For example in one study (Wu et al., 2014), participants were shown a curve to trace but the actual learning was evaluated on another shape that they were unaware of. This meant that the only way participants could improve on this task was to discover this task goal through trial and error – i.e., identify what the shape of the curve they were being rewarded on. While these prior results advance our knowledge by showing that humans can use motor variability to explore new solutions, in our view, they are less likely to be relevant for many real-life contexts where the task goal is known to the learner in advance. In contrast to these paradigms, in our study, the task goal was known to the learner in advance and learning primarily involved controlling motor variability over multiple trials – we believe this may more closely reflect real-life contexts in motor learning.

Overall, these results caution against the use of 'observed' motor variability as a predictor of future learning (Ranganathan and Newell, 2010b; Ranganathan et al., 2020). The observed variability in a given context is only a 'snapshot' of the system's behavior and may not fully reflect the full potential of the system, which may explain why predictions using variability outside of the specific task context are likely to be less useful. Our results are consistent with the conclusion (He et al., 2016) that there is no single relation between variability and learning that generalizes to all contexts, and highlight the need for further work using tasks representative of real-world learning to fully understand the role of variability in motor learning (Haar et al., 2020). Furthermore, the results also highlight the need to better understand the phenomenon of flexibility in motor learning and if specific exploration strategies for moving from one solution to another (for e.g., abrupt vs. gradual change) can be used during training to enhance flexibility.

AUTHOR CONTRIBUTIONS

RR, MHL and CK conceived and designed research.

ML and SC performed experiments.

RR, ML, SC and RL analyzed data.

RR, MHL and CK interpreted results of experiments.

RR prepared figures.

RR drafted manuscript.

RR, ML, SC, RL, MHL and CK edited and revised manuscript.

RR, ML, SC, RL, MHL and CK approved final version of manuscript.

DATA ACCESSIBILITY

The data associated with this manuscript are available at https://osf.io/8zqpr/.

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