

EXAMINING THE SPATIAL AND TEMPORAL PROPERTIES OF
UNCONSTRAINED MOTOR SKILL LEARNING

by

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Doctor of Philosophy at George Mason University

by

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DEDICATION

This is dedicated to my grandmother Emma McKenna. She emphasized the importance of education to both her children and grandchildren. I know she would be proud of this accomplishment.

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I would like to thank my family for their unwavering support while on this journey toward earning my PhD. To my husband, Will, thanks for supporting me throughout graduate school. We were not always together; it was not always easy; but we made it. Thank you for editing my papers, listening to complaints, and endless worries, and for sharing many beers to celebrate little successes along the way. To my parents, Bill and Linda, thank you for being there. Your countless visits were always something I looked forward to, especially when I was in Virginia by myself. There was nothing Wednesday night dinner, a bike ride, and beers could not fix. Thank you for supporting me in everything that I have done and trusting my vision for my education and career. To Jennifer Jones, my color guard partner and first friend I made in Virginia, thank you for inviting me to join the staff at Freedom. Rehearsal was a chance to escape from reality and enjoy the art we created.

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ABSTRACT

EXAMINING THE SPATIAL AND TEMPORAL PROPERTIES OF UNCONSTRAINED MOTOR SKILL LEARNING

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There are at least two types of motor learning: motor adaptation and motor skill learning. Motor adaptation is characterized by fast changes to simple, constrained movement, where the goal is to counter a perturbation and return to baseline performance. Motor skill learning is defined by slow changes to complex, unconstrained movement where the goal is to improve beyond baseline performance (Krakauer et al. 2012, 2014). Previous work has established several spatial and temporal properties of motor adaptation including spatial and temporal generalization. Spatial generalization describes the transfer of motor learning from a trained to untrained spatial configurations. Similarly, temporal generalization describes the transfer of motor learning from a trained to untrained movement speeds. This dissertation aims to determine whether these known spatial and temporal properties of motor adaptation, also apply to motor skill learning. Dancers are an ideal population of motor skill experts to study because dance technique requires

dancers to move consistently through space and in time with music or a metronome. This dissertation is designed to answer three research questions: 1) Do dancers spatially navigate better than non-dancers with and without vision? 2) Can dancers transfer motor skills from trained to novel spatial contexts? 3) Can dancers transfer motor skills from trained to novel speeds? We utilized motion capture technology to continuously measure dancers and non-dancers' movement throughout their performance on each task. Our results suggest that spatial navigation for both dancers and non-dancers deteriorates when vision is restricted, but dancers outperform non-dancers when navigating complex configurations both with and without vision. In addition, our results imply that dancers are able to transfer motor skills from trained to untrained spatial contexts and speeds. Taken together, the results of this dissertation demonstrate that some of the known spatial and temporal properties of motor adaptation also apply to motor skill learning.

EXPERIMENT ONE: SPATIAL NAVIGATION OF DANCERS AND NON-DANCERS WITH AND WITHOUT VISION

Introduction

Spatial navigation is an important skill required for humans to appropriately interact with the environment. A wide variety of studies have examined the ability of humans to navigate through space, however, a large portion of these studies required participants to remain still and navigate through virtual environments. A somewhat small subgroup of these studies have required humans to walk during a spatial navigation task (Ehinger et al. 2014; Commins et al. 2013; Sun et al. 2004), but many do not measure the movement of the subjects continuously throughout each trial of the experiment. The current study intends to examine human spatial navigation using motion capture to measure the specific location of humans as they actively move through their environment.

Vision is widely accepted as the sensory system most heavily used by humans to navigate through their environment. This is evidenced by severe navigational impairments in blind humans (Thinus-Blanc and Gaunet, 1997, Ekstrom, 2015) and the presence of neurons in the human hippocampus that respond specifically to visual landmarks (Ekstrom et al., 2003; Janzen and van Turenout, 2004). Several blind-walking studies suggest that humans can navigate through their environment without vision, but tend to walk slower (Hallemans et al. 2010), adjust step length (Courtine and

Schieppati, 2003), increase variance of movement trajectory (Courtine and Schieppati, 2003), and demonstrate a reduction in upper body stability (Iosa et al. 2012). Other studies have found no effect of lack of vision on walking (Ruddle and Lessels, 2006; Kallie et al. 2002). But, again, the vast majority of these studies did not continuously measure whole body movement.

Humans have a range of ability to spatially navigate. Spatial navigation has been shown to improve due to expertise in some motor skills. For example, Danion et al. (2000) asked gymnasts to walk, steer a wheel chair, and verbally direct a person pushing them in a wheel chair with and without vision. They found that when vision was unavailable, gymnasts deviated from the desired straight line path, but outperformed other motor skill experts (soccer, tennis, handball, and basketball players). Danion et al. (2000) speculated that the superior performance observed in gymnasts could be a result of improved proprioceptive sense that comes with extensive gymnastics training, but may not be required for other motor skills. Similarly, extensive dance training leads to cognitive benefits over non-dancers including a heightened sense of body awareness and orientation within the environment (Fonseca et al. 2014; Margaret et al. 2014). Dancers also have an increased ability to integrate proprioceptive signals compared to non-dancers; dancers tend to utilize proprioceptive information more than non-dancers when vision information is present (Jola et al., 2011). Thus, dance training represents an acquired expertise in spatial navigation.

In the current study, we examined the whole body movements of dancers and non-dancers as they navigated specific spatial configurations. Utilizing motion capture,

we monitored the body position throughout each trial and examined the effect of vision on the performance (trial-to-trial variance and accuracy with respect to the ideal path trajectory). We tested dancers and non-dancers in three different patterns with and without vision. These results provide insight into the role of vision and body representation expertise on spatial navigation tasks requiring whole body movements.

Methods

Participants

Twenty subjects volunteered to participate in this experiment. All participants had no known neurological impairment and were naive to the purpose of this study, which consisted of walking in specific spatial patterns with and without vision. Subjects did not receive any training before data collection, and each individual completed one 1-hour session. A group of ten female students age 18-22 enrolled in the George Mason University School of Dance comprised the “dancer” group. Ten subjects (2 men and 8 women, 18-30 years of age) who had no prior dance experience comprised the “non-dancer” group. Prior dance experience was defined as participating in dance classes regularly for more than one year. The study protocol was approved by the George Mason University Institutional Review Board. All participants gave informed consent.

Experimental Setup

Motion capture technology was used to monitor subjects’ position within a 6.45 m by 4.50 m rectangular space. Twenty Optitrack Prime 13 cameras were mounted in a dance studio in the George Mason University School of Dance (Figure 1).

Schematic of the Motion Capture Setup

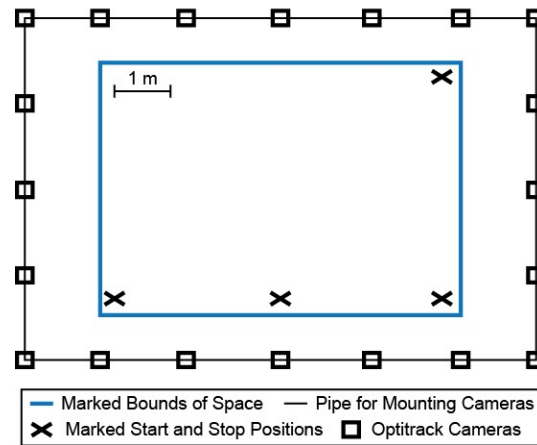


Figure 1 Schematic of the Motion Capture Setup. Twenty Optitrack Prime 13 cameras were mounted on a pipe just below the ceiling of the dance studio. The bounds of the space where motion capture data was collected reliably was marked in blue tape on the floor. The start and stop locations of the spatial configurations were marked on the floor with an X.

The Optitrack baseline marker set ($n = 37$ markers) was applied to each subject (Figure 2). Three-dimensional position data were collected at 120 Hz for each of the 37 markers.

Example Skeleton in Motive

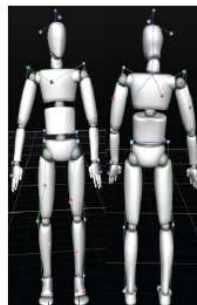


Figure 2 Skeleton Recreation. Subjects were fitted with a motion capture suit and markers were placed in specified locations based on Optitrack guidelines for the baseline marker set. Optitrack software utilized the position of the markers in space to recreate a skeleton which moved in real-time with the subject.

The rectangular space was marked on the floor with tape and subjects were instructed to stay within these bounds throughout the duration of the experiment. Four white X's marked the start and stop locations for the three walking patterns of interest: circle, zigzag 1, and zigzag 2 (Figure 3).

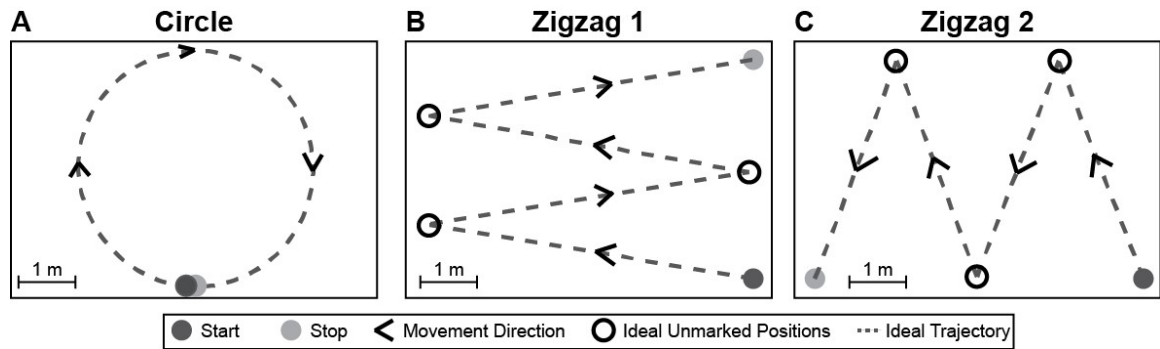


Figure 3 Movement Patterns from Bird's Eye View Perspective. In each pattern, the dark gray filled circle represents the start position and the light gray filled circle represents the end position. Arrows indicate the direction of movement. Open black circles indicate the changes in direction which were not explicitly marked on the floor. Dotted lines show the ideal movement trajectory for the A) circle, B) zigzag 1, and C) zigzag 2 patterns.

Task

Subjects were shown Figures 3A, B and C to familiarize themselves with the required walking pattern at the beginning of each block of trials. The experimenter explicitly pointed out the location of the start and stop positions marked on the floor. The locations where subjects should change direction in the zigzag patterns were not explicitly marked on the floor and subjects were not instructed where they should occur. Thus, these transition points were completely estimated by the subjects. At the beginning of each trial, subjects were asked to start with their body facing the front of the room for

both the circle and zigzag 2 patterns, and facing the side for the zigzag 1 pattern. During each trial, a metronome played at 110 beats per minute and subjects were told to take one step on each click of the metronome. On trials without vision, a blindfold was placed on subjects at the start position. To signal the end of the trial, subjects were told to stop and put their feet together once they felt they had reached the end location. On trials where a subject stepped outside of the blue tape, subjects were instructed to stop and the trial was repeated. This occurred 40 times out of 340 attempted trials (11.7%). Following each no vision trial, the experimenter guided subjects back to the start position and corrected their body position. The blindfold was removed after all no vision trials were completed for the given walking pattern.

Experimental Procedure

Subjects were asked to walk in three different patterns, a circle and two zigzag patterns, and ten trials were recorded for each pattern; a block of five trials with vision and a block of five trials without vision. The order of the patterns was counterbalanced across subjects and the order of vision and without vision blocks was randomized.

Analysis of Body Motion

The position of the body (hip trajectory) was determined using the average location of the four markers on the hips. The velocity of the body was calculated based on the change in position in the horizontal and vertical dimensions of the body position. The start (end) of a trial was represented by the point in time where the body velocity increased (decreased) to 0.05 m/s. We determined the duration of the movement from movement start to end and converted this to a percentage from 0% to 100%. We then

examined the hip trajectory at each 0.5% increment. The hip trajectory was then averaged across each trial within a given block of trials (e.g. circle with vision, zigzag 1 without vision) and then across subjects within the dancer or non-dancer groups. The ideal pattern was based on the position of the start and end markers on the floor. For both ideal zigzag patterns, the second change in direction was the midpoint between the start and end locations. For the ideal zigzag 1, the first and third changes in direction were determined by dividing the distance between the start and midpoint position and the midpoint and the end position in the vertical dimension, respectively, and 15 cm from the outer bounds of the space (marked in blue tape) in the horizontal dimension. For the ideal zigzag 2, the first and third changes in direction were determined by dividing the distance between the start and midpoint position and the midpoint and the end position in the horizontal dimension, respectively, and 15 cm from the outer bounds of the space in the vertical dimension. The diameter of the ideal circle was 4.20 m (15 cm inside the bounds of the rectangular space).

To examine consistency of movement over the course of each trial, we calculated the number of steps taken and the total time taken. For the zigzag 1 and zigzag 2 trials, we divided the trial into four segments based on the changes in direction. For zigzag 1 trials, changes in direction were defined by a change from positive to negative or negative to positive horizontal distance traveled between any two points in each subject's hip trajectory. For zigzag 2 trials, changes in direction were defined by a change from positive to negative or negative to positive vertical distance traveled between any two points in each subject's hip trajectory. We defined the completion of a step of the left

(right) foot as the point where the height-position data of the marker on the outside of the foot left (right) foot decreased below the value of the height-position data of the marker on the outside of the right (left) foot. We then summed the number of steps on the left and right feet between changes in direction for the zigzag patterns and over the course of the whole trial for the circle pattern, averaged across trials within a block, then across subjects. The time was calculated between the changes in direction for the zigzag patterns and over the course of the whole trial for the circle pattern and then averaged across trials within a block, then across subjects.

We also examined the hip trajectory of an example subject for the dancer and non-dancer groups (Figure 4). Here, we quantified accuracy and precision. Accuracy refers to the closeness of data to the task goal (e.g. in the game of darts, accuracy refers to the closeness of darts to the bullseye) and precision refers to the consistency or spread of data (e.g. in the game of darts, precision refers to how close darts are clustered relative to each other). To examine each subject's accuracy, we compared each hip trajectory within a given block of five trials to the ideal pattern by calculating the mean squared error (MSE) (Figure 4, top bar graphs). We will refer to this calculation as mean squared error relative to the ideal pattern or MSE_i . To quantify precision of the hip trajectory, we calculated the mean squared error between the average hip trajectory for a given block of trials ($n=5$) to each individual trial's actual hip trajectory (Figure 4, bottom bar graphs). We will refer to this calculation as the mean squared error relative to the average hip trajectory or MSE_m . We then examined the group data where we averaged the hip trajectory across a block of five trials for each subject, then across subjects (Figure 5).

Here, we quantified accuracy by calculating the MSE_i for a block of trials for each subject, then across subjects (Figure 5, top insets). We also quantified precision by calculating the MSE_m for a given block of trials for each subject, then averaged across subjects (Figure 5, bottom insets).

To evaluate the effect of lack of vision on accuracy (precision) of spatial navigation, we plotted the average MSE_i (MSE_m) on no vision trials versus the average MSE_i and (MSE_m) on vision trials for each subject in Figure 6 (Figure 7). To ensure the data was normally distributed we performed Anderson-Darling tests and took the logarithm (base 10) of all the data for this analysis. Data points that fell on the unity line represented subjects that were unaffected by the lack of vision. Points that fell above the unity line represented subjects that experienced difficulty in navigation with the lack of vision.

Statistical Analysis

Statistical significance of the effect of vision and effect of dance experience on time elapsed, steps taken, MSE_i , and MSE_m , and was determined using 2-way ANOVAs. Paired, one-tailed t-tests were utilized for post-hoc comparison of the dancer group performance across the vision and no vision condition and non-dancer group performance across the vision and no vision condition. Two-sample, one-tailed t-tests were utilized for post-hoc comparison of the dancer and non-dancer group performance in each vision condition. Error bars and shading in Figure 4 represent standard deviation. Error bars and shading in Figure 5 represent standard error. To ensure data was normally distributed, we ran Anderson-Darling tests and transformed data by taking the logarithm when necessary.

All statistical analyses were performed with MATLAB, and for all tests the significance level was 0.05.

Results

Comparison of duration and steps required during path navigation

In order to compare performance between the two groups (dancers versus non-dancers), we first quantified the number of steps taken and time elapsed from the start to the end of each trial to examine the consistency of movement throughout each trial. For the circle pattern, we found no main effect of group, condition, or an interaction for the number of steps taken throughout each trial which suggests that dancers and non-dancers required the same number of steps regardless of whether vision was provided in the circle pattern (2-way ANOVA, $p = 0.26$ for group, $p = 0.20$ for condition, and $p = 0.38$ for interaction). We also found no main effect of group, vision, or an interaction for the number of steps taken during segment 1 (2-way ANOVA, $p = 0.20$ for group, $p = 0.56$ for condition, and $p = 0.52$ for interaction), segment 2 (2-way ANOVA, $p = 0.41$ for group, $p = 0.53$ for condition, and $p = 0.87$ for interaction), segment 3 (2-way ANOVA, $p = 0.18$ for group, $p = 0.61$ for condition, and $p = 0.89$ for interaction), or segment 4 (2-way ANOVA, $p = 0.96$ for group, $p = 0.73$ for condition, and $p = 0.97$ for interaction) for the zigzag 1 pattern. In addition, we found no main effect of group, vision, or an interaction for the number of steps taken during segment 1 (2-way ANOVA, $p = 0.87$ for group, $p = 0.38$ for condition, and $p = 0.82$ for interaction), segment 2 (2-way ANOVA, $p = 0.72$ for group, $p = 0.94$ for condition, and $p = 0.90$ for interaction), segment 3 (2-way ANOVA, $p = 0.96$ for group, $p = 0.61$ for condition, and $p = 0.93$ for interaction), or segment 4 (2-

way ANOVA, $p = 0.35$ for group, $p = 0.98$ for condition, and $p = 0.75$ for interaction) for the zigzag 2 pattern. Together, these results indicate that dancers and non-dancers required the same number of steps regardless of whether vision was available in both zigzag patterns.

When we considered time elapsed for the circle pattern, we found no main effect of group, condition, or an interaction which suggests dancers and non-dancers took the same amount of time for start to finish of a circle pattern trial regardless of whether vision was available (2-way ANOVA, $p = 0.15$ for group, $p = 0.07$ for condition, and $p = 0.62$ for interaction). We examined the time elapsed during the zigzag 1 pattern and found no significant main effects of vision or condition, or an interaction for segment 1 (2-way ANOVA, $p = 0.36$ for group, $p = 0.57$ for condition, and $p = 0.47$ for interaction), segment 2 (2-way ANOVA, $p = 0.39$ for group, $p = 0.46$ for condition, and $p = 0.78$ for interaction), segment 3 (2-way ANOVA, $p = 0.15$ for group, $p = 0.49$ for condition, and $p = 0.94$ for interaction), or segment 4 (2-way ANOVA, $p = 0.17$ for group, $p = 0.11$ for condition, and $p = 0.84$ for interaction). This indicates that dancers and non-dancers took similar amounts of time to complete zigzag 1 trials regardless of whether or not they used vision. When we examined time elapsed during each segment of the zigzag 2 pattern, we found no significant main effect of group, condition, or an interaction for segment 1 (2-way ANOVA, $p = 0.56$ for group, $p = 0.63$ for condition, and $p = 0.86$ for interaction), segment 2 (2-way ANOVA, $p = 0.89$ for group, $p = 0.81$ for condition, and $p = 0.99$ for interaction), and segment 3 (2-way ANOVA, $p = 0.99$ for group, $p = 0.42$ for condition, and $p = 0.97$ for interaction) of the pattern. However, we did find a main effect of

condition, but not for group or interaction for the final segment of the zigzag 2 pattern (2-way ANOVA, $p = 0.09$ for group, $p = 0.03$ for condition, and 0.27 for interaction). This suggests that a lack of vision influenced the amount of time subjects took only in the final segment of the zigzag 2 pattern.

Dancer and non-dancer, example comparison

We examined the average hip trajectory of an example dancer and an example non-dancer for each block of trials (Figure 4). We chose these subjects because their hip trajectories were accurate examples of the group average trajectories. Ideal trajectories are shown as thick black lines (see Methods). Thin dark (with vision) and light (without vision), red (dancer) and blue (non-dancer) lines show the average hip trajectory for a block of trials ($n=5$). Shading represents the standard deviation. Bar graphs show the MSE_i (top) and MSE_m (bottom) with units of cm^2 for each block of trials.

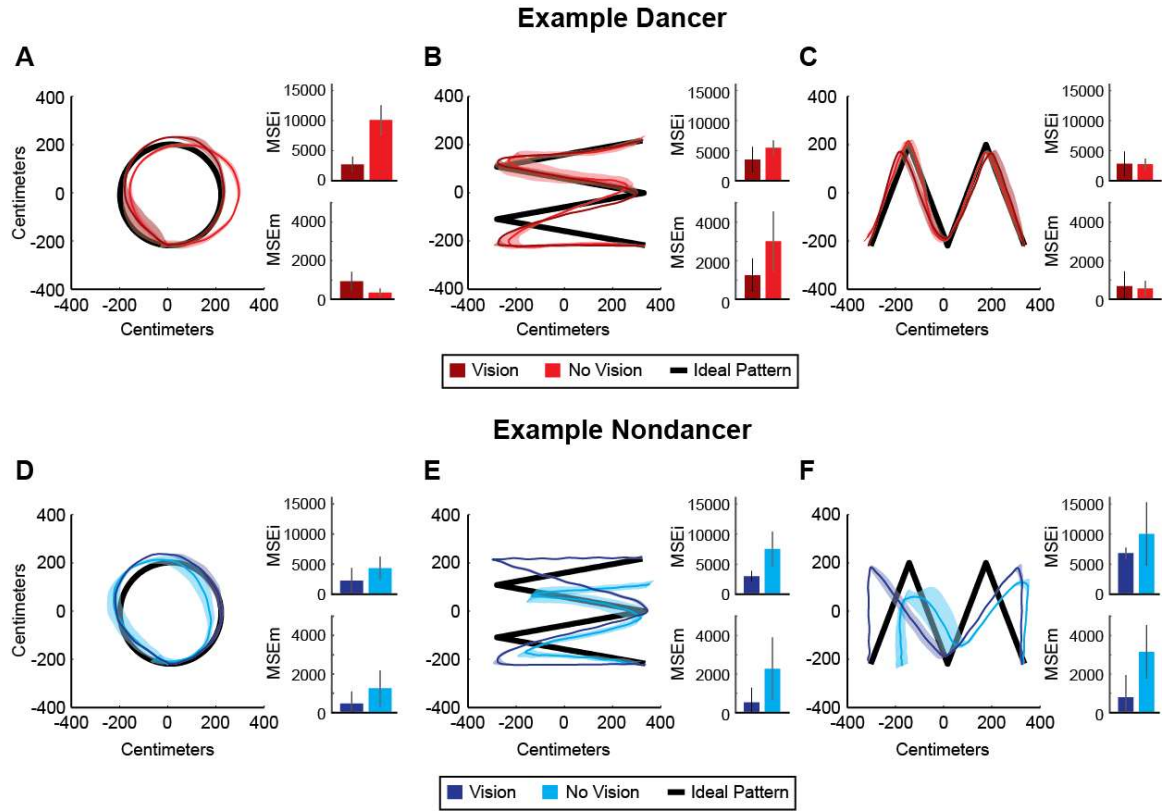


Figure 4 Example Dancer and Non-dancer. A) B) and C) represent single subject data from one dancer. D) E) and F) represent single subject data from one non-dancer. Red bars and traces show data from the example dancer. Blue bars and traces show data from the example non-dancer. Darker shades show data from the vision condition and lighter shades represent data from the no vision condition. Thick black traces show the ideal patterns. In each panel, the top bar graph shows MSE_i and the bottom bar graph shows MSE_m . The units for the MSE measures are cm^2 . Thin black lines on the bars show standard deviation.

For the example dancer and non-dancer, the MSE_i was higher for the no vision conditions for the circle (mean $\pm$ SD: dancer vision: $2737 \pm 1304 \text{ cm}^2$ dancer no vision: $10103 \pm 2462 \text{ cm}^2$ non-dancer vision: $2251 \pm 2125 \text{ cm}^2$ non-dancer no vision: $4342 \pm 1914 \text{ cm}^2$) and zigzag 1 patterns (mean $\pm$ SD: dancer vision: $3532 \pm 2122 \text{ cm}^2$, dancer no vision: $5493 \pm 1212 \text{ cm}^2$, non-dancer vision: $2999 \pm 860 \text{ cm}^2$, non-dancer no vision: $7503 \pm 2900 \text{ cm}^2$) which suggests both example subjects' hip trajectories were less accurate on no vision trials. The dancer had higher MSE_m for the circle when vision was available

(mean $\pm$ SD: dancer vision: $924 \pm 501 \text{ cm}^2$ dancer no vision: $347 \pm 208 \text{ cm}^2$) which implies that the dancer performed more precisely without vision in the circle condition. The non-dancer on the other hand had higher MSE_m on the no vision trials than on vision trials for the circle pattern (mean $\pm$ SD: non-dancer vision: $466 \pm 632 \text{ cm}^2$ non-dancer no vision: $1264 \pm 916 \text{ cm}^2$) which implies that the non-dancer performed less precisely when vision was unavailable. Both the dancer and non-dancer had higher MSE_m when vision was eliminated for the zigzag 1 pattern (mean $\pm$ SD: dancer vision: $1240 \pm 882 \text{ cm}^2$, dancer no vision: $3007 \pm 1552 \text{ cm}^2$, non-dancer vision: $530 \pm 750 \text{ cm}^2$, non-dancer no vision: $2264 \pm 1637 \text{ cm}^2$). This suggests that both subjects performed the zigzag 1 pattern less precisely when vision was not available.

For the zigzag 2 pattern, the dancer's MSE_i and MSE_m for the vision and no vision conditions was not significantly different (mean $\pm$ SD, MSE_i dancer vision: $2835 \pm 2039 \text{ cm}^2$ dancer no vision: $2761 \pm 922 \text{ cm}^2$, MSE_m dancer vision: $680 \pm 765 \text{ cm}^2$ dancer no vision: $556 \pm 394 \text{ cm}^2$) which suggests that the dancer performed equally accurately and precisely when vision was eliminated in this condition. The non-dancer had higher MSE_i and MSE_m in the zigzag 2 pattern when vision was eliminated (mean $\pm$ SD, MSE_i non-dancer vision: $6803 \pm 959 \text{ cm}^2$, non-dancer no vision: $10010 \pm 5248 \text{ cm}^2$, MSE_m non-dancer vision: $792 \pm 1148 \text{ cm}^2$ non-dancer no vision: $3149 \pm 1386 \text{ cm}^2$), revealing that the non-dancer performed less accurately and less precisely when vision was not available.

Dancer and non-dancer, group comparison

We studied the group average hip trajectories for each block of trials (Figure 5).

As in Figure 4, the ideal trajectories are shown as thick black lines, thin dark (with vision) and light (without vision), red (dancer) and blue (non-dancer) lines show the group average hip trajectory for a block of trials ($n=10$), and shading represents the standard error. Bar graphs show the MSE_i (top) and MSE_m (bottom) in units of cm^2 for each block of trials.

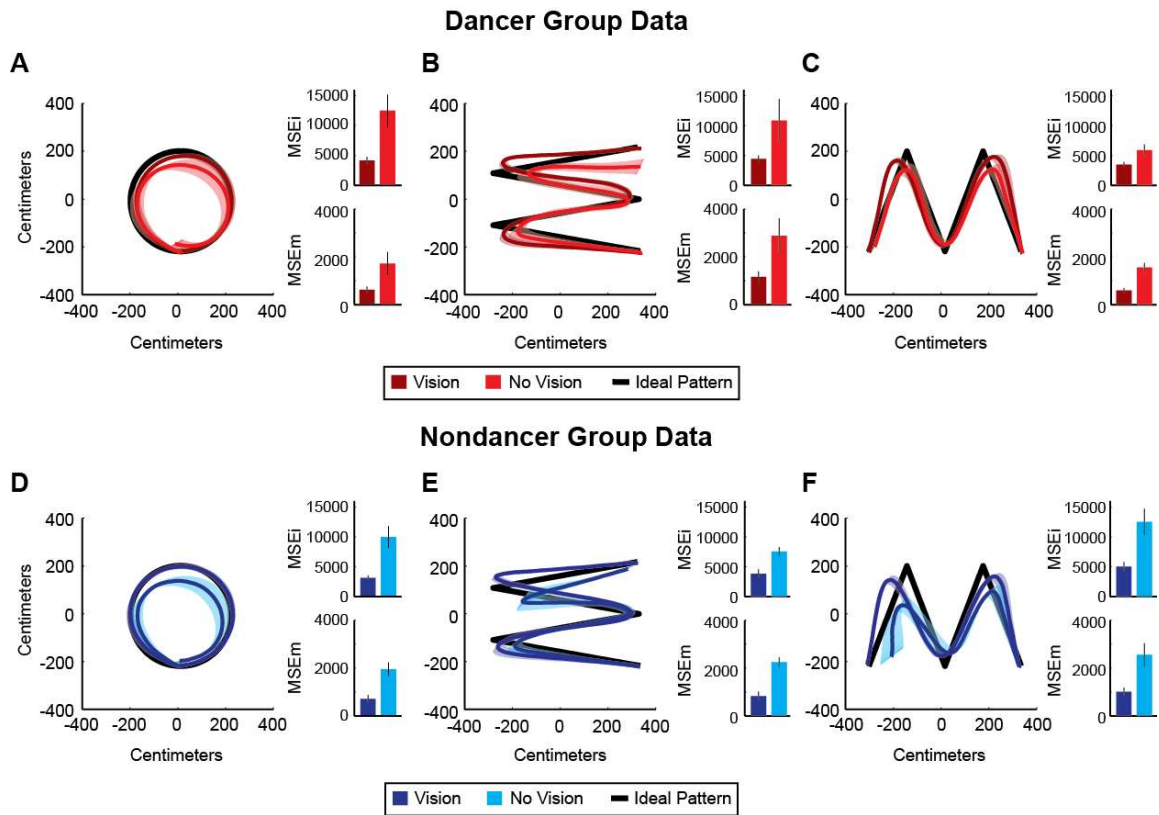


Figure 5 Dancer and Non-dancer Group Data. A) B) and C) show dancer group data. D) E) and F) show non-dancer group data. Red bars and traces show data from the dancer group. Blue bars and traces show data from the non-dancer group. Darker shades show data from the vision condition and lighter shades represent data from the no vision condition. Thick black traces show the ideal patterns. In each panel, the top bar graph shows

MSE_i and the bottom bar graph shows MSE_m. The units for the MSE measures are cm². Thin black lines on the bars show standard error.

For the circle pattern, MSE_i was not significantly different for the dancer and non-dancer groups, but there was a main effect of condition (2-way ANOVA, $p = 0.31$ for group, $p < 0.01$ for condition, and $p = 0.66$ for interaction). Post-hoc tests revealed that MSE_i was lower when vision was available compared to when it was unavailable for both the dancer (paired, one-tailed t-test, $p < 0.01$) and non-dancer groups (paired, one-tailed t-test, $p < 0.01$) in the circle pattern. Together these data suggest that the both dancers and non-dancers' hip trajectories were equally accurate in the circle pattern, but both groups were less accurate when vision was restricted (Figure 5A, D top graphs).

In the zigzag 1 pattern, MSE_i was not significantly different for group, but there was a main effect for condition (2-way ANOVA, $p = 0.31$ for group, $p = 0.01$ for condition, and $p = 0.48$ for interaction). Post-hoc tests revealed that MSE_i was significantly lower when vision was available compared to when it was unavailable for the non-dancer group (paired, one-tailed t-test, $p < 0.01$) in the zigzag 1 pattern. The same post-hoc test did not reach significance for the dancer group (paired, one-tailed t-test, $p = 0.06$) in the zigzag 1 pattern. This suggests that dancers and non-dancers performed equally accurately in the zigzag 1 pattern, but only the non-dancer group performed less accurately when vision was not available (Figure 5B, E).

In the zigzag 2 pattern, MSE_i was significantly different for group and condition (2-way ANOVA $p < 0.01$ for group, $p < 0.01$ for condition, and $p = 0.05$ for interaction) (Figure 5C, F). Post-hoc tests revealed that MSE_i was lower when vision was available

compared to when it was unavailable for both dancers (paired, one tailed t-test, $p < 0.01$) and non-dancers (paired, one tailed t-test, $p < 0.01$) in the zigzag 2 pattern. Post-hoc tests also showed that MSE_i was lower for dancers than for non-dancers both when vision was (two-sample, one tailed t-test, $p = 0.04$) and was not available (two-sample, one tailed t-test, $p < 0.01$) in the zigzag 2 pattern. This suggests that dancers performed more accurately than non-dancers overall, but both groups performed less accurately when vision was restricted.

For the circle pattern, MSE_m was not significantly different for the dancer and non-dancer groups, but there was a main effect of condition (2-way ANOVAs, $p = 0.60$ for group, $p < 0.01$ for condition, and 0.80 for interaction). Post-hoc tests revealed that MSE_m was lower when vision was available compared to when it was unavailable for both dancers (paired, one-tailed t-test, $p = 0.04$) and non-dancers (paired, one-tailed t-test, $p < 0.01$) in the circle pattern. Together these data suggest that the both dancers and non-dancers' hip trajectories were equally precise in the circle pattern, but both groups performed less precisely when vision was restricted (Figure 5A, D).

In the zigzag 1 pattern, MSE_m was not significantly different for group, but there was a main effect for condition (2-way ANOVA, $p = 0.24$ for group, $p < 0.01$ for condition, and $p = 0.71$ for interaction). Post-hoc tests revealed that MSE_m was lower when vision was available compared to when it was unavailable for both the dancers (one-tailed t-test, $p = 0.03$) and non-dancers (one-tailed t-test, $p < 0.01$) in the zigzag 1 pattern. This suggests that dancers and non-dancers performed with equal precision in the

zigzag 1 pattern, but both groups performed less precisely when vision was restricted (Figure 5B, E).

In the zigzag 2 pattern, MSE_m was significantly different for group and condition (2-way ANOVA, $p = 0.02$ for group, and $p < 0.01$ for condition, and $p = 0.31$ for interaction) (Figure 5C, F). Post-hoc tests revealed that MSE_m was lower when vision was available compared to when vision was unavailable for both the dancer (paired, one tailed t-test, $p < 0.01$) and non-dancer groups (paired, one tailed t-test, $p < 0.01$) in the zigzag 2 pattern. Post-hoc tests also showed that MSE_m was lower for dancers compared to non-dancers both when vision was (two-sample, one-tailed t-test, $p = 0.03$) and was not available (two-sample, one tailed t-test, $p = 0.04$) in the zigzag 2 pattern. This suggests that dancers performed more precisely than non-dancers, but both groups performed less precisely when vision was restricted.

To examine the effect of lack of vision on the accuracy of the hip trajectory, we plotted the average MSE_i for no vision trials versus the MSE_i for vision trials for each subject (Figure 6). We took the logarithm of the raw data for this figure to ensure the data was normally distributed for statistical analysis. In this figure, points that fell on the unity line indicate subjects whose accuracy were not affected by lack of vision. That is, the MSE_i for the vision and no vision trials were equal in this case. Points that fell above the unity line indicate subjects whose hip trajectories were less accurate with a lack of vision; the MSE_i for the no vision trials was greater than for the vision trials. Points that fell below the unity line indicate subjects whose hip trajectories were more accurate with a lack of vision; the MSE_i for the no vision trials was less than for the vision trials.

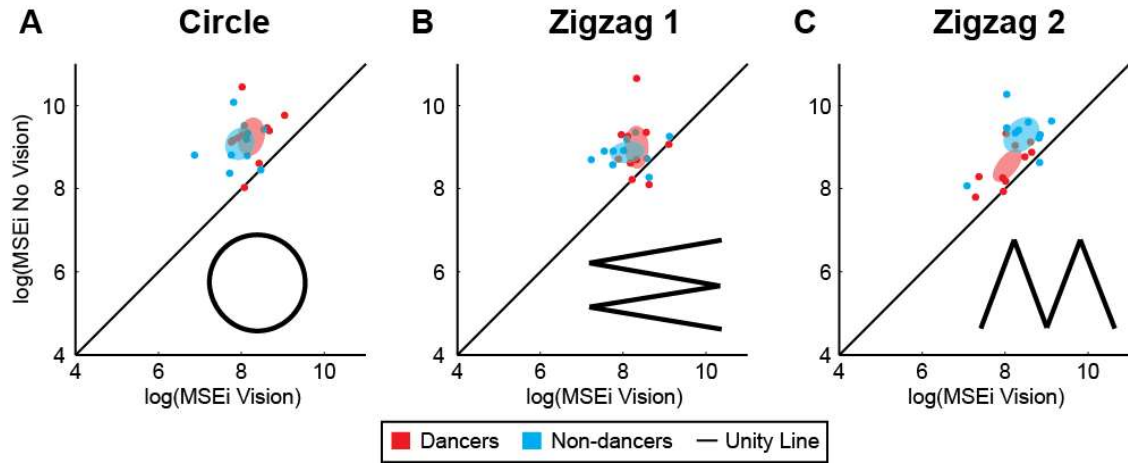


Figure 6 MSE_i Scatterplot for the A) Circle B) Zigzag 1 and C) Zigzag 2 patterns. MSE_i for the no vision condition was plotted with respect to MSE_i for the vision condition. Filled, small circles show average data over five trials for each dancer (red) and nondancer (blue). Red and blue ellipses represent the two standard errors around the group means for the dancer and non-dancer groups, respectively. The thin black line is the unity line. Thick black traces show an example shape of each pattern.

For the circle pattern, there was a significant main effect of condition, but no significant main effect of group or an interaction (2-way ANOVA, $p = 0.19$ for group, $p < 0.01$ for condition, and $p = 0.77$) (mean $\pm$ SEM: dancer vision: 8.24 ± 0.14 , dancer no vision: 9.25 ± 0.20 , non-dancer vision: 7.97 ± 0.15 , non-dancer no vision: 9.08 ± 0.17) (Figure 6A). This suggests that dancers and non-dancers were equally accurate, but the lack of vision influenced accuracy of both groups.

For the zigzag 1 pattern, we found a significant main effect of vision, but no main effect of group or interaction (2-way ANOVA, $p = 0.30$ for group, $p < 0.01$ for condition, and $p = 0.74$ for interaction) (mean $\pm$ SEM: dancer vision: 8.33 ± 0.11 , dancer no vision: 9.00 ± 0.23 , non-dancer vision: 8.10 ± 0.18 , non-dancer no vision: 8.88 ± 0.10) (Figure

6B). This suggests that both dancers and non-dancers were similar in their accuracy, but both experienced a change in accuracy when vision was eliminated.

For the zigzag 2 pattern, there was a significant main effect of group and condition, but no interaction (2-way ANOVA, $p < 0.01$ for group, $p < 0.01$ for condition, $p = 0.26$ for interaction) (mean $\pm$ SEM: dancer vision: 8.05 ± 0.15 , dancer no vision: 8.56 ± 0.17 , non-dancer vision: 8.39 ± 0.19 , non-dancer no vision: 9.29 ± 0.19) (Figure 6C). This suggests that the dancers were more accurate relative to the ideal than non-dancers in the zigzag 2 pattern and both groups experienced a change in accuracy when vision was eliminated. Importantly, our results demonstrate that when the spatial navigation task was more complex, like in the zigzag 2 configuration, dancers outperformed non-dancers in terms of accuracy both when vision was available and restricted.

To examine the effect of lack of vision on precision, we plotted the average MSE_m for no vision trials versus the MSE_m for vision trials for each subject (Figure 7). As above, we determined the logarithm of the raw data for this figure to ensure the data was normally distributed for statistical analysis. In this figure, points that fell on the unity line indicate subjects whose precision of hip trajectory was not affected by lack of vision; the MSE_m for the vision and no vision trials were equal. Points that fell above the unity line indicate subjects whose precision of hip trajectory decreased with a lack of vision; the MSE_m for the no vision trials was greater than for the vision trials. Points that fell below the unity line indicate subjects whose hip trajectories were more precise with a lack of vision; the MSE_m was lower for the no vision trials than the vision trials.

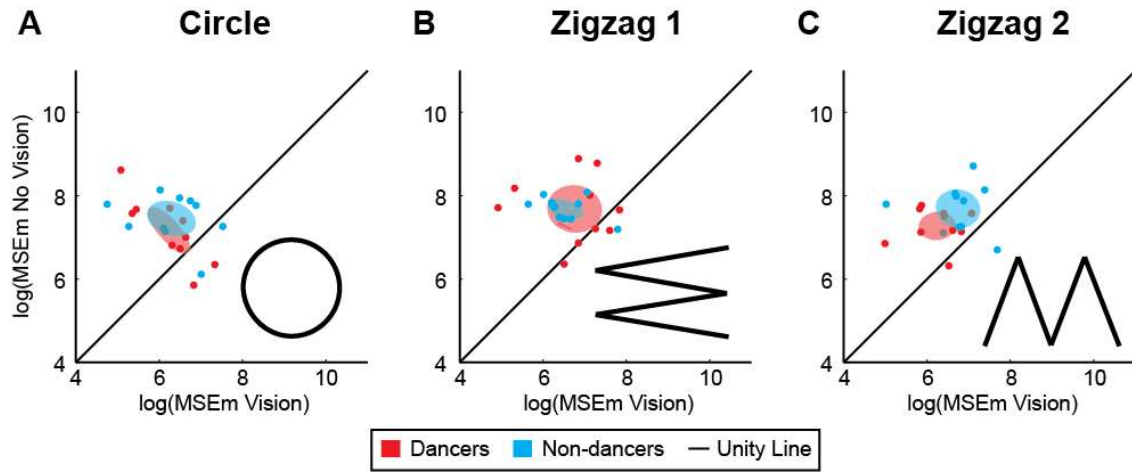


Figure 7 MSE_m Scatterplot for the A) Circle B) Zigzag 1 and C) Zigzag 2 patterns. MSE_m for the no vision condition was plotted with respect to MSE_m for the vision condition. Filled, small circles show average data over five trials for each dancer (red) and nondancer (blue). Red and blue ellipses represent the two standard errors around the group means for the dancer and non-dancer groups, respectively. The thin black line is the unity line. Thick black traces show an example shape of each pattern.

For the circle pattern, there was a significant main effect of condition, but no significant main effect of group or an interaction (2-way ANOVA, $p = 0.47$ for group, $p < 0.01$ for condition, $p = 0.64$ and for interaction) (mean $\pm$ SEM: dancer vision: 6.23 ± 0.23 , dancer no vision: 7.17 ± 0.25 , non-dancer vision: 6.29 ± 0.26 , non-dancer no vision: 7.44 ± 0.19) (Figure 7A). This suggests that dancers and non-dancers were equally precise in their hip trajectories, but the lack of vision influenced precision of both groups.

For the zigzag 1 pattern, we found a significant main effect of vision, but no main effect of group or interaction (2-way ANOVA, $p = 0.62$ for group, $p < 0.01$ for condition, and $p = 0.63$ for interaction) (mean $\pm$ SEM: dancer vision: 6.76 ± 0.30 , dancer no vision: 7.68 ± 0.26 , non-dancer vision: 6.54 ± 0.19 , non-dancer no vision: 7.68 ± 0.09) (Figure 7B). This suggests that both dancers and non-dancers were similar in their precision, but both experienced a change in precision when vision was eliminated.

For the zigzag 2 pattern, there was a significant main effect of group and condition, but no interaction (2-way ANOVA, $p = 0.02$ for group, $p < 0.01$ for condition, and $p = 0.82$ for interaction) (mean $\pm$ SEM: dancer vision: 6.24 ± 0.19 , dancer no vision: 7.27 ± 0.14 , non-dancer vision: 6.74 ± 0.23 , non-dancer no vision: 7.67 ± 0.19) (Figure 7C). This suggests that the dancers were more precise in their hip trajectory than non-dancers in the zigzag 2 pattern and both groups experienced a change in precision when vision was eliminated. Critically, our results demonstrate that when the spatial navigation task was more complex, like in the zigzag 2 configuration, dancers outperformed non-dancers in terms of precision both when vision was available and restricted.

Discussion

Here we found that for each spatial configuration, the accuracy and precision of hip trajectories of dancers and non-dancers were affected by the lack of vision. This demonstrated that dance expertise does not aid in spatial navigation when vision is restricted. We also found that dance expertise did not aid in the accuracy or precision of walking simple spatial configurations like the zigzag 1 and circle patterns. However, dance expertise did allow for more accurate and more precise performance of complex spatial configurations like the zigzag 2 pattern. Thus, our data suggest that dance expertise does aid in the spatial navigation of complex, but not simple spatial configurations.

Neural activation during spatial navigation

Neuroimaging studies have identified the importance of the hippocampus and the parahippocampal region in human navigation (Aguire et al. 1998; Agurie et al. 1996;

Maguire et al. 1998). These structures are necessary for the memory aspects of spatial navigation and it is suggested that spatial navigation deteriorates with age due to a decrease in this visual memory (Moffatt et al., 2001). Interestingly, these same brain regions also respond to visual stimuli (Cameron et al. 2001; Epstein et al. 2003; Epstein and Kanwisher, 1998; Kreiman et al. 2000; Ojemann et al. 2002). This, again, highlights the importance of the visual system for accurate spatial navigation in humans. When vision is restricted however, these areas receive less input which may account for both dancers and non-dancers decrease in performance when vision was eliminated.

Effects of dance experience on motor control

Previous studies have identified some tasks in which dance experience provides an advantage over non-dancers. Dancers have been shown to have improved postural control (Rein et al., 2011) and to be able to hold postures longer (Crofts et al., 1996) than non-dancers. These studies suggest that dance expertise improve postural control in static positions. Dance expertise has also been shown to improve balance proficiency and distance traveled in a beam walking task (Sawers and Ting, 2015). This improved balance proficiency has been linked to improved neural control of movement as evidenced by more consistent motor modules with less coactivity of muscles in dancers compared to non-dancers (Sawers et al., 2015). Taken together, these studies imply that dance expertise improves balance in both static and dynamic balance control tasks. Our results add to this body of motor control research to show that dance expertise provides an advantage when navigating complex spatial configurations.

There is also evidence to suggest that the advantages dance expertise provides are eliminated when vision is not available. Golomer et al. (1999) tested the postural sway of dancers of varying age. They found that the most experienced dancers were more dependent on vision than the younger dancers. de Mello et al. (2017) also found that ballet dancers had more postural sway than non-dancers in a single-leg stance when vision was restricted. These results could be a reflection of how dancers are taught to use their visual system during their training. For example, spotting is a technique used both to balance and to prevent dizziness while turning. This use of the visual system during spotting is a fundamental component of dance expertise. Our results further demonstrate dancers' reliance on the visual system in motor control tasks; dance expertise did not provide any advantage in spatial navigation over non-dancers when vision was restricted.

We also found that dancers and non-dancers performed similarly in two of the three spatial configurations. It is possible that this may be a result of the simplicity of the two configurations and the simplicity of the walking task. However, when the spatial configuration was more complex in the zigzag 2 pattern, dancers outperformed non-dancers. This suggests that spatial navigation may be independent of body representation. Alternatively, when asked to perform more complex skills along the same path, body representation may be more critical for accurate performance. Our next study intends to examine this by having dancers perform choreography in the same spatial configurations and determine whether they are able to transfer these motor skills from one spatial context to another.

EXPERIMENT TWO: SPATIAL GENERALIZATION OF UNCONSTRAINED MOTOR SKILLS

Introduction

Motor learning describes the changes in movements that occur with practice or experience. Recently, Shmuelof and Krakauer (2012, 2014) provided a meaningful distinction between two categories of motor learning: motor adaptation and unconstrained motor skill learning. Motor adaptation is characterized by fast behavioral changes in response to a perturbation that induces a systematic error (Held, 1965; Shadmehr and Mussa-Ivaldi 1994; Krakauer, 2009). In this case, motor learning returns performance to baseline levels. In contrast, motor skill learning requires slower changes in behavior that lead to improvements in performance beyond baseline levels (Schmidt, 1975; Wulf et al. 2010). If motor adaptation and unconstrained motor skill learning are both properties of motor learning, then the features observed in motor adaptation (retention, generalization to untrained contexts, etc.) should also apply to motor skill formation.

Generalization, one feature of motor adaptation, refers to the ability to transfer learning from a trained context to an untested context. Generalization has been studied extensively using several motor adaptation paradigms including visuomotor rotation (Krakauer, 2009), force-field adaptation (Criscimagna-Hemminger et al. 2003), and split-belt treadmill walking (Reisman et al. 2009, Vasudevan and Bastian 2010, Savin et al. 2014). Through these studies, generalization has been studied across movement speeds

and extents (Goodbody and Wolpert 1998; Mattar and Ostry 2010; Joiner et al. 2011), configurations (Shadmehr and Mussa-Ivaldi, 1994; Shadmehr and Moussavi, 2000; Malfait et al. 2002), effectors (Criscimagna-Hemminger et al. 2003, Malfait et al. 2004, Taylor et al. 2011, Joiner et al. 2013), and directions (Donchin et al. 2003; Thoroughman and Taylor, 2005; Hwang et al. 2006; Fernandes et al. 2012). Currently, however, few studies have determined the extent generalization is also a property of motor skill learning.

Here, we will focus specifically on spatial generalization which has been studied extensively in motor adaptation paradigms, particularly force-field adaptation. Force-field adaptation is commonly studied using a robotic manipulandum. Subjects make constrained reaching movements where the goal is to place a cursor in a goal target. During baseline movements, the robotic manipulandum moves freely and subjects make straight reaching movements unperturbed. At the beginning of the training period, a force proportional in magnitude and orthogonal in direction is applied to the robotic handle. Initially, subjects' movements take a curved path and subjects apply little force to the handle. By the end of training, subjects learn to apply a force to the handle that corresponds to the force that the robot applies and subjects make straighter movements between targets (Shadmehr and Mussa-Ivaldi, 1994).

Previous work has shown that aftereffects in response to a force-field perturbation also occur in novel workspaces (Shadmehr and Mussa-Ivaldi, 1994) which suggests that adaptation to perturbations can generalize to new contexts. Malfait et al. (2002) expanded upon this and identified that adaptation to force-field perturbations generalizes from one

arm configuration to another as long as the joint displacements remain the same. This suggests that motor adaptation is tied to intrinsic coordinates, and much less to joint velocities. Force-field adaptation has also been demonstrated to generalize from a learned body posture to a novel posture (Ahmed and Wolpert, 2009). While it is clear that generalization occurs in a wide variety of the spatial context changes, it remains unclear whether these observations would occur for skilled, unconstrained movement tasks.

To study generalization of motor skills, we examined dancers performing a phrase of choreography in a trained and untrained spatial contexts. Dance is an ideal motor skill for study because ballet technique requires that movements be performed in precise ways which allows individual dancers to perform skills consistently from repetition to repetition (Hopper et al., 2018). In addition, ballet training ensures that multiple dancers on stage together will perform skills in an aesthetically similar way. Dancers are also trained to move in time with music or a metronome which allows for a consistent performance across dancers with respect to time. Previous work has found that dance training leads to some cognitive benefits over non-dancers including a heightened sense of body awareness and orientation within the environment (Fonseca et al. 2014; Margaret et al. 2014). The current study aims to examine the generalization of motor skills, so we chose dancers as our model for experts of spatial awareness, orientation within the environment, and motor skill.

In the current study, we examined dancers performing a phrase of choreography that was learned in one spatial configuration, and then tested in two novel configurations. Utilizing motion capture cameras and analysis, we monitored body position throughout

each trial. We examined the accuracy of the dancers' performance of the desired configurations and the consistency of their performance from trial to trial. Our results provide insight into the extent generalization occurs in tasks requiring highly skilled, unconstrained movements.

Methods

Participants

Ten subjects volunteered to participate in this experiment. All participants were female, age 18-22, had no known neurological impairment, and were naive to the purpose of this study, which consisted of performing complex dance movements in different spatial configurations. All subjects were enrolled in the George Mason University School of Dance and had completed more than twelve years of dance experience, defined as participating in weekly dance classes, prior to participation in the study. Subjects did not receive any training before data collection, and each individual completed one 1-hour session. The study protocol was approved by the George Mason University Institutional Review Board. All participants gave informed consent.

Experimental Setup

Motion capture cameras were used to monitor subjects' position within a 6.45 m by 4.50 m rectangular space. Twenty Optitrack Prime 13 cameras were mounted in a dance studio in the George Mason University School of Dance (Figure 1). The Optitrack baseline marker set ($n = 37$ markers) was applied to each subject (Figure 2). Three-dimensional position data were collected at 120 Hz for each of the 37 markers.

The rectangular space was marked on the floor with tape and subjects were instructed to stay within those bounds through the duration of the experiment. Four X's marked the start and stop location for the trained and the novel spatial configurations (training: zigzag 1, test: circle and novel zigzag).

Task

Dancers learned a phrase of choreography via video recordings. Two of the videos were slow demonstrations of the choreography; a peer showed the specific movements required in the phrase and the timing of those movements. In one of the demonstration videos, the camera filmed the peer from the front, and the other demonstration video filmed the peer from the back. Two other videos were examples of the peer performing the choreography at the trained speed (110 beats per minute (bpm)) and in the trained configuration (zigzag 1 pattern). One example video was filmed from the front perspective and one was filmed from the back. Both example videos had audio of a metronome set to 110 bpm. Dancers were able to watch these videos as many times as they needed to feel confident in their ability to perform the choreography on their own. The phrase of choreography was composed of eight sets of three counts for a phrase total of 24 counts. To complete one trial, the phrase of choreography was repeated twice for a trial total of 48 counts. At the ideal tempo, the duration of one trial was 26.18 seconds (48 beats at 110 bpm). The choreography was written such that dancers would make the trained zigzag 1 pattern as they traveled through the rectangular space (Figure 8). At the beginning of the training block and each test block, dancers were shown the desired pattern like those shown in Figure 8 and the experimenter explicitly pointed out the start

and stop locations marked on the floor. Dancers were not able to practice the circle or novel zigzag patterns prior to data collection. The same phrase of choreography was used through the duration of the experiment.

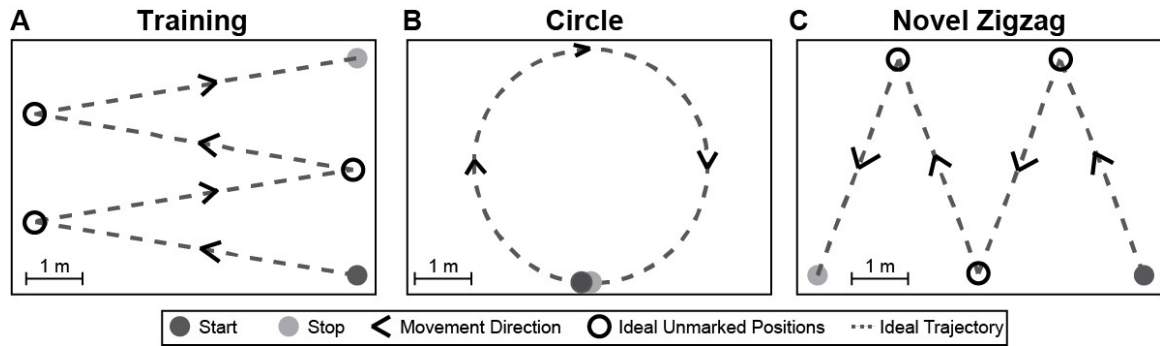


Figure 8 Ideal Movement Trajectories from Bird's Eye View Perspective. In each pattern, the dark gray filled circle represents the start position and the light gray filled circle represents the end position. Arrows indicate the direction of movement. Open black circles indicate the changes in direction which were not explicitly marked on the floor. Dotted lines show the ideal movement trajectory for the A) training, B) circle, and C) novel zigzag patterns.

Experimental Procedure

Dancers first completed a training period where they performed a block of ten trials in the trained zigzag 1 configuration. Following this training period, dancers were asked to perform two test blocks of four trials in the two test configurations: circle and novel zigzag. The order of the test blocks was randomized for each subject. During each trial, a metronome played at 110 bpm.

Analysis of body motion

The position of the body (hip trajectory) was determined using the average location of the four markers on the hips. The velocity of the body was calculated based

on the change in position in the X and Y dimensions of the body position. The start (end) of a trial was represented by the point in time where the body velocity increased (decreased) to 0.05 m/s. We then determined the duration of the movement from movement start to end and converted this to a percentage from 0% to 100%. We then examined the hip trajectory at each 0.5% increment. The hip trajectory was then averaged across each trial within a block of training or test trials and then across subjects.

The ideal pattern was based on the position of the start and end tapes marked on the floor. For both ideal zigzag patterns (trained and novel), the second change in direction was the linear midpoint between the start and end locations. For the ideal trained pattern, the first and third changes in direction were determined by dividing the distance between the start and midpoint position and the midpoint and the end position in the Y dimension, respectively, and 15 cm from the outer bounds of the space based on the blue tape in the X dimension. For the ideal novel zigzag, the first and third changes in direction were determined by dividing the distance between the start and midpoint position and the midpoint and the end position in the X dimension, respectively, and 15 cm from the outer bounds of the space based on the blue tape in the Y dimension. The diameter of the ideal circle was 4.20 m (15 cm inside the bounds of the rectangular space).

To examine the consistency of movement across conditions, we calculated the total time taken to complete each trial. The time was calculated from the start to the stop of each trial, averaged across trials within a block, then across subjects.

To determine how accurately dancers were able to adjust their movements from the training pattern to the novel zigzag pattern, we scaled their movement from the training pattern to most closely match their movement from the novel zigzag pattern. We compared the scaling the dancers actually performed to the ideal scaling based on the ideal training and novel zigzag patterns. We first identified the horizontal and vertical scaling of the ideal training pattern that resulted in the lowest MSE when compared to the ideal novel zigzag pattern. Here we rotated the ideal training pattern so the start and end locations line up with those from the novel zigzag pattern. We then identified the ideal scaling of the horizontal and vertical position points from the rotated ideal training pattern such that the scaled horizontal and vertical position points and the points from the ideal novel zigzag pattern have the lowest MSE. We found that multiplying the horizontal position data from the rotated ideal training pattern by 1.47 and the vertical position data from the rotated ideal training pattern by 0.69 resulted in the lowest MSE between the ideal novel zigzag pattern and the scaled data (Figure 9).

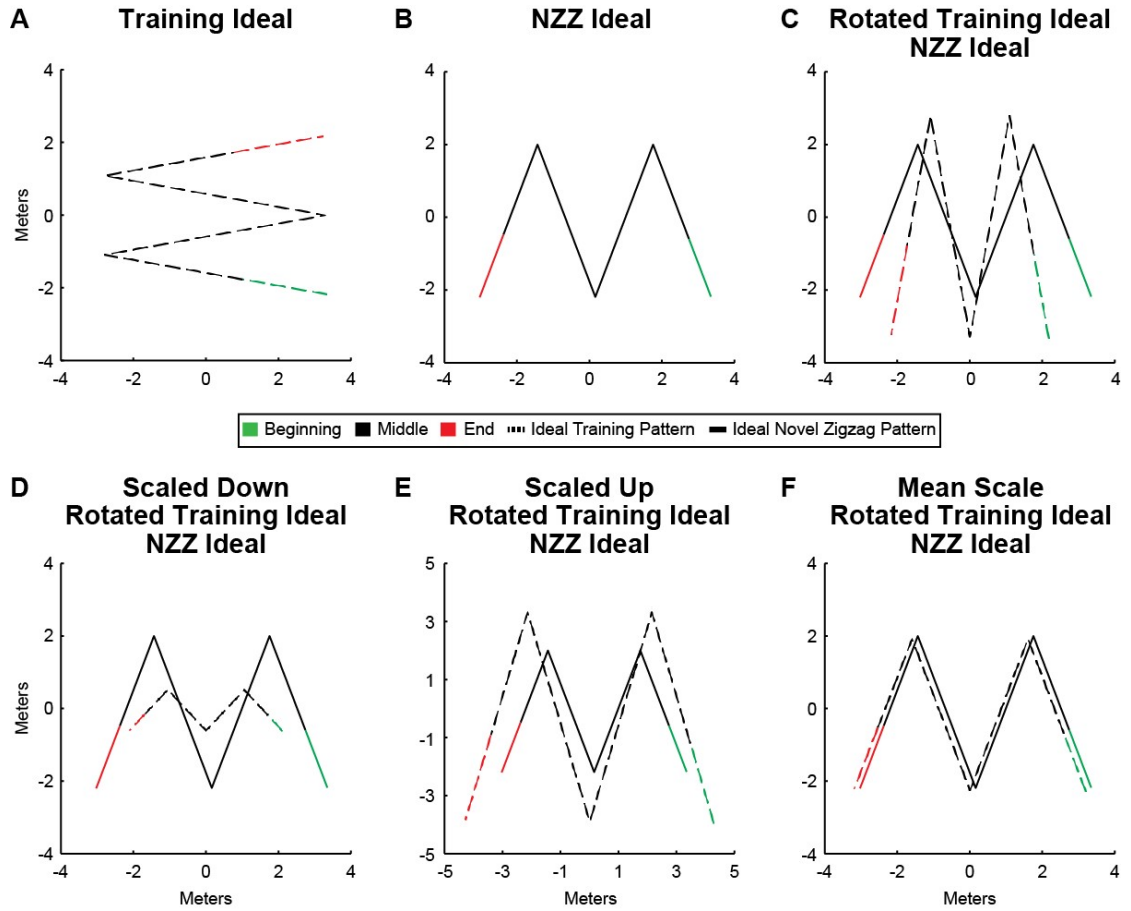


Figure 9 Illustration of Calculating the Ideal Spatial Scaling Based on Ideal Training and Novel Zigzag Patterns. Dashed traces represent the ideal training pattern. Solid traces represent the ideal novel zigzag pattern. Green, black, and red sections represent the beginning, the middle, and the end of the ideal patterns, respectively. A) Ideal training pattern. B) Ideal novel zigzag pattern. C) Ideal novel zigzag and ideal training pattern rotated to match the dimensions of the novel zigzag pattern. D) Ideal novel zigzag pattern plotted with the rotated ideal training pattern scaled down in both the horizontal and vertical dimensions. E) Ideal novel zigzag pattern plotted with the rotated ideal training pattern scaled up in both the horizontal and vertical dimensions. F) Ideal novel zigzag pattern plotted with the ideally scaled and rotated training pattern where we found the minimum MSE between the two traces.

To determine the actual scaling dancers performed, we first rotated and then scaled the average training pattern from each subject from 0.97 to 1.97 by 0.005 in the horizontal dimension and 0.185 to 1.185 by 0.005 in the vertical dimension. We then found the MSE between each scaled training pattern and the actual data from each trial of the novel zigzag pattern (Figure 10). We averaged the MSEs across novel zigzag pattern

trials, then across subjects. The MSEs were plotted in a heat map (Figure 12). We also found the horizontal and vertical scaling each dancer used and plotted the average over all dancers and the ideal scaling based on the ideal training and novel zigzag patterns (Figure 12).

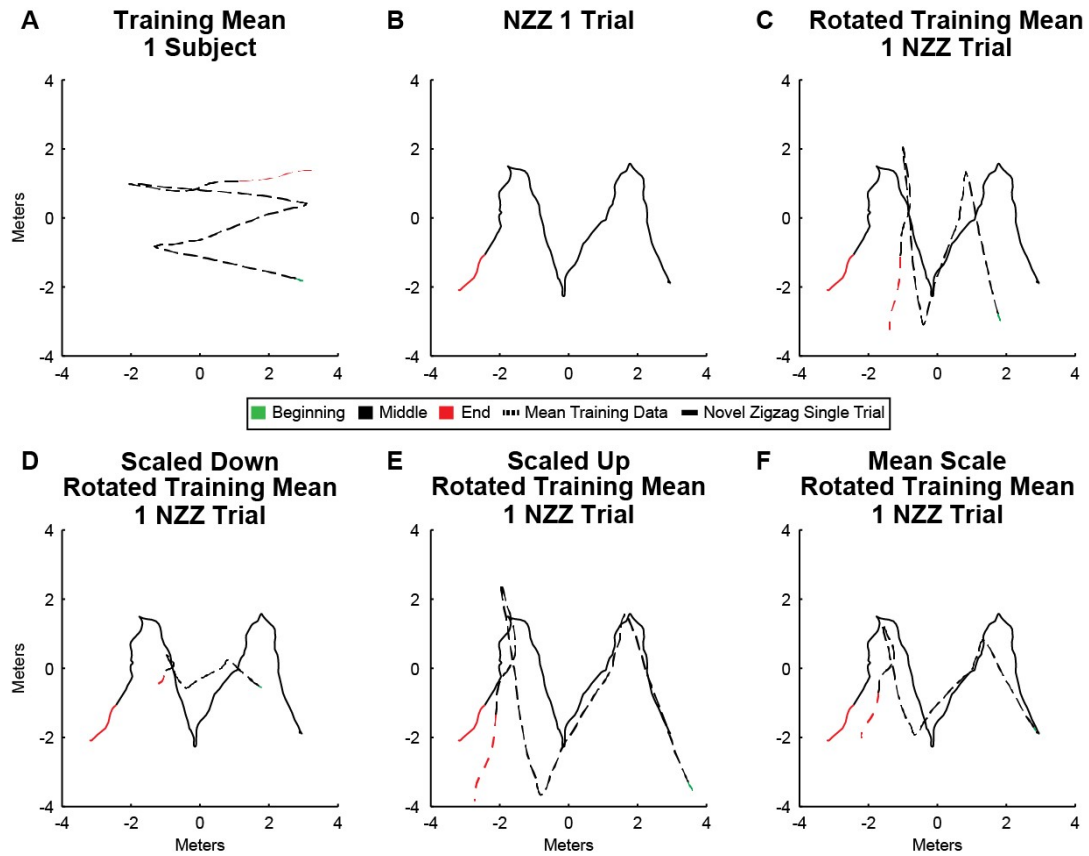


Figure 10 Illustration of Calculating the Each Subject's Spatial Scaling Based on Mean Training Data and Data from a Single Novel Zigzag Trial. Dashed traces represent one subject's mean hip trajectory in the training pattern. Solid traces represent the hip trajectory on a single novel zigzag trial. Green, black, and red sections represent the beginning, middle, and end of the trajectories, respectively. A) Mean hip trajectory for one subject in the training pattern. B) Hip trajectory from one trial in the novel zigzag pattern. C) Single trial novel zigzag hip trajectory and mean training hip trajectory rotated to match the dimensions of the novel zigzag trial. D) Single trial novel zigzag hip trajectory plotted with the rotated mean training hip trajectory scaled down in both the horizontal and vertical dimensions. E) Single trial novel zigzag hip trajectory plotted with the rotated mean training hip trajectory scaled up in both the horizontal and vertical dimensions. F) Single trial novel zigzag hip trajectory plotted with the rotated mean training hip trajectory scaled in the horizontal and vertical dimensions where we found the minimum MSE between the two traces.

We also examined the hip trajectory of each trial relative to the ideal pattern and to the mean hip trajectory for each block of training or test trials (Figure 11). To quantify the accuracy of the hip trajectories, we calculated the mean squared error (MSE) between the hip trajectory on each trial and the ideal pattern. We will refer to this calculation as mean squared error relative to the ideal pattern or MSE_i . In Figure 11D, we calculated the MSE_i for each subject within a given block of trials, then averaged across subjects. To examine the precision of hip trajectory, we calculated the MSE between the hip trajectory on each trial and the mean hip trajectory for the respective block of training or test trials. We will refer to this calculation as the mean squared error relative to the mean hip trajectory or MSE_m . In Figure 11E, we calculated the MSE_m for each subject within a given block of trials, then averaged across subjects. The units for all measures of MSE are cm^2 .

Statistical Analysis

A one-way ANOVA was performed to identify whether there was a difference in the average time to complete trials in the trained and test patterns. We also performed two one-way ANOVAs to test whether there was a difference in MSE_i or MSE_m for the three spatial configurations. Because we found a main effect for MSE_i , we also performed paired t-tests to determine which pair or pairs of the three conditions contained a significant difference in MSE_i . We used a Bonferroni correction to adjust for multiple comparisons. To determine whether the average horizontal and vertical scaling was significantly different from the known ideal horizontal and vertical scaling, we performed

two one-tailed t-tests. All statistical analyses were performed with MATLAB, and for all tests the significance level was 0.05.

Results

Comparison of time elapsed during trials in each spatial configuration

We first quantified the amount of time dancers required to complete the training, circle, and novel zigzag pattern trials. The repeated phrase of choreography was the same for each of the patterns. Therefore, the time used to complete each pattern should have been approximately equal provided performance was not different between spatial configurations. A one-way ANOVA revealed that there was no significant difference in the average time taken to complete training, circle, and novel zigzag patterns ($p = 0.35$). The dancers took 28.5 ± 0.6 , 27.1 ± 0.7 , and 28.1 ± 0.7 seconds on average to complete trials in the training, circle, and novel zigzag conditions, respectively. This suggests that dancers performed the choreography consistently in time despite the change from trained to untrained spatial configurations.

Comparison of performance to the ideal trajectory and mean path for each pattern

We then examined the hip trajectories (Figure 11). We first plotted the average hip trajectory across all subjects for each pattern (Figure 11A, B, and C). We then calculated the MSE_i between the hip trajectory on each trial and the ideal pattern (Figure 11D) and the MSE_m between the hip trajectory on each trial and the average hip trajectory for each pattern (Figure 11E). A one-way ANOVA found that there was a significant difference between the MSE_i for the three different patterns ($p = 0.04$). Post-hoc tests with a Bonferroni correction for multiple comparisons revealed that the MSE_i

for the novel zigzag pattern was lower than for the training pattern (one-tailed, t-test $p < 0.01$). This suggests that the dancers perform more accurately in the novel zigzag condition than in the training condition. A one-way ANOVA comparing the MSE_m for the three patterns revealed no significant difference between the three patterns ($p = 0.52$). This implies that the dancers performed the three patterns equally precisely.

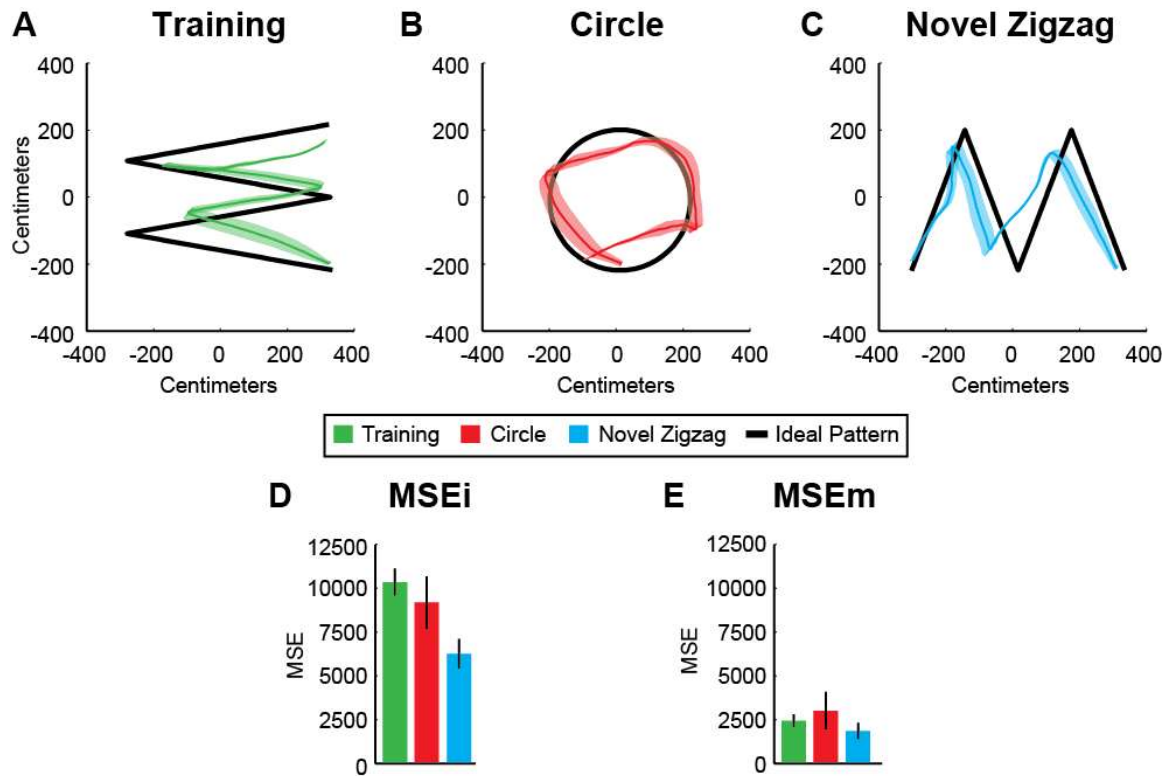


Figure 11 Hip Trajectories and MSE_i and MSE_m . Average hip trajectories are plotted with the ideal trajectory for each of the three patterns: A) training, B) circle, and C) novel zigzag. Thick black traces represent the ideal trajectory for each pattern. Thin colored traces represent the average hip trajectory across ten subjects. Shading represents standard error. Green represents data from the training condition. Red shows data from the circle condition and blue shows data from the novel zigzag pattern. The mean squared error relative to the ideal (MSE_i) and mean squared error relative to the mean hip trajectory (MSE_m) are plotted in the bar graphs with units of cm² in D) and E). Thin black lines on bars represent the standard error.

Analysis of spatial scaling between configurations

Finally, we compared the horizontal and vertical scaling of the training hip trajectories dancers performed and the ideal scaling they should have applied in order to accurately perform the novel zigzag pattern. The surface plot of MSE values shows low values of MSE in cooler colors and higher values of MSE in hotter colors (Figure 12). The thick black lines indicate the ideal scaling of the training pattern that results in the lowest MSE between the scaled training pattern and the ideal novel zigzag pattern ($1.47 * \text{ideal rotated training horizontal data}$ and $0.69 * \text{ideal rotated training vertical data}$). The dashed lines indicate the group average of the horizontal and vertical scaling that resulted in the lowest MSE between the actual rotated and scaled training data and the actual data from the novel zigzag pattern.

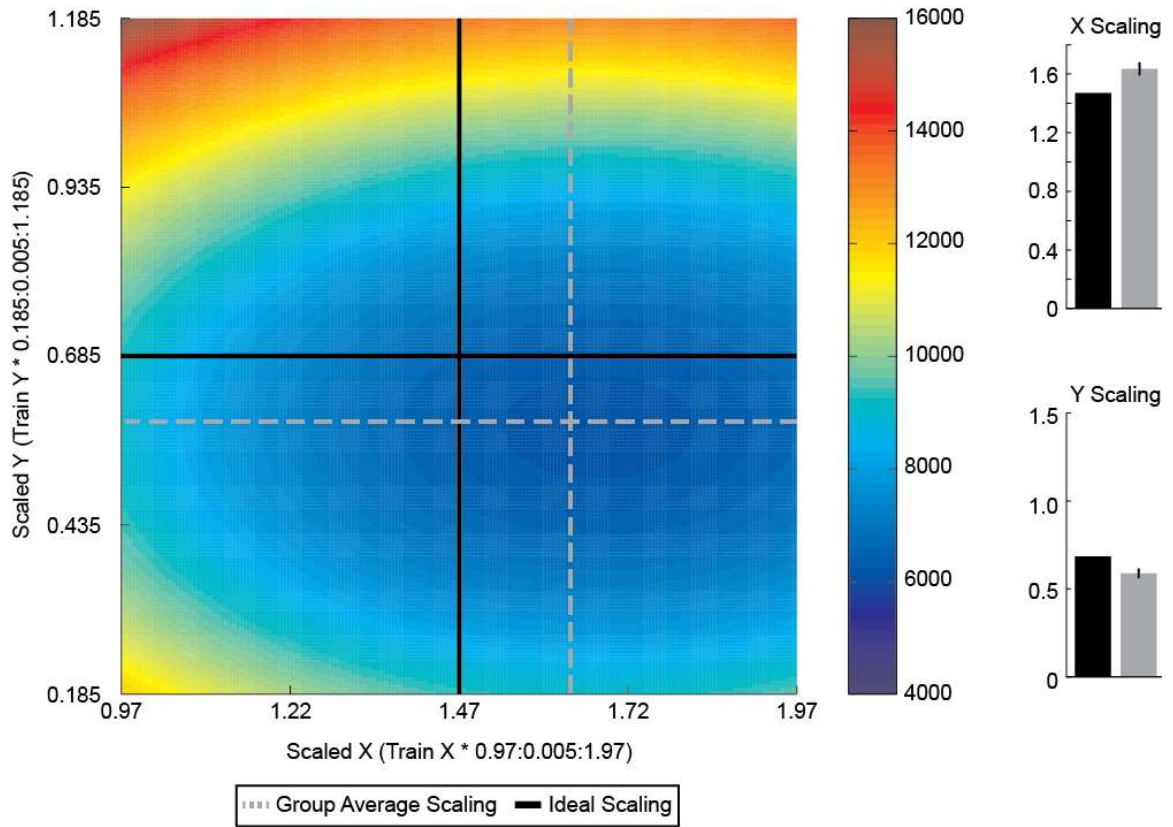


Figure 12 Ideal Horizontal and Vertical Spatial Scaling of the Training Pattern to Match the Novel Zigzag Pattern Performance. Heat map represents the scaling of the horizontal data from the training pattern on the X axis and scaling of the vertical data from the training pattern on the Y axis. Each point in this figure represents the MSE between the data from the novel zigzag pattern and the scaled horizontal and vertical data from the training pattern. Warm colors show high MSE values and cooler colors show lower MSE values with units of cm^2 . The thick black lines represent the ideal horizontal and vertical scaling based on the ideal training and novel zigzag patterns. Gray dashed lines represent the average scaling that resulted in the lowest MSE between the scaled training positional data and the actual positional data from the novel zigzag pattern. The top bar graph shows the ideal horizontal scaling based on the ideal patterns in black and the group average of the actual horizontal scaling in gray. The bottom bar graph shows the ideal vertical scaling based on the ideal patterns in black and the group average of the actual vertical scaling in gray. Thin black lines represent the standard error.

The group average horizontal scaling was identified as 1.64 ± 0.05 (mean $\pm$ SE) times the rotated training horizontal data and the group average vertical scaling was identified as 0.59 ± 0.03 (mean $\pm$ SE) times the rotated training vertical data. We ran two t-tests to identify whether the group averages for the horizontal and vertical scaling of the actual data differed from the scaling based on the ideal patterns. We found that the actual

horizontal scaling was significantly greater than 1.47 (one-tailed t-test, $p < 0.01$) and the actual vertical scaling was significantly less than 0.69 (one-tailed t-test, $p < 0.01$). This indicates that dancers tended to overestimate the upscaling they needed to transform the training pattern to the novel zigzag pattern in the horizontal dimension and tended to overestimate the downscaling needed to transform the training pattern to the novel zigzag pattern in the vertical dimension.

Discussion

Collectively, our results suggest that spatial generalization does occur in the case of unconstrained motor skills. We found that dancers moved in the desired patterns with equal precision in the trained and novel contexts. Additionally, dancers performed with equal accuracy for the trained and circle pattern and performed more accurately in the novel zigzag pattern. Finally, dancers were able to scale their movements from the trained pattern to the novel zigzag pattern though they tended to overestimate the upscaling needed in the horizontal dimension and overestimate the downscaling needed in the vertical dimension.

To better understand the underlying neural processes of generalization, Brayanov et al. (2012) evaluated whether intrinsic or extrinsic representations are used in generalization of motor adaptation. They identified that both intrinsic and extrinsic representations are used when transferring learning from a training to an untrained context. When considering our results, it is likely that dancers utilized both intrinsic and extrinsic representations while transferring motor skills from the trained pattern to the test patterns.

Brayanov et al. (2012) also posit that a collection of neurons may encode the memory of generalization of simple movement using a gain-field combination of intrinsic and extrinsic representations. It is possible that these same neurons contribute to the motor memories dancers' utilize to transfer motor skills to new contexts. This hypothesis could be tested and confirmed using functional magnetic resonance imaging, but the skilled motor learning task would need to involve only hand or wrist movements as in Shmuelof et al. (2012) due to the limitations of brain imaging which require subjects to remain still during scans.

In the future, we will examine the whole-body movement in three dimensions. Here, we will determine how consistent dancers perform the choreography over the course of each trial. More specifically, we intend to examine the variability of the arm and leg movements across trials in the training and test blocks in order to quantify the consistency of the dancers' movements despite the change in spatial context. We expect that the dancers' movement will have very low variability within each subject, but also across subjects. We expect the change in spatial context will have very little effect on the variability of the movement which would provide further evidence that dancers are able to transfer motor skills from a trained to an untrained spatial configuration.

EXPERIMENT THREE: TEMPORAL GENERALIZATION OF UNCONSTRAINED MOTOR SKILL

Introduction

The previous study established that dancers are able to transfer motor skill learning from a trained spatial configuration to untrained spatial configurations. Thus, our results suggest that generalization may be a property of both motor adaptation and motor skill learning. In the subsequent study, we further examined generalization of motor skill learning, but in this case we tested the extent dancers are able to transfer skill learning from a trained to untrained performance speeds.

Generalization of learning across movement speeds and extents has been demonstrated using simple, confined movements (Goodbody and Wolpert 1998; Mattar and Ostry 2010; Joiner et al. 2011). In each of these studies, subjects completed a force-field adaptation task where subjects were asked to counter a velocity-dependent force that was applied orthogonally to the direction of movement. Goodbody and Wolpert (1998) found near linear transfer of adaptation from slow to fast movements. These results, however, could be explained by the random presentation of force-fields of differing magnitude. Scheidt et al. (2001) found that when varying magnitudes of force-field are presented, subjects adapt to the average of those force-fields. Later, Mattar and Ostry (2010) found level extrapolation of adaptation from trained to untrained speeds. Their study, however, increased both speed and extent simultaneously, so their results could be

attributed to contextual effects. Joiner et al. (2011) addressed the study design issues that could have contributed to previous conflicting results. Importantly, Joiner et al. (2011) trained subjects to move to a target within a specified movement duration (speed), then tested transfer of force-field adaptation to a shorter movement duration (faster speed). They found that approximately 74% of adaptation transferred from the longer to the shorter movement duration. Their results definitively show generalization of motor adaptation across movement speeds, but it remains unknown whether this effect can be observed in motor skill learning.

Dancers provide an interesting population to study temporal generalization of motor skills because they are often asked to perform these tasks during the process of learning and perfecting choreography. Dancers often learn choreography at slower speeds and then perform that choreography at faster speeds with music. Similarly, a choreographer or teacher may ask dancers to perform at slower or faster tempos to teach dancers differences in the weight and flow of movement. Sgouramani and Vatkis (2014) evaluated dancer and non-dancer timing judgments using a production task where subjects were asked to stop a video when they felt a certain amount of time had passed. They found that dance expertise was associated with lower variability in these timing judgments.

In addition, dancers have been shown to display more interpersonal synchrony than dyads of non-dancers (Sofianidis and Hatzitaki, 2012) which suggests that dancers are better able to integrate timing cues in order to synchronize movement with a partner than non-dancers. Interestingly, when dancers were asked to perform a four-minute

phrase of choreography without music or timing cues, dancers tended to speed up the choreography and end fourteen seconds early. This 5% difference was attributed more to memory errors (forgetting segments of choreography) rather than internal timing errors (Stevens et al. 2009). It appears that dancers have a superior ability to judge timing, integrate time cues to guide movement, and perform motor skills consistently in time without any time cues. This information suggests that dancers may have an advantage in transferring motor skills from trained to untrained speeds, but their ability to do this has yet to be studied or quantified.

In the current study, we examined dancers performing a phrase of choreography in a trained tempo (110 bpm) and then tested transfer to several untrained tempos (55 bpm, 88 bpm, 99 bpm, 121 bpm, 132 bpm, and 165 bpm). We utilized motion capture analysis to monitor dancers' body position throughout each trial. Our results provide insight into the ability of humans to transfer motor skills from experienced movement speeds to unexperienced movement speeds. We intend to further establish that temporal generalization is not just a property of motor adaptation, but is also a property of motor skill learning.

Methods

Participants

Ten subjects volunteered to participate in this experiment. All participants were female, age 18-22, had no known neurological impairment, and were naive to the purpose of this study, which consisted of performing a complex movement sequence at different speeds. All subjects were enrolled in the George Mason University School of Dance and

had completed more than 12 years of dance experience, defined as participating in weekly dance classes, prior to participation in the study. Subjects did not receive any training before data collection, and each individual completed one 1-hour session. The study protocol was approved by the George Mason University Institutional Review Board. All participants gave informed consent.

Experimental Setup

Motion capture cameras and markers were used to monitor subjects' position within a 6.45 m by 4.50 m rectangular space. Twenty Optitrack Prime 13 cameras were mounted in a dance studio in the George Mason University School of Dance (Figure 1). The Optitrack baseline marker set ($n = 37$ markers) was applied to each subject (Figure 2). Three-dimensional position data were collected at 120 Hz for each of the 37 markers.

The rectangular space was marked on the floor with tape and subjects were instructed to stay within those bounds through the duration of the experiment. Two X's marked the start and stop location for each trial.

Task

Dancers learned a phrase of choreography via video recordings. Two of the videos were slow demonstrations of the choreography; a peer showed the specific movements required in the phrase and the timing of those movements. In one of the demonstration videos, the camera filmed the peer from the front, and the other demonstration video filmed the peer from the back. Two other videos were examples of the peer performing the choreography at the trained speed, 110 bpm; one example video filmed from the front perspective, and one from the back. Both example videos had audio

of a metronome set to 110 bpm. Dancers were able to watch these videos as many times as they needed to feel confident in their ability to perform the choreography on their own. The phrase of choreography was composed of eight sets of three counts for a phrase total of 24 counts. To complete one trial, the phrase of choreography was repeated twice for a trial total of 48 counts. At the trained tempo, the duration of one trial was ideally 26.18 seconds (48 beats at 110 bpm). The choreography was written such that dancers would make a zigzag pattern as they traveled through the rectangular space (Figure 13). The example videos showed the peer performing the zigzag pattern. Dancers were also shown Figure 13 so they could clearly see the ideal pattern and the experimenter explicitly pointed out the start and stop locations marked on the floor. The same phrase of choreography was used throughout the duration of this experiment.

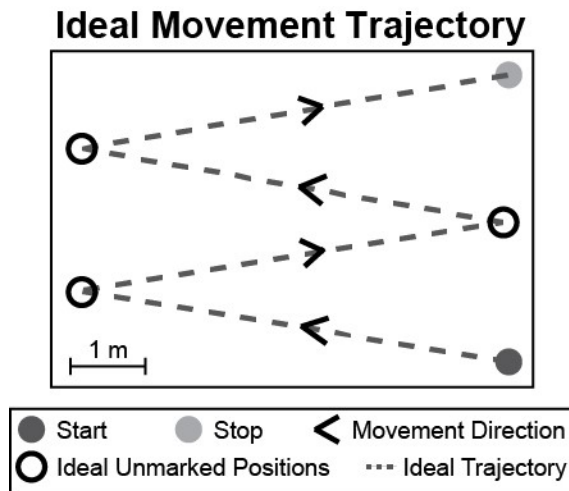


Figure 13 Ideal Movement Trajectory. The dark gray filled circle represents the start position and the light gray filled circle represents the end position. Arrows indicate the direction of movement. Open black circles indicate the changes in direction which were not explicitly marked on the floor. Dotted lines show the ideal movement trajectory for the trial.

Experimental Procedure

Dancers first completed a training period where they performed a block of ten trials at the trained speed, 110 bpm. Following this training period, dancers were asked to perform one block of four trials at each of the test tempos (55, 88, 99, 121, 132, and 165 bpm), for a total of six test periods. These tempos represent 10%, 20%, and 50% increases and decreases in tempo. The extremely low and extremely high tempos were chosen in order to collect data at speeds dancers were less likely to perform accurately. The order of the test tempos was randomized for each subject. During each trial, a metronome clicked at the desired tempo.

Analysis of body motion

The position of the body (hip trajectory) was determined using the average location of the four markers on the hips. The velocity of the body was calculated based on the change in position in the horizontal and vertical dimensions of the body position. The start (end) of a trial was represented by the point in time where the body velocity increased (decreased) to 0.05 m/s. We then determined the duration of the movement from movement start to end and converted this to a percentage from 0% to 100%. We then examined the hip trajectory at each 0.5% increment. The hip trajectory was then averaged across each trial within a block of trials at a given tempo and then across subjects. The ideal pattern was based on the position of the start and end positions marked on the floor. The second change in direction or the halfway point of the pattern was the linear midpoint between the start and end locations. The first and third changes in direction were determined by dividing the distance between the start and midpoint

position and the midpoint and the end position in the vertical dimension, respectively, and 15 cm from the outer bounds of the space in the horizontal dimension.

To examine the consistency of movement across trials, we calculated the total distance traveled during each trial. Distance traveled was calculated using change in horizontal and vertical position of the body at each 0.5% of the hip trajectory. The distance traveled over the course of each 0.5% of the trial was summed for each trial, averaged across trials within a block, then across subjects (Figure 14).

We also examined the hip trajectories (Figure 15) and quantified accuracy and precision for each tempo. To quantify accuracy, we calculated the mean squared error (MSE) between the actual hip trajectory on each trial and the ideal pattern. We refer to this calculation as MSE_i . To quantify precision, we calculated the MSE between the hip trajectory on each trial and the mean hip trajectory for a block of trials for a given tempo. We refer to this calculation as MSE_m . In Figure 16A and 16B, we calculated the MSE_i for each subject within a given tempo condition and plotted this versus the MSE_m for each subject within a given tempo condition. All MSE values have units of cm^2 . We also plotted the ellipse representing two standard errors around the group mean for each tempo condition. Figure 16A has squared axes with the same values on each axis. In Figure 16B, we zoom in on the X axis to better show the distribution of dancers and the group data ellipses.

To determine how accurately dancers were able to scale the speed of their movements from the training tempo to the test tempos, we scaled the timing of their movement at the trained tempo by known amounts and identified the tempo that most

closely matched the speed of actual movement in the test tempo trials. We first identified the ideal scaling based on the time dancers should have taken to complete each trial. For the trained tempo, each trial should have taken 26.18 s (48 beats at 110 bpm). The duration of the trial for 55 bpm, 88 bpm, 99 bpm, 121 bpm, 132 bpm, and 165 bpm tempos ideally should be 52.36 s, 32.73 s, 29.09 s, 23.80 s, 21.82 s, and 17.45 s in duration, respectively. With this information, we identified the ideal scaling should be necessary to align test trials to the ideal in time. The ideal constant scalars used to multiply the training time stamps to match the ideal time stamps for the 55 bpm, 88 bpm, 99 bpm, 121 bpm, 132 bpm, and 165 bpm trials were 2, 1.25, 1.11, 0.91, 0.83, and 0.67, respectively.

To determine the actual scaling dancers performed in each of the test patterns, we first scaled the average timestamps ($n = 200$ timestamps) from the training trials for each dancer from 0.80 to 2.20, 1.05 to 1.45, 0.91 to 1.31, 0.71 to 1.11, 0.63 to 1.03, and 0.47 to 0.87 by 0.01 for the 55 bpm, 88 bpm, 99 bpm, 121 bpm, 132 bpm, and 165 bpm trials, respectively. This gave us 41 sets of scaled training time stamps for each test tempo. For each of the 41 sets of scaled training timestamps, we examined the position of the actual hip trajectory at each of the 200 timestamps. This gave us a new hip trajectory based on the scaled timestamps. With the 41 sets of scaled timestamps, we found 41 hip trajectories for each dancer for each test trial. We calculated the MSE between these 41 hip trajectories and the actual hip trajectory for each test trial. We did this process for each test trial, averaged the MSEs across the four test trials at each tempo. We found the scaling of the training timestamps that produced the minimum MSE for each dancer. We

converted this actual scaling back to the equivalent tempo and plotted this as a function of the ideal tempo in each tempo condition. We also calculated and plotted the group average of the actual tempo each dancer used based on the scaling of the trained tempo (Figure 17).

Statistical Analysis

A one-way ANOVA was performed to identify whether there was a difference in the average distance traveled in the trained and test patterns. We performed post-hoc t-tests to determine which conditions differed in distance traveled. We used a Bonferroni correction to adjust for multiple comparisons. To determine whether the average scaling was significantly different from the known ideal tempo for each tempo condition, we performed six two-tailed t-tests. All statistical analyses were performed with MATLAB, and for all tests the significance level was 0.05.

Results

To quantify the consistency of movement, we first examined the distance dancers traveled during the trained and test tempos (Figure 14). Because the ideal movement trajectory was the same for the training and test conditions, we expected that the distance traveled in each condition would be approximately equal across tempos. However, a one-way ANOVA revealed a significant difference in the distance traveled for the conditions ($p < 0.01$). Post-hoc tests revealed significant differences in distance traveled for the following pairs of tempos: 55 bpm and 121 bpm (paired, two-tailed t-test $p = 0.03$), 55 bpm and 165 bpm (paired, two-tailed t-test $p < 0.01$), 88 bpm and 132 bpm (paired, two-tailed t-test $p = 0.01$), 88 bpm and 165 bpm (paired, two-tailed t-test $p < 0.01$), 99 bpm

and 165 bpm (paired, two-tailed t-test $p < 0.01$), 110 bpm and 165 bpm (paired, two-tailed t-test $p < 0.01$), 121 bpm and 165 bpm (paired, two-tailed t-test $p < 0.01$), and 132 bpm and 165 bpm (paired, two-tailed t-test $p < 0.01$). Each post-hoc test was Bonferroni corrected for multiple comparisons. Dancers traveled less distance in 121 bpm trials and 132 bpm compared to 55 bpm trials and 88 bpm trials, respectively. Also, dancers traveled less during the 165 bpm trials than all other tempo conditions. Taken together these results suggest that dancers tended to travel less at faster tempos, particular at the fastest tempo.

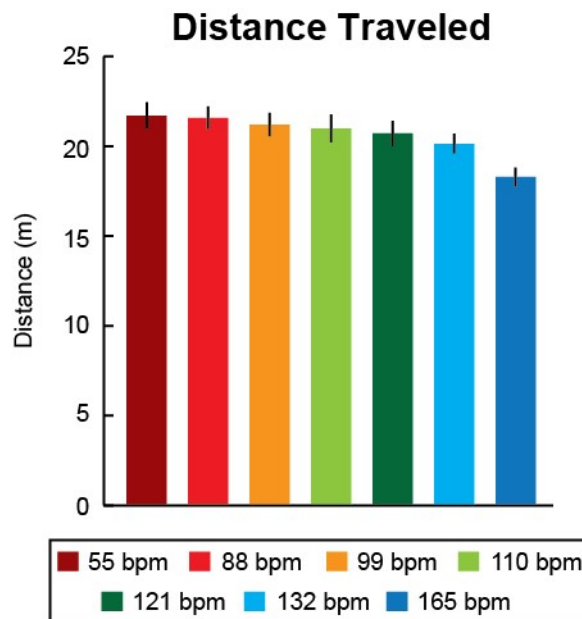


Figure 14 Total Distance Traveled in Each Tempo Condition in Meters. Bars show the group average of the total distance traveled during training and test tempos. Dark red, red, orange, light green, dark green, cyan, and blue bars represent data from the 55 bpm, 88 bpm, 99 bpm, 110 bpm, 121 bpm, 132 bpm, and 165 bpm trials, respectively. Black lines on bars show standard error.

We then examined the hip trajectories for each tempo condition (Figure 15). Here, thin colored lines show the group average hip trajectories for each condition and shading represents the standard error. Thick black traces show the ideal zigzag pattern.

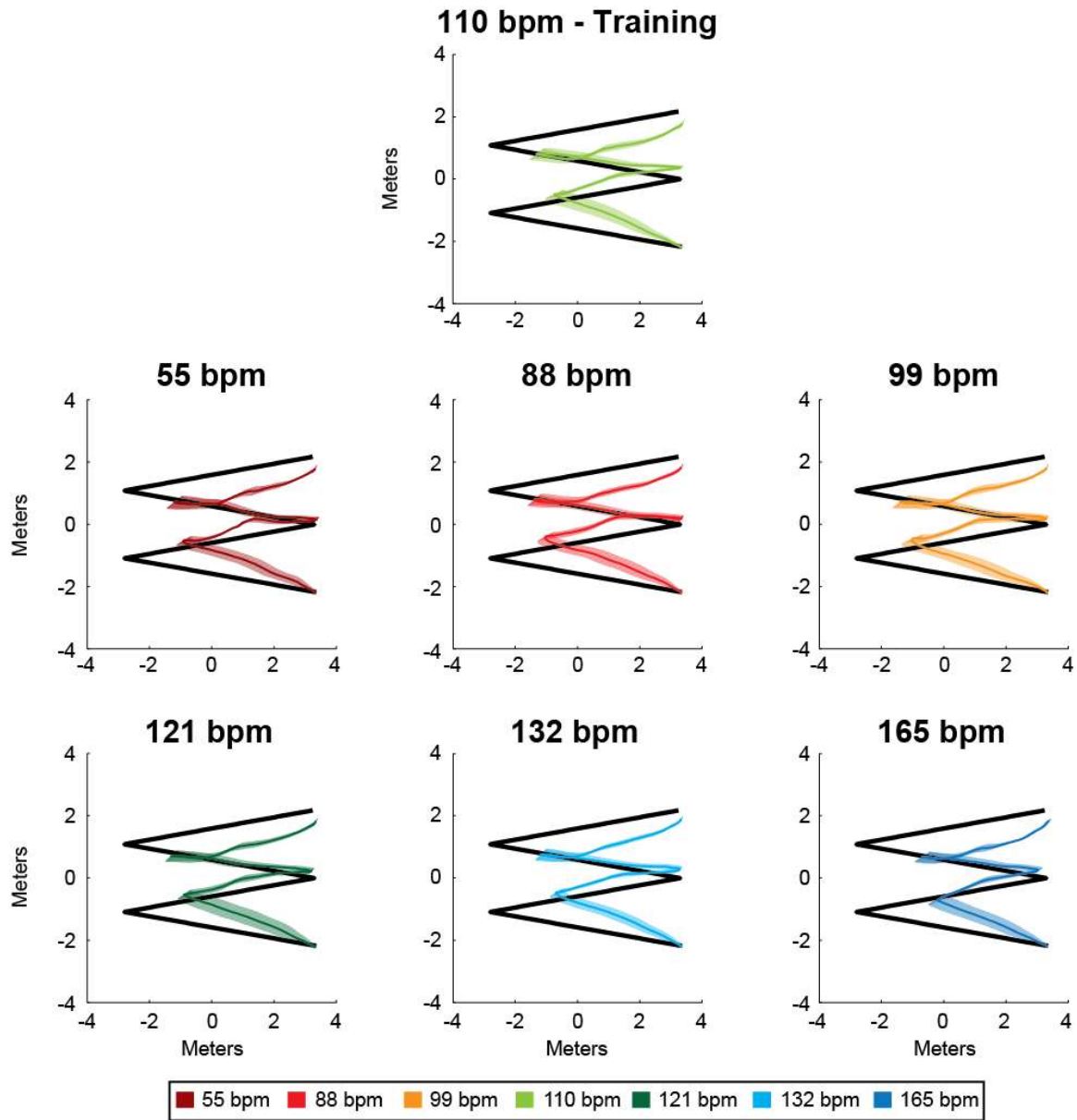


Figure 15 Average Hip Trajectories for Each Tempo. Average hip trajectories are plotted with the ideal trajectory for each of the seven tempos. Thick black traces represent the ideal trajectory. Thin colored traces

represent the average hip trajectory across ten subjects. Shading represents standard error. Dark red, red, orange, light green, dark green, cyan, and blue traces and shading represent data from the 55 bpm, 88 bpm, 99 bpm, 110 bpm, 121 bpm, 132 bpm, and 165 bpm trials, respectively.

To evaluate dancers' accuracy in performing the ideal zigzag pattern, we calculated the MSE between each actual hip trajectory and the ideal pattern (MSE_i). A one-way ANOVA revealed no significant difference in the MSE_i for the tempo conditions ($p = 0.52$). This suggests that dancers performed with equal accuracy at the trained and each of the test tempos. To evaluate the precision of hip trajectory, we calculated the MSE between each hip trajectory and the mean hip trajectory for a given condition (MSE_m). A one-way ANOVA revealed there was no significant difference in the MSE_m for the tempo conditions ($p = 0.12$). This suggests that dancers' hip trajectories were equally precise when performing at the trained tempo and each of the untrained tempo compared to the other conditions. In Figure 16, we plotted the MSE_i versus MSE_m for each dancer in each tempo condition and the ellipse representing two standard errors around the group mean. The unity line represents the location where accuracy and precision values are equal. All of the data points and ellipses fall above the unity line which illustrates how much greater the MSE_i was compared to the MSE_m for every dancer in every tempo condition. This indicates that dancers are much more precise, than they are accurate in their performance of the ideal trajectory.

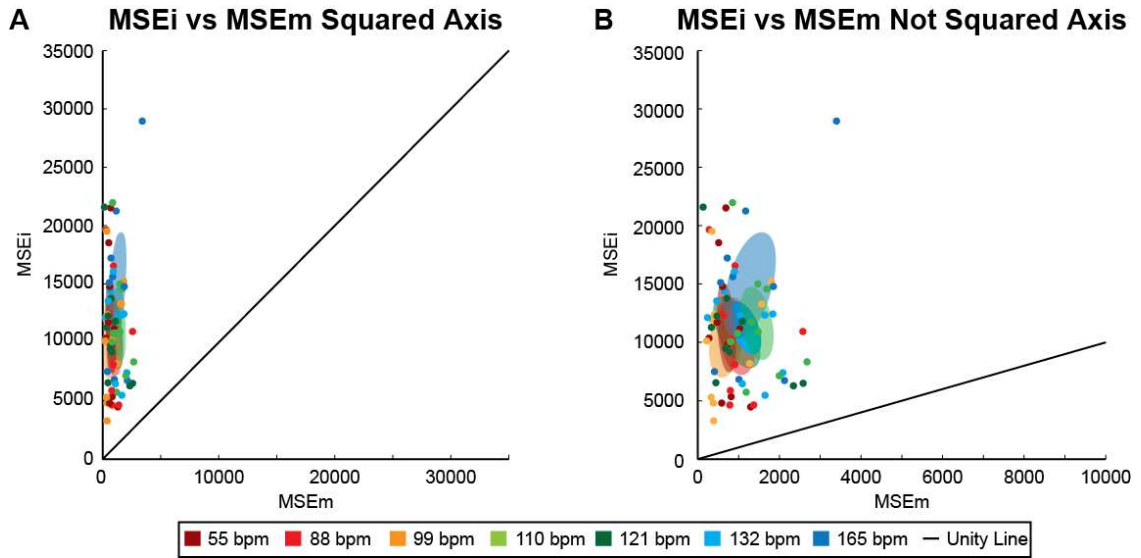


Figure 16 MSEi versus MSEm. A) MSEi versus MSEm with the same X and Y axes. B) MSEi versus MSEm with uneven X and Y axes. Small filled circles represent the average MSEi and MSEm for each of the ten subjects in each of the seven tempo conditions. MSE values have units of cm^2 . Ellipses represent two standard errors around the group mean in each tempo condition. Dark red, red, orange, light green, dark green, cyan, and blue represent data from the 55 bpm, 88 bpm, 99 bpm, 110 bpm, 121 bpm, 132 bpm, and 165 bpm trials, respectively. Thin black lines represent the unity line.

To determine how well dancers were able to adjust their speed to the novel tempos, we scaled the timestamps from the training data and identified the scaling that led to the lowest MSE between the trajectory based on the scaled timestamps and the actual trajectory dancers performed in the test conditions (see Methods). We plotted each dancer's scaled tempo versus the ideal tempo to evaluate how effectively dancers adjusted to the novel tempos (Figure 17).

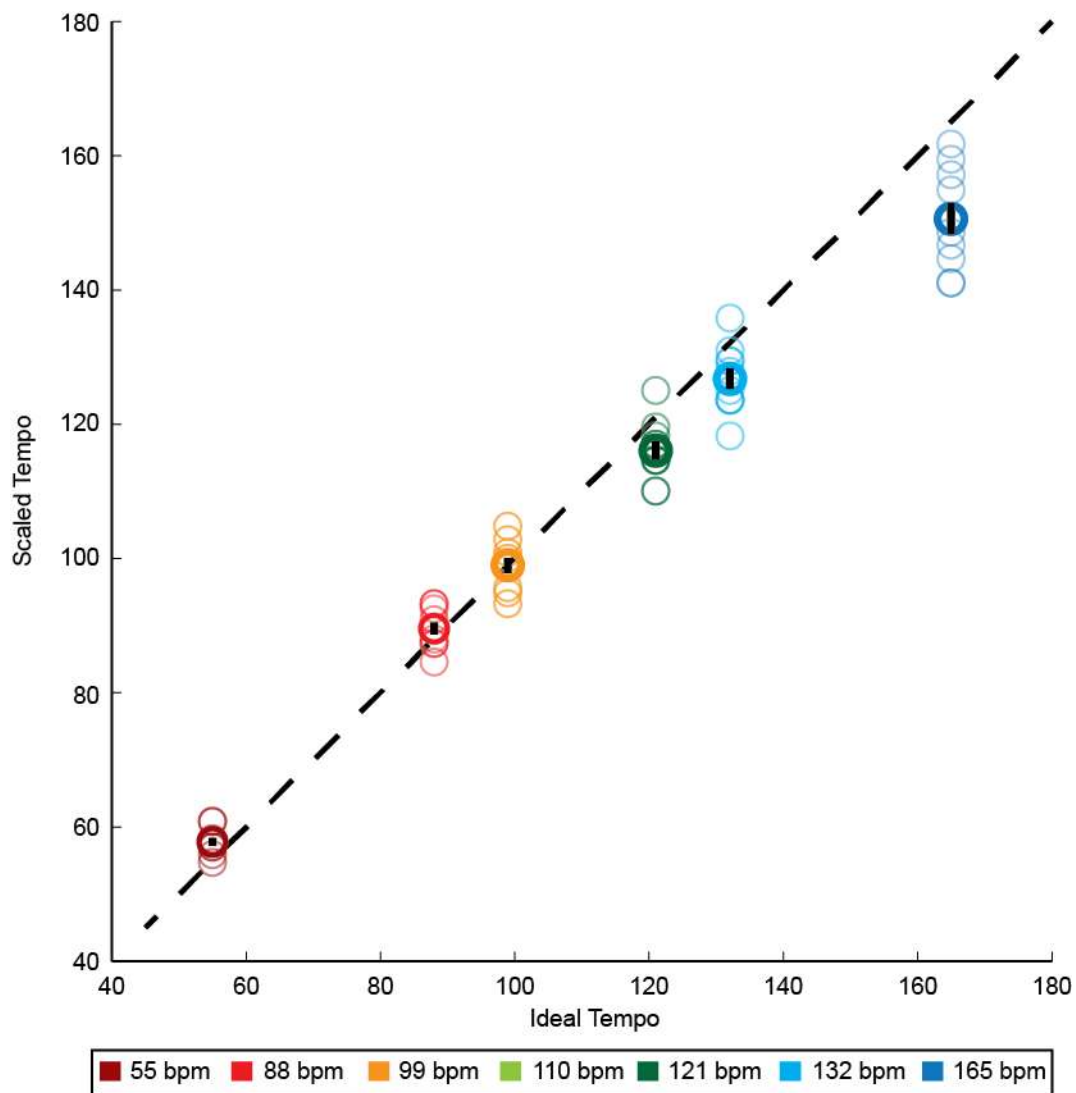


Figure 17 Scaled Versus Ideal Tempo. The thick, dashed black line represents the unity line where the scaled tempo and the ideal tempo are equal. Thin colored circles represent each dancer's average of the scaled tempo that led to the lowest MSE between the scaled trajectory and the actual hip trajectory. Thick colored circles represent the group average of the scaled tempos. Thin black lines show standard error. Dark red, red, orange, light green, dark green, cyan, and blue circles represent data from the 55 bpm, 88 bpm, 99 bpm, 110 bpm, 121 bpm, 132 bpm, and 165 bpm trials, respectively.

The scatterplot shows that dancers match the ideal tempo in the 88 bpm and 99 bpm conditions. We ran two-tailed t-tests to comparing the scaled and the ideal tempo for the 88 bpm and the 99 bpm conditions and found no significant differences between the

scaled and ideal tempos (88 bpm: $p = 0.11$ and 99 bpm: $p = 0.96$). This suggests that dancers were able to accurately adjust their speed to match the ideal tempo at these tempos. We ran four t-tests comparing the scaled and the ideal tempo; one t-test for the 55 bpm, 121 bpm, 132 bpm, and 165 bpm conditions. Each t-test revealed significant differences between the scaled and ideal tempos (55 bpm: $p < 0.01$, 121 bpm: $p = 0.01$, 132 bpm: $p < 0.01$, and 165 bpm: $p < 0.01$). This suggests that for the 55 bpm condition, dancers scaled their movement, but undershot the temporal decrease necessary to perform at the slowest speed (i.e. they scaled to tempos faster than the ideal). In addition, for the 121 bpm, 132 bpm, and 165 bpm conditions, dancers scaled their movement, but undershot the temporal increase necessary to perform at the faster than trained speeds (i.e. they scaled to tempos slower than the ideal). Taken together, these results suggest that dancers scale their speed well at intermediate tempos (88 bpm and 99 bpm), but tend to undershoot the necessary scaling for extreme tempos (55bpm, 121 bpm, 132 bpm, and 165 bpm).

Discussion

Collectively, our results suggest that dancers are able to transfer motor skill learning from trained to untrained speeds, but there is a threshold at which dancers can no longer accurately perform the task at the new speeds. We found that dancers are able to maintain the distance they travel and accurately match their hip trajectories to the ideal pattern at novel speeds until they were asked to perform the choreography at 165 bpm, the fastest speed. Dancers also performed more precisely than they did accurately compared to the ideal trajectory. In addition, dancers were able to scale their movements

accurately in time to lower speeds, but not the extreme at 55 bpm. They were not able to accurately scale their movements in time to higher speeds. This suggests that dancers may be able to transfer motor skills more accurately to novel slower speeds compared to novel faster speeds.

Zijlstra et al. (1995) identified a relationship between stride length and step frequency when walking was constrained. When subjects were asked to walk in time with a metronome (1 step on each beat), subjects increased the frequency of stepping with increasing tempo, but did not adjust their step length. Critically, the maximum tempo this study examined was 125 bpm. This study predicts that when frequency is increased, but the number of steps remains constant, distance traveled should remain constant. However, we found that dancers traveled less distance when they performed at the fastest tempo. Perhaps at the fastest tempo, the dancers in our study were forced to take shorter steps in order to transfer their weight in time. By testing the faster tempos, particularly 165 bpm, we may have found a threshold where step size must decrease in order for step frequency to match the task demands.

Previous work has also quantified preferred movement speeds for simple, unconstrained movement tasks. Collyer et al. (1994) had subjects freely tap their finger at a rate that was comfortable without any outward timing cues. They found average preferred tapping rates for the first few trials (subjects tended to tap faster after the first few trials) at inter-response intervals of 460 to 490 milliseconds. These inter-response intervals correspond to a tempos of 122 to 130 bpm. Kay et al. (1987) also found preferred inter-response intervals of 490 milliseconds (122 bpm) when subjects freely

tapped one hand; however, when subjects were asked to tap at their preferred speed with alternating hands, average preferred speeds were slower. These tasks suggest that humans may have a preferred speed to perform specific tasks, but that this speed varies depending upon the complexity of the task. Based on dancers' limited ability to scale their movements to novel speeds in our experiment, dancers may prefer to perform the given choreography between 88 and 110 bpm.

Another important consideration is that there is a physical limitation to how accurately the dancers can perform the movement at extremely high and extremely low speeds. The dynamical systems theory of motor control explains that movement arises from the interaction between the subsystems of the body, the environment, and the specific task. Ester Thelen demonstrated that motor control depends on the physics that underlie movement, not just the top-down signals from the brain (Thelen, 2005). Thelen and Fisher (1982) showed that the stepping reflex observed in babies disappears and then reappears, but is a result of weak leg muscles, not a spontaneous loss of motor control ability. This highlights importance of the physics behind the movement we asked dancers to perform. In the phrase of choreography, dancers performed a cartwheel. The dynamical systems theory would suggest that a potential reason we found dancers unable to scale their speed to higher tempos and extremely low tempos is that they physically could not perform a cartwheel as quickly or as slowly as the tempo demanded. We studied these extreme speeds specifically to quantify dancers' physical limitations, so we expected dancers to be unable to match the extreme speeds, 55 bpm and 165 bpm.

Future directions for this experiment include examining the whole-body movement of the dancers in three dimensions. We will evaluate the consistency of movement each dancer performs within blocks of training and test trials. In addition, we will quantify the consistency of movement across dancers. To do this, we will quantify the variability of limb movement across trials. We expect that the variability of limb movement will be low at speeds around the trained tempo, but will increase when the speed increases and decreases to the extreme tempos. We expect that these data will confirm dancers' ability to transfer motor skill learning from trained to novel speeds.

SUMMARY, LIMITATIONS, AND FUTURE DIRECTIONS

Summary

Collectively, the three experiments described above provide insight to the spatial and temporal properties of unconstrained motor skills.

Our first study examined the ability of dancers and non-dancers to navigate in three spatial configurations with and without vision. We found that both dancers and non-dancers' performance was negatively influenced when vision was restricted, but dancers performed better than non-dancers in more complex spatial configurations.

Our second study examined whether dancers are able to transfer a phrase of skilled movement from a trained spatial context to two untrained contexts. Here, we found dancers performed with equal precision in the trained and untrained contexts and dancers performed more accurately in an untrained context than the trained context. In addition, dancers were able to scale their movement from the trained pattern to a novel zigzag pattern, but tended to overestimate the necessary upscaling in the horizontal dimension and overestimate the necessary downscaling in the vertical dimension. Together, these results suggest that dancers are able to transfer movement from a trained to untrained spatial contexts.

Finally, our third study examined whether dancers are able to transfer a phrase of skilled movement from a trained to novel speeds. We found that dancers performed with

equal accuracy and precision in each tempo condition. We also found that dancers are able to temporally scale their movement to intermediate tempos, but scale less accurately at extremely high and extremely low tempos. Our results indicate that dancers can transfer choreography from trained to untrained speeds, but tend to perform this task less accurately at extremely fast and extremely slow speeds.

Limitations

The contents of the room we used to collect data were constantly changing. The metronome was roughly placed in the same location for every subject, but we did not have a way to ensure that this was true. Particularly on trials without vision in experiment 1, dancers and non-dancers could have used the auditory cue of the metronome to determine their position in the room. This cue, therefore, may have been in slightly different location from subject to subject. The room also had chairs, tables, and other objects on the perimeter. Dancers and non-dancers may have guided their movement based on the location of these objects, but these objects were in different locations for each subjects. This could have influenced the behavior of dancers and non-dancers.

In addition, it was possible for markers to fall off in the middle of a trial. Though this happened infrequently, it did require elimination of a trial that was partially completed from analysis. On the rare occasion this happened, subjects gained experience in whatever task they had been performing due to this extra trial where we could not use the data. This could influence the results to suggest that subjects performed better than they did given the additional, unmeasured experience they gained.

Similarly, it was possible for subjects to step outside of the bounds of the space when they were blindfolded in no vision trials in experiment 1 which led us to stop and eliminate a partially completed trial from analysis. Though this happened infrequently, dancers and non-dancers experienced a trial that was not measured in our results. This could have influenced the performance of dancers and non-dancers because they were stopped in a random location and brought back to the start position. They may have used the proprioceptive cues from the guided return to correct their next movement.

Future Directions

The current studies examine movement of dancers and non-dancers using only two-dimensional data from our motion capture system. The future direction of the two generalization studies is to examine the movement of the dancers in three dimensions. We are collaborating with computer scientists at University of California, Davis to analyze our data. We will measure the variability of the limb and head movement across tempo conditions and spatial contexts. What we expect to see is that the variability of the limb movement will be similar in both trained and untrained contexts. The dancers are extremely good at being able to perform the choreography with new task demands, so we anticipate that there will be little variability despite changing contexts.

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