



Differential control of task and null space variability in response to changes in task difficulty when learning a bimanual steering task

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Received: 7 September 2018 / Accepted: 30 January 2019 / Published online: 9 February 2019
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Abstract

The presence of motor redundancy means that movement variability can be split into a ‘task-space’ component that affects task performance, and a ‘null space’ component which has no effect on task performance. While the control of task-space variability during learning is essential, because it is directly linked to performance, how the nervous system controls null space variability during learning has not been well understood. One factor that has been hypothesized to govern the change in null space variability with learning is task difficulty, but this has not been directly tested. Here, we examined how task difficulty influences the change in null space variability with learning. Healthy, college-aged participants ($N=36$) performed a bimanual steering task, where they steered a cursor through a smooth W-shaped track of a certain width as quickly as possible while attempting to keep the cursor within the track. Task difficulty was altered by changing the track width and participants were split into one of the three groups based on the track width that they practiced on—wide, narrow, or progressive (where the width of the track progressively changed from wide to narrow over practice). The redundancy in this task arose from the fact that the position of the cursor was defined as the average position of the two hands. Results showed that movement time depended on task difficulty, but all groups were able to decrease their movement time with practice. Learning was associated with a reduction in null space variability in all groups, but critically, there was no effect of task difficulty. Further analyses showed that while the task-space variability showed an expected speed–accuracy tradeoff with movement time, the null space variability showed a qualitatively different pattern. These results suggest differential control of task and null space variability in response to changes in task difficulty with learning, and may reflect a strong preference to minimize overall movement variability during learning.

Keywords Variability · Synergy · Null space · Task difficulty · Bimanual · UCM

Introduction

The large number of degrees of freedom in the human body creates redundancy, which means that most motor tasks can be accomplished through multiple movement solutions (Bernstein 1967). For example, when reaching to a location in 3D space, the human arm has at least 7 degrees of freedom at the joint level, which means that there are multiple arm postures that can be used to reach that location (Turvey et al. 1982). This example of mechanical redundancy allows

movement variability to be decomposed into two components—(1) a ‘task space’ (or goal-relevant) component, where the variability directly affects the task outcome and (2) a ‘null space’ (or goal-equivalent) component, where variability has no effect on the task outcome (Cusumano and Cesari 2006; Domkin et al. 2002; Mosier et al. 2005; Müller and Sternad 2004; Scholz and Schöner 1999). Understanding how the nervous system controls these two components of variability when learning a novel task is critical from both theoretical and applied viewpoints.

Although it is apparent that task-space variability must be controlled with learning due to its direct link to task performance, the role of null space variability with learning remains rather unclear (Wu and Latash 2014). On one hand, there is evidence that overall movement variability (i.e., both task and null space variability) generally decreases with learning (Darling and Cooke 1987; Ranganathan and Newell

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2010; Shmuelof et al. 2012), indicating that even in the presence of many solutions, there is a tendency to use certain ‘preferred’ solutions. However, on the other hand, reducing null space variability could also be considered ‘wasted effort’, since it has no impact on task performance (Todorov and Jordan 2002). Moreover, reducing null space variability may also be counter-productive, since the presence of null space variability may allow flexibility to accommodate perturbations or secondary tasks (Latash 2012; Rosenblatt et al. 2014; Zhang et al. 2008). A recent review (Latash 2010) revealed a mixed pattern of results—in some tasks, there was an increase in null space variability (relative to the task-space variability) with learning, whereas in others, there was a decrease. One potential hypothesis raised to explain this pattern of results was task difficulty—simple tasks with lower task difficulty generally showed greater reduction in null space variability, whereas complex tasks with higher task difficulty led to relative preservation of the null space variability. These results point to a need to clarify the role of task difficulty in the change of null space variability in learning.

However, a major limitation of inferring the role of task difficulty from prior work is the necessity to make comparisons between learning completely different tasks (e.g., pointing at a target vs. multi-finger force production). Although it seems intuitive that some tasks may be more difficult than others, there is no common metric of task difficulty across these different tasks, which is critical to quantitatively test this hypothesis. Here, we overcome this limitation using a single task that could be varied on a quantifiable metric of task difficulty. Specifically, we used a steering task, where participants had to steer a cursor through a track while staying within a track. This paradigm allowed us to manipulate task difficulty by altering the width of the track while holding all other experimental factors constant.

The goal of this study was to examine the effect of manipulating task difficulty on the change in null space variability with learning. Participants performed a bimanual steering task, where the goal was to steer a screen cursor through a desired track of specified width as quickly as possible without crossing the boundaries of the track. Critically, the screen cursor position was determined as an average of the position of the two hands, which meant that the same cursor path could be achieved by different combinations of hand paths. We manipulated the task difficulty by adjusting the track width: in two groups (wide and narrow), the track width was held constant throughout practice, and in a third group (progressive), we changed the track width during practice. We evaluated the change in null space variability with learning. Based on the task difficulty hypothesis (Latash 2010), we hypothesized that there would be a reduction in variability with learning in both cases, but that the group with higher task difficulty (i.e., the narrow group)

would show higher amounts of null space variability relative to the group with easier task difficulty. As a second exploratory aim, we also examined if progressive modification of task difficulty (gradually moving from lower to higher task difficulty) had a differential effect on the use of null space variability relative to the groups that practiced with the same level of task difficulty throughout.

Methods

Participants

Participants were 36 healthy college-aged adults (age range 20–24 years, 20 females). Participants received extra course credit for participation. All participants provided informed consent and the procedures were approved by the Institutional Review Board at Michigan State University.

Apparatus

We used a bimanual manipulandum (KINARM Endpoint Lab, BKIN Technologies, ON), which consists of two separate robotic arms that allow motion in a 2D horizontal plane. A handle located at the end of each arm could be grasped by participants. Participants were seated on a height-adjustable chair, and looked into a screen at around 45 degree angle below eye level (Fig. 1a). The visual information was presented in such a way that the objects on the screen appear to be located in the plane of the hands. Kinematic data from both handles were sampled at 1000 Hz.

Task description

The participants controlled a cursor of diameter 4 mm and steered it from start position to end position along a smooth W-shaped track of length 738 mm (Fig. 1b). The goal of the participants was to do this as quickly as possible while maintaining the cursor within the track. The width of the track was always visible to the participant—both the track (i.e., the ‘allowed region’), and the surrounding region were highlighted in different colors. When the cursor deviated from the track, the surrounding region changed color serving as a visual cue to help maintain the cursor within the track. Regardless of the track width, the center of the track always remained in the same position in the workspace for all participants and conditions.

Cursor mapping

The position of the cursor (X_C , Y_C) was displayed at the average position of the two hand locations (X and Y coordinates of the left and right hands), making the task redundant

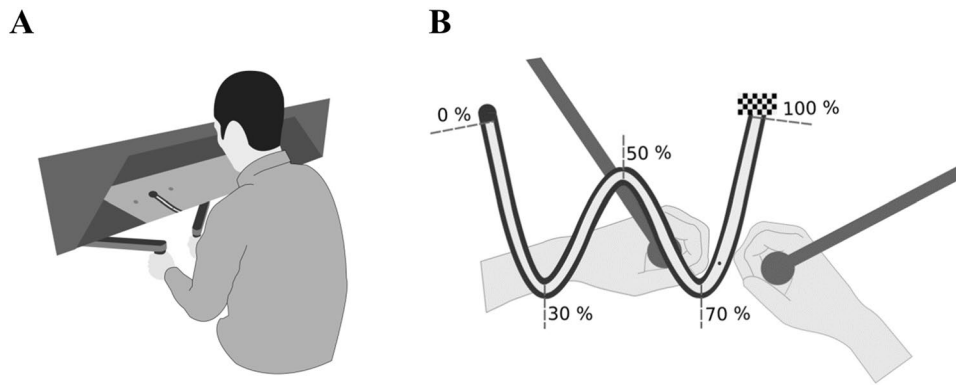


Fig. 1 Experimental setup. **a** Schematic of experimental apparatus. Participants held the handles of a bimanual manipulandum and looked into a screen that displayed the image in the same plane as their hands. Participants could not see their hands directly. **b** Task schematic. Participants were asked to steer a cursor through the W-shaped track as quickly as possible from start to finish while main-

taining the cursor inside the track. The position of the cursor was displayed at the average position of the two hands (hands were not visible to the participant). We specifically focused on variability at five specific points on the path (0%, 30%, 50%, 70%, and 100%). Hands and the robot handles are drawn only for the sake of clarity and are not to scale

(Diedrichsen 2007). This 4-to-2-mapping can be represented as follows (Liu and Scheidt 2008; Mosier et al. 2005):

$$C = \begin{bmatrix} X_C \\ Y_C \end{bmatrix} = \begin{bmatrix} 0.5 & 0.5 & 0 & 0 \\ 0 & 0 & 0.5 & 0.5 \end{bmatrix} \begin{bmatrix} X_L \\ X_R \\ Y_L \\ Y_R \end{bmatrix} = AH,$$

where C is the cursor position, A is the ‘mapping matrix’, and H is the vector of hand positions.

Procedures

At the start of each trial, participants saw two individual cursors (one for each hand), which allowed them to position each hand in its own start circle—this was done to ensure that the two hands always started at the same position for each trial. Once each hand reached its start position, the individual cursors disappeared and were replaced by a single cursor at the average position of the two hands. Participants then moved this cursor towards the finish position as fast as possible staying within the width of the track. Participants were asked to ‘pass through’ the finish box (i.e., they did not have to stop the cursor at the finish box).

To encourage participants to go faster while staying inside the track, participants were shown a ‘Points Score’ at the end of the trial that reflected their task performance—higher scores (max 100 points) were generated for faster times and for staying inside the track. Participants received a penalty in proportion to the time they took to complete the whole movement (t_m) and the time that the cursor spent outside the track (t_o) (see equation below). If the cursor completely went outside even the surrounding region, they were awarded zero points on that trial:

$$\text{Points score} = 100 - 0.1 * (t_m)^2 - 0.5 * (t_o)^2.$$

Experimental protocol

Participants were divided into three groups ($n = 12/\text{group}$)—narrow, progressive, and wide, based on the track width during practice (Fig. 2). All participants initially performed a familiarization block of 10 trials on the wide track, where they familiarized themselves with the task and the scoring system. Subsequently, each group practiced on a different track width over 2 days of practice. The narrow group had a 6 mm wide track,

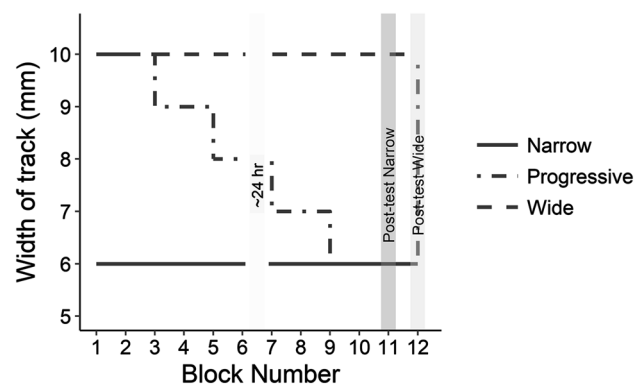


Fig. 2 Experimental protocol for the three groups of participants. Each block of practice consisted of 24 trials with a ~24-h break between blocks 6 and 7. The wide and narrow groups practiced with track widths of 10 mm and 6 mm, respectively, throughout the experiment. For the progressive group, the track width was reduced during practice (blocks 1–10) by 1 mm every 2 blocks, going from 10 mm in block 1 to 6 mm by block 9. After the last practice block (block 10), the progressive group faced a 6 mm track on block 11 (the same as the narrow group), and a 10 mm track on block 12 (the same as the wide group). These two blocks essentially served as post-tests for comparisons with narrow and wide groups, respectively

the wide group had a 10 mm wide track, and the width for these two groups remained constant throughout all 12 blocks of the experiment (1 block = 24 trials). For the progressive group, the track width started at 10 mm (i.e., the same as the wide group) and was then gradually reduced by 2 mm after every two blocks until it reached 6 mm (the same as the narrow group). After 10 blocks of practice, the progressive group performed one block of trials on the narrow setting (6 mm) on block 11, and one block of trials on the widest setting (10 mm) in block 12. Participants in the progressive group were not explicitly informed about the changes in track width, although the width of the track was visible to them.

Data analysis

Movement time

Based on our task instruction, the primary variable of interest was movement time. Movement time was measured as the time between the instant when the participant moved the cursor out of the start circle and the instant when the cursor moved into the finish box.

Error percentage

Because participants also had an accuracy requirement of staying inside the track, the error percentage was computed as the time duration that the cursor stayed outside the track in any given trial expressed as percentage of the movement time of that trial.

Task and null space variability

Because of the redundancy in the task, participants could maintain the same cursor position with differing positions of the individual hands. Therefore, the variability in hand positions could be further decomposed into task and null space variability (Liu and Scheidt 2008; Mosier et al. 2005; Ranganathan et al. 2013).

The path from each trial was divided into 51 spatially equidistant points from the start to the end. At each point, the corresponding hand positions from all trials in that block were extracted into a matrix H (see “Cursor mapping”) and the Moore–Penrose inverse matrix was used to decompose the hand positions into null space and task-space components. Based on the mapping matrix A defined in the “Cursor mapping”, the null space (H_n) and task-space (H_t) decomposition of hand positions were calculated as

$$H_t = A' * (A * A')^{-1} * A * H$$

$$H_n = (I_4 - A' * (A * A')^{-1} * A) * H,$$

where I_4 is an identity matrix of size 4×4 . The variances of these null and task components of the hand positions were computed and summed to obtain total null space and task-space variability at each spatial point.

Statistical analysis

Based on the experimental design, we refer to blocks 1–10 as the ‘practice blocks’ and blocks 11–12 as the ‘post-test blocks’. Specifically, block 11, which was used to compare the progressive and narrow groups is referred to as post-test narrow; and block 12, which was used to compare the progressive and wide groups is referred to as post-test wide.

Analysis of practice blocks

The data from the first and last practice blocks (i.e., blocks 1 and 10) were analyzed to evaluate the effects of practice and task difficulty. For movement time and error percentage, we used a two-way repeated measures ANOVA (practice \times group), with practice being the repeated measure. For the task and null space variability, we used a three-way repeated measures ANOVA (practice \times path location \times group), with practice and path location being repeated measures. Here, path location refers to five spatial points (0%, 30%, 50%, 70%, and 100%) on the cursor path measured as a percentage of the total length of the path. The approximate locations of these path locations for any given block are shown in Fig. 1b.

Analysis of post-tests

To evaluate the effect of progressive practice, we analyzed the post-tests focusing on the two groups which practiced on the same track width (thereby removing the effect of task difficulty). In the post-test narrow, we compared the narrow and progressive groups, and in the post-test wide, we compared the wide and progressive groups. For each post-test, we used a one-way ANOVA (group) to analyze differences in movement time and error percentages and a two-way repeated measures ANOVA (path location \times group), with path location being the repeated measure, to analyze differences in task and null space variabilities.

The significance level was set at $\alpha = 0.05$. Post-hoc comparisons were adjusted using the Bonferroni correction and Greenhouse–Geisser corrections were applied to account for violations in sphericity.

Results

First, we examined null and task variabilities in each block and removed participants, whose variability fell outside the Tukey’s fences ($Q3 + 1.5 * IQR$ and $Q1 - 1.5 * IQR$,

Q1 = lower quartile, Q3 = upper quartile, and IQR = interquartile range). There were 6 such outliers in total, which reduced the sample sizes to 10 in each group.

Movement time

Practice

As expected, both task difficulty and practice influenced the movement time (Fig. 3a). Participants in the narrow and wide groups were able to reduce movement time with practice, but the progressive group did not show changes in movement time with practice (because the task difficulty was constantly increased in this group). The analysis of the practice blocks revealed a significant main effect of group [$F(2,27) = 34.05, p < 0.001$], practice [$F(1,27) = 59.05, p < 0.001$] and a significant group \times practice interaction [$F(2,27) = 16.27, p < 0.001$]. Pairwise Bonferroni adjusted comparisons for the group \times practice interaction showed: block 1—that movement times were longer for the narrow group compared to the wide and progressive groups ($p < 0.001$), whereas there was no significant difference between the progressive vs. wide ($p = 0.268$), block

10—movement times for the wide group were significantly smaller than both narrow and progressive groups ($p < 0.001$), but there was no significant difference between the narrow vs. progressive ($p > 0.999$).

Post-tests

Progressive practice did not facilitate reduction in movement time on the narrow track, and led to a small but significant increase in the movement time on the wide track. Comparisons in the post-test narrow revealed no significant differences between progressive and narrow groups [$F(1,18) = 0.79, p = 0.379$]. In the post-test wide, movement times were higher for the progressive group compared to the wide group [$F(1,18) = 6.03, p = 0.024$].

Error percentage

Practice

Overall, the error percentage was low for all groups (between 5 and 15%) (Fig. 3b). Participants in the narrow and wide groups had nearly constant movement error percentages

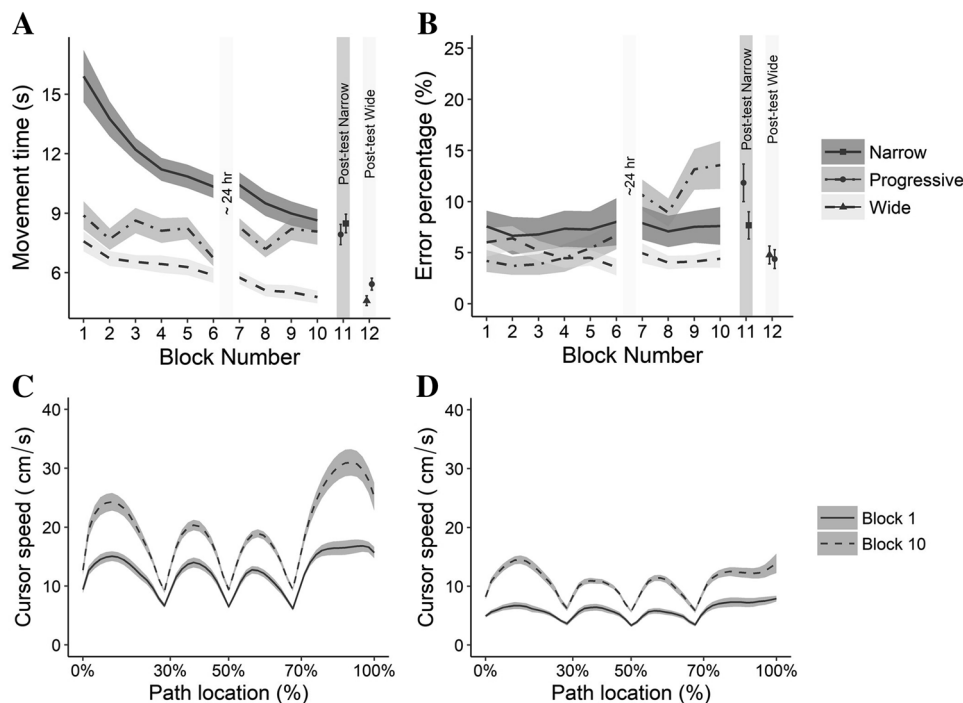


Fig. 3 **a** Average movement time in each group as a function of practice. Movement times were affected by track width and practice. Blocks 1–10 represent the practice phase and blocks 11 and 12 represent the post-tests. There was a ~24 h break between blocks 6 and 7. **b** Average error percentage in each group as a function of practice. Error percentages were generally low, and remained constant throughout practice, except for the progressive group. Average cursor

speeds throughout the path for **c** wide group and **d** narrow group in the first and last practice block. Increases in speed with practice were more pronounced during the straighter portions of the track when compared to the curved portions of the track. Note that the cursor speed at 0% (even though participants started the trial at rest) is not zero, because the 0% was defined outside of the start region. Error bars represent one standard error (between-participant)

throughout practice, whereas the progressive group had an increasing movement error percentage (because of the gradual increase in task difficulty). The analysis of practice blocks revealed a significant main effect of practice [$F(1,27)=9.12, p=0.005$] and a significant group \times practice interaction [$F(2,27)=15.76, p<0.001$]. Pairwise Bonferroni adjusted comparisons for the group by practice interaction showed: block 1—no significant differences between groups: progressive vs. narrow ($p=0.130$), progressive vs. wide ($p=0.88$) and narrow vs. wide ($p>0.99$), block 10—error percentages were higher for progressive in comparison to the wide ($p=0.013$) and there were no significant differences between progressive vs. narrow ($p=0.170$) or narrow vs. wide ($p=0.682$). The main effect of group was also not significant [$F(2,27)=1.78, p=0.187$].

Post-tests

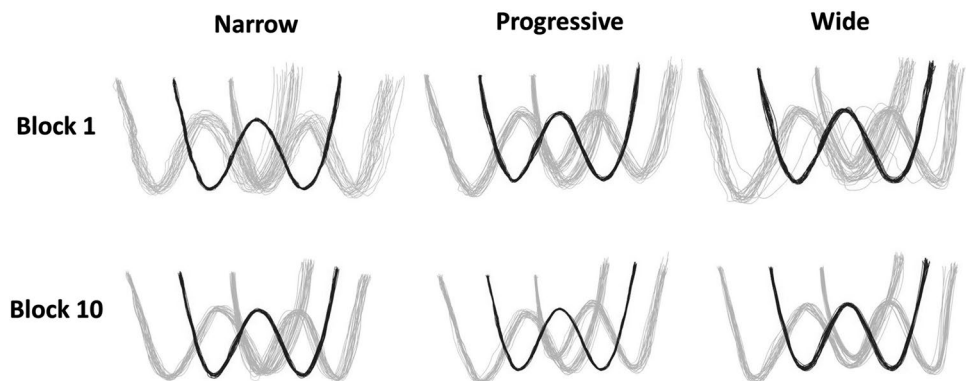
Progressive practice did not significantly affect the error percentage both on the narrow and wide tracks. Comparisons in the post-test narrow revealed no significant differences between progressive vs. narrow [$F(1,18)=3.37, p=0.082$] and comparisons in the post-test wide revealed no significant difference between progressive vs. wide [$F(1,18)=0.10, p=0.753$].

In addition to overall movement time, we also analyzed the speed of the cursor throughout the path (Fig. 3c, d). The average speed of the cursor in the narrow and wide groups increased from the first to the last block of training throughout the path, but there was a bigger change in the straighter portions of the track, compared to the curved portions.

Task-space variability

Cursor and hand trajectories of all trials in block 1 and block 10 of practice for a representative participant in each group are shown in Fig. 4.

Fig. 4 Sample trajectories (cursor, left and right hand) from one participant in each group are shown for first block of practice (block 1) and last block of practice (block 10). Cursor trajectories are shown in black, and the left and right hand trajectories are shown in grey. The individual hand trajectories become less variable with practice even though cursor variability remains roughly the same



Practice

Task-space variabilities are shown as a function of path location for the first (block 1) and last block (block 10) of practice (Fig. 5a, b). Because the track width essentially constrains the task-space variability, we expected to see group differences as a result of our experimental manipulation. In agreement, there was a significant effect of group [$F(2,27)=11.86, p<0.001$], path location [$F(2.7,73.3)=92.03, p<0.001$] and a significant interaction effect group \times path location [$F(5.4,73.3)=11.49, p<0.001$].

Pairwise comparisons for the group \times path location interaction showed the following trends: while there were no significant differences between the groups at the 0% path location, the narrow group had smaller variability than the wide group throughout the rest of the path ($p_s<0.001$). The narrow group also had smaller variability than the progressive group almost through the entire path (path location at 30% $p=0.007$; 50% $p=0.032$, 70% $p=0.147$, 100% $p<0.001$), whereas the wide group had higher variability than the progressive group throughout the path except at the end (30% $p=0.077$, 50% $p=0.033$, 70% $p=0.035$, 100% $p>0.99$). There were no other significant effects—practice [$F(1,27)=0.01, p=0.911$], practice \times group [$F(2,27)=0.86, p=0.433$], practice \times path location [$F(2.2,60.4)=1.32, p=0.273$], and group \times practice \times path location [$F(4.5,60.4)=0.39, p=0.834$].

Post-tests

Practicing with progressive widths did not affect task-space variability on either of the post-tests (Fig. 6a, b). In post-test narrow, there was a significant effect of path location [$F(3.1,56.1)=60.49, p<0.001$] and a significant interaction effect group \times path location [$F(3.1,56.1)=3.28, p=0.025$]. Pairwise comparisons at various path locations revealed a significant difference between the progressive and narrow groups generally in the latter half of the trajectory – 70% path location ($p=0.022$), but the 50% path

Fig. 5 Average task-space variability for each group in **a** first practice block (block 1) and **b** last practice block (block 10). Task-space variability differed between groups, but did not change significantly with learning. Average null space variability for each group in **c** first practice block and **d** last practice block. Null space variability was similar between the groups and showed reductions from the first to last block. Error bars indicate one standard error (between-participant)

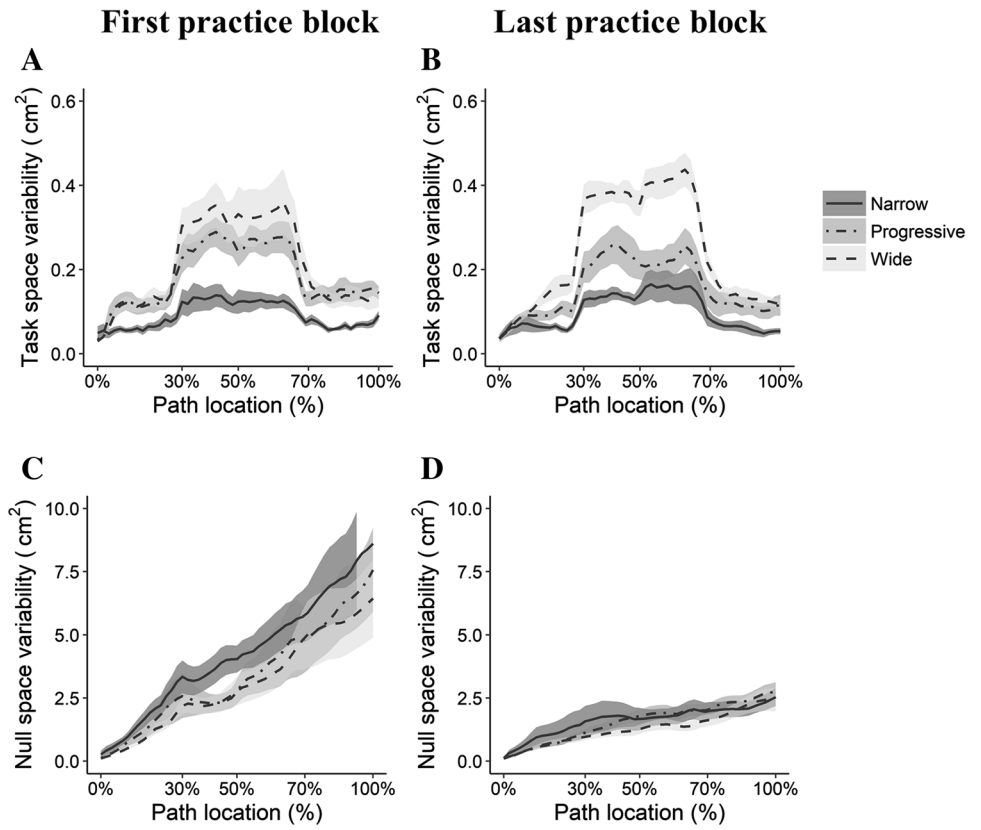
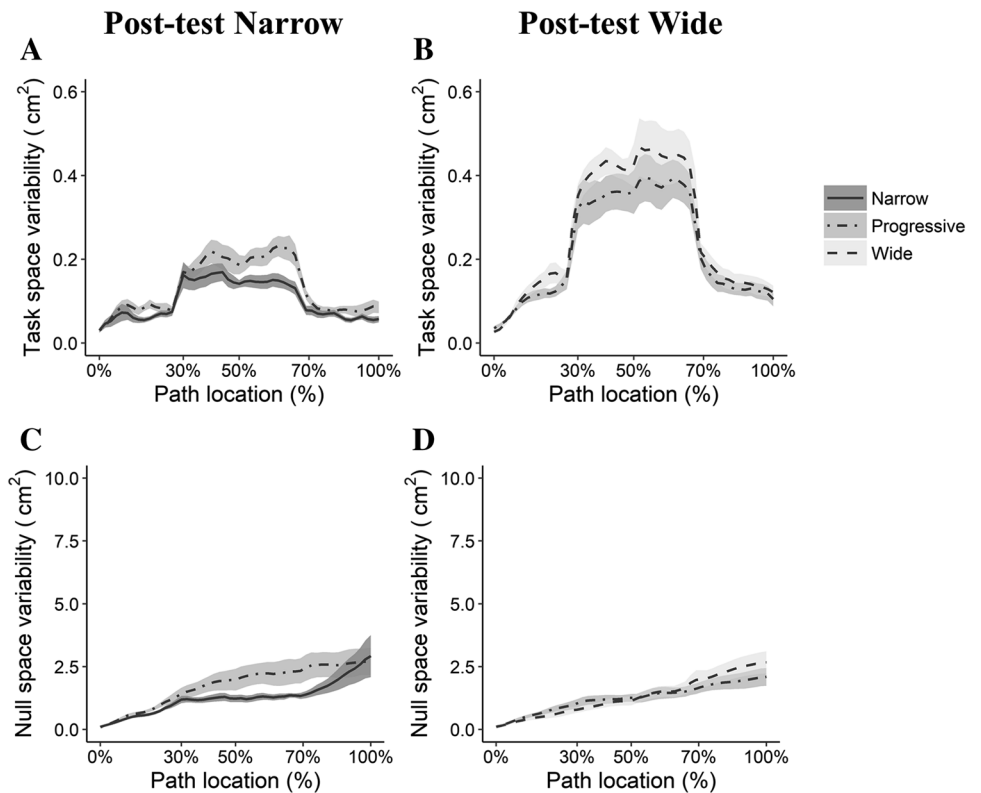


Fig. 6 Average task-space variability for the relevant groups in **a** post-test narrow (block 11) and **b** post-test wide (block 12). Average null space variability for the relevant groups in **c** post-test narrow and **d** post-test wide blocks. There were no advantages to progressive practice either in task or null space variability in both post-tests. Error bars indicate one standard error (between-participant)



location ($p = 0.109$) and 100% path location ($p = 0.107$) were not significant. Group differences were not significant in the first half of the trajectory – 0% path location ($p = 0.928$), 30% path location ($p = 0.765$). There was no significant effect of group [$F(1,18) = 2.80$, $p = 0.110$].

In post-test wide, there was a significant effect of path location [$F(2.4,43.9) = 44.05$, $p < 0.001$] which was similar to the effect seen in practice. There was no significant effect of group [$F(1,18) = 0.55$, $p = 0.465$], or group \times path location [$F(2.4,43.9) = 0.43$, $p = 0.690$].

Null space variability

Practice

Null space variabilities are shown as a function of path location for first (block 1) and last block (block 10) of practice (Fig. 5c, d). We observed that (1) null space variability showed an increasing trend along the path from start to finish and (2) there was a reduction in null space variability with practice for all groups and for all blocks. Comparisons of null space variability revealed a significant effect of practice [$F(1,27) = 30.65$, $p < 0.001$], path location [$F(1.3,36.7) = 57.79$, $p < 0.001$], and practice \times path location [$F(1.3,34.5) = 15.71$, $p < 0.001$]. Pairwise comparisons between blocks 1 and 10 at various path locations yielded an overall decrease in variability throughout the path at all path locations ($p < 0.001$) except at the 0% path location ($p = 0.296$). Importantly, there was no significant effect of group [$F(2,27) = 1.518$, $p = 0.237$], or other interactions—group \times practice [$F(2,27) = 1.27$, $p = 0.296$], group \times path location [$F(2.7,36.7) = 0.38$, $p = 0.924$], and practice \times group \times path location [$F(2.5,34.5) = 0.47$, $p = 0.872$].

Post-tests

Progressive practice did not affect null space variability on either post-test (Fig. 6c, d). In post-test narrow, there was a significant effect of path location [$F(1.7,30.8) = 20.56$, $p < 0.001$] which showed a similar increasing trend from start to finish. There was no significant effect of group [$F(1,18) = 0.93$, $p = 0.346$], or group \times path location [$F(1.7,30.8) = 1.21$, $p = 0.304$].

Similarly, in post-test wide, there was a significant effect of path location [$F(1.8,33.8) = 47.18$, $p < 0.001$], showing a similar increasing trend from start to finish. There was no significant effect of group [$F(1,18) = 1.17$, $p = 0.292$], or group \times path location [$F(1.8,33.8) = 2.55$, $p = 0.095$].

Variabilities as a function of movement time

Finally, to examine speed–accuracy effects, we examined null and task-space variabilities for all participants as a function of movement time in the first and last block of practice, i.e., block 1 and block 10 (Fig. 7a, b). For this analysis, the task and null space variabilities were averaged across all path locations for each participant. Because the scatter plots indicated that relation was not linear, we used the Spearman's ranked correlation (ρ) to compute the correlation.

Task-space variability exhibited a speed–accuracy trade-off both early and late in learning—i.e., shorter movement times were associated with higher task-space variability. This was indicated by a significant negative correlation for both block 1 ($\rho = -0.69$, $p < 0.001$) and block 10 ($\rho = -0.81$, $p < 0.001$). However, null space variability showed a qualitatively different pattern of results. Rather than a speed–accuracy tradeoff (i.e., a negative correlation), the observed correlation was positive early in block 1 ($\rho = 0.455$, $p = 0.012$) and was not significant in block 10 ($\rho = 0.13$, $p = 0.479$).

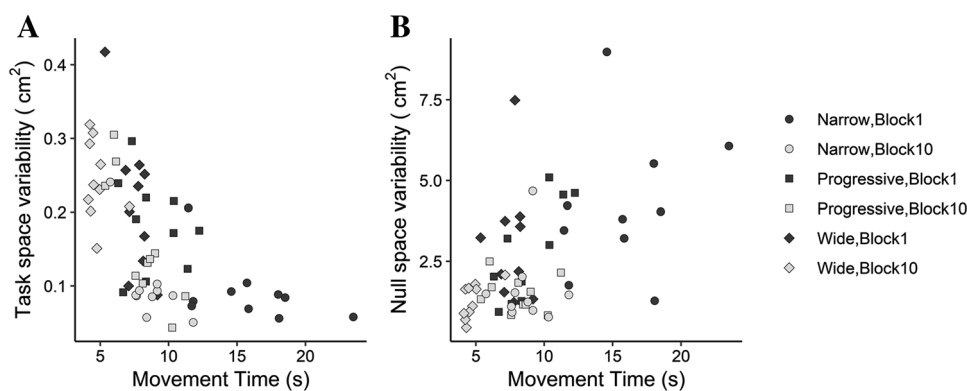


Fig. 7 **a** Average task space and **b** average null space variability plotted against movement time in the first practice block (black symbols) and the last practice block (grey symbols). Each symbol represents a participant. Task-space variability shows a negative correlation in

both practice blocks, indicating a speed–accuracy tradeoff, whereas the null space variability shows a qualitatively different pattern, going from a slightly positive correlation in block 1 to a non-significant correlation in block 10

Discussion

The goal of the study was to examine changes in null space variability when learning tasks of different difficulty. Participants performed a bimanual steering task through a W-shaped track and we modulated the task difficulty using the width of the track. Based on the task difficulty hypothesis (Latash 2010), we hypothesized that the narrow group would show higher amounts of null space variability relative to the wide group. Our results did not support the hypothesis—although both task difficulty and practice had an effect on the movement time (indicating that the manipulation worked and there was learning), there was no effect of task difficulty on the null space variability. Instead, with practice, null space variability simply showed an overall reduction for all groups. With regard to our exploratory aim on progressive practice, we found that practicing with progressive difficulty did not have any beneficial effects (and in some measures even had slightly worse performance) relative to the groups that practiced with constant difficulty.

Effect of task difficulty on performance

Because error percentages were generally low for all groups and fairly constant, movement time was treated as the primary performance variable. Changing task difficulty had anticipated effects: movement times in the narrow track were longer relative to the wide track, indicating a speed–accuracy tradeoff (Fitts 1954). Even though original version of the Fitts' law task was developed for discrete point-to-point movements, other versions for path-based control have been developed (Accot and Zhai 1997). Such a tradeoff between movement time and accuracy (imposed by the track width) has been attributed to signal-dependent noise (Harris and Wolpert 1998; Schmidt et al. 1979). However, with practice, participants were able to complete the task faster, which is consistent with the idea that learning results in reduced motor variability (Darling and Cooke 1987; Georgopoulos et al. 1981; Gottlieb et al. 1988; Huber et al. 2016; Shmuelof et al. 2012).

Effect of task difficulty on movement variability

However, because this task was redundant, we could further examine how participants changed their performance with learning. First, we observed that the task-space variability was constrained mainly by the track width and did not change with learning, which is consistent with the idea that participants did not reduce their task-space variability

any more than what was required to do the task. When we examined the null space variability, however, there was no effect of task difficulty; instead, the main change was simply an overall reduction with practice in all groups. In other words, as participants learned to move faster through the same track, their hand paths from trial-to-trial became more consistent, leading to a reduction in the amount of null space variability (even though the cursor variability was unaffected). These results are somewhat contradictory to the predictions of a two stage learning model (Latash 2010). In this model, the first stage of learning, which is more pronounced for tasks with higher task difficulty, should lead to strengthening of motor synergies (i.e., a relative preservation of the null space variability), followed by an optimization process (where null space variability may be decreased). Instead, we found that regardless of task difficulty, there was almost a steady reduction in null space variability during learning.

A simple explanation for these results is that our manipulation of task difficulty was simply not large enough—i.e., the wide and narrow groups did not differ sufficiently enough in task difficulty to create significant differences in the null space variability. However, we think that this explanation is unlikely, because the effect of task difficulty is clearly seen in the movement time; the narrow group almost took twice as long as the wide group throughout the entire practice duration.

This raises the question—what is the purpose of reducing null space variability with learning if it has no effect on task performance? There are two possibilities—first, the previous literature on the learning of redundant tasks has argued that reductions in null space variability could be a reflection of learning the metric properties of the task space (Mosier et al. 2005) or the learning of an inverse map from cursor coordinates to hand coordinates (Liu et al. 2010; Ranganathan et al. 2013). Second, because the task here focused on reduction of variability, the reduction in individual hand variability (and, therefore, null space variability) could also be due to use-dependent or ‘model-free’ learning—in other words, repetition of successful movements (Diedrichsen et al. 2010; Shmuelof et al. 2012). This is also consistent with evidence that high amounts of null space variability may impair this use-dependent learning mechanism and affect subsequent learning, even if it does not affect immediate performance (Cardis et al. 2017; Ranganathan and Newell 2013). While the current study was not designed to address the mechanisms of how this variability was reduced with learning—i.e., reduction in motor noise vs. increased error correction gains (Hasson et al. 2016), the results show that null space variability, although having no effect on performance, is also tightly controlled with learning.

Control of task and null space variability

Interestingly, when considering performance at a single timepoint (i.e., ignoring the learning aspect), the task and null space variability showed patterns both within- and across participants, that were consistent with an optimal feedback control framework (Todorov and Jordan 2002). At the within-participant level, when we examined task variability along the track, task-space variability was higher in the middle of the track compared to the start and end. However, when we examined the null space variability, we found an increasing trend throughout the path from start to finish, consistent with other evidence in static force production tasks (Shim et al. 2004). This is also consistent with the optimal feedback control, because the system had nothing to gain by ‘correcting’ null space deviations (since they would be wasted effort), and therefore, the variability simply accumulated throughout the path.

At the between-participant level, we also found that while the task-space variability showed the typical speed–accuracy tradeoff (i.e., shorter movement times associated with higher task-space variability), the null space variability showed a qualitatively different pattern, where faster movement times generally resulted in lower null space variability, particularly early in learning. These results are also consistent with optimal feedback control (Todorov and Jordan 2002)—as participants went faster, there was less time for feedback-based compensation between the two hands, and therefore, participants would have had to be more consistent with both hands (i.e., use less null space variability) to still be successful at the task.

Effect of progressive practice

Finally, we examined the progressive group to investigate if changing task difficulty had any beneficial transfer effects (Day 1956). We observed no benefits to gradually increasing task difficulty level relative to the groups that practiced with constant track width. In both post-tests, the progressive group did not outperform the group that had practiced on the constant track width (narrow or wide). In the post-test narrow condition, we in fact observed a higher null and task-space variability in the progressive group, indicating that the progressive group had a carry-over effect of practicing with wider track widths, and, therefore, had slightly higher overall variability. In general, the results support a “specificity” account of learning (Baker et al. 1950; Bachman 1961; Henry 1958; Woodworth and Thorndike 1901), where the best performance was obtained by direct practice on the to-be-learned condition.

There are a number of important caveats that need to be addressed. First, from a task paradigm perspective, in our task, participants were required to maintain task-space

variability, but were free to select movement time. There is some evidence that instructions have an effect on the use of redundancy—for example, in well-learned reaching movements, participants required to maintain the same movement time across task difficulty show changes in the use of null space variability (Tseng et al. 2003); however, this effect seems to disappear if participants self-select the movement time (Greve et al. 2015). Because our task was more novel, we expected to see if the non-significant differences found in Greve et al. were due to ‘ceiling’ effects of using a well-learned behavior, but surprisingly, even in this novel task, we did not see differences in null space variability. Second, the mean position of the track was never changed during the experiment, which meant that participants really did not have to explore during learning; instead, they only needed to reduce the movement time while maintaining the task variability. Although this argues against the use of null space variability as a buffer to avoid increased task-space variability (Todorov and Jordan 2002), this lack of exploration could have also resulted in decreased null space variability. Therefore, it is plausible that learning in this task mainly involved the ‘second stage of learning’ (Latash 2010) (i.e., where null space variability is decreased in favor of an optimization process). While this is outside the scope of the current study, introducing task variations to enhance motor exploration (such as manipulating the position of the channel, or the contribution of the hands to the shared cursor) may be ways to examine if the null space variability is critical to exploration.

In summary, we found that task difficulty did not have any differential effects on the use of null space variability. Null space variability decreased with practice, even as movement times got faster. These results suggest that in tasks involving the reduction of variability, the nervous system may use null space variability early on in learning but rely on the strategy of reducing overall variability regardless of task difficulty.

Acknowledgements This material is based upon work supported by the National Science Foundation under Grants nos. 1703735 and 1823889.

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