Summer 2022

Effects of Positive Social Comparative Feedback During Practice on Motor Sequence Learning, Performance Expectancies, and Resting State Connectivity

Allison Foster Lewis

EFFECTS OF POSITIVE SOCIAL COMPARATIVE FEEDBACK DURING PRACTICE ON MOTOR SEQUENCE LEARNING, PERFORMANCE EXPECTANCIES, AND RESTING STATE CONNECTIVITY

by

Allison Foster Lewis

Bachelor of Arts
University of North Carolina at Chapel Hill, 2010

Doctor of Physical Therapy
Medical University of South Carolina, 2014

Submitted in Partial Fulfillment of the Requirements

For the Degree of Doctor of Philosophy in

Exercise Science

Arnold School of Public Health

University of South Carolina

2022

Accepted by:

Jill C. Stewart, Major Professor

Stacy Fritz, Committee Member

Sara Wilcox, Committee Member

Dirk den Ouden, Committee Member

Tracey L. Weldon, Vice Provost and Dean of the Graduate School

DEDICATION

I dedicate this dissertation to my son, Cam Lewis, who is the joy of my life. I would also like to honor my father-in-law, A. Camden Lewis, whose life inspired me to be tenacious in pursuit of my career and aspirations.

ACKNOWLEDGEMENTS

First, I would like to thank my mentor, Jill Stewart, for her commitment, patience, expertise, and friendship. I would not have succeeded on this path without you. To Stacy Fritz, my secondary mentor, I thank you for encouraging me to start down this path. You inspired me to take a leap, and you continue to inspire me by leading with kindness. I would also like to thank my dissertation committee members, Sara Wilcox and Dirk den Ouden, and other mentors, Sheri Silfies, Alicia Flach, and Elizabeth Regan, for supporting me throughout this process. Each of you contributed to my growth and success. I appreciate your commitment to me throughout my doctoral training.

To my colleagues and friends: Thank you to Jessica Baird, Rachel Bohnenkamp, Lynn Johnson, Makenzie Myers, and Charles Smith for helping with data collection, but more importantly for their friendship and moral support.

To my parents, Sally and Mike Foster: Thank you for modeling hard work and commitment. You taught me to press forward in the face of challenges and defeat, which is the single most important skill for surviving doctoral training.

To Will: You are exceptional. Your unwavering love and support is unparalleled. You were the guiding force that nudged me forward, never allowing me to be overcome with self-doubt. I cannot imagine a greater demonstration of love and selflessness.

ABSTRACT

Positive social comparative feedback indicates to the learner that they are performing better than others. While this type feedback supports motor skill learning in some tasks, the effect of social comparative feedback on motor sequence learning remains unknown. In addition, the OPTIMAL theory predicts that positive social comparative feedback may trigger a dopaminergic response in the brain. However, no studies have utilized neuroimaging techniques to investigate this question. Therefore, the aim of these studies was to determine the effect of positive social comparative feedback on motor sequence learning, performance expectancies, and resting state connectivity of dopaminergic neural pathways.

In the first study, forty-eight individuals practiced a joystick-based sequence task and were divided into three feedback groups: CONTROL (no performance feedback), RT ONLY (response time only feedback), and RT+POS (response time plus positive social comparison). Participants attended sessions on two consecutive days: Day 1 for motor skill acquisition and Day 2 for retention testing. Performance related expectancies were measured before and after motor practice and at retention. The RT+POS and CONTROL group showed better overall performance/learning compared with the RT ONLY group. However, the RT+POS showed the highest peak velocities, and the CONTOL

group showed the shortest path distances. Overall, the RT+POS and CONTROL showed increases in perceived competence while the RT ONLY group did not. The results of this study suggest that feedback content is an important consideration during motor practice, since feedback without social context (RT ONLY) was detrimental, and since feedback may be leveraged to bias motor practice towards higher movement speeds versus spatial accuracy.

In the second study, thirty individuals practiced the same motor task and were divided into two feedback groups: RT ONLY and RT+POS. The study protocol was similar, with magnetic resonance imaging added before and after motor practice. The RT+POS group showed an increase in functional connectivity between the ventral tegmental area and the left nucleus accumbens, brain regions along the mesolimbic dopamine pathway. The RT+POS group showed better overall performance than the RT ONLY group at acquisition. Similar to the first study, the RT+POS showed higher peak velocities than the RT ONLY group. Overall, both groups showed increases in performance expectancies that were not different by group. The results of the brain connectivity analysis support the OPTIMAL theory prediction that positive social comparative feedback may trigger a dopaminergic response in the brain.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Behavioral practice is the foundation of restorative motor rehabilitation. However, the optimal structure of behavioral practice, including specific influences of feedback variations on behavior and neural network activation, remain unknown. Feedback is defined as any information provided to the learner during practice about their performance (Schmidt & Lee, 2011). Feedback can provide a learner with knowledge of the results of their performance (i.e., accuracy or speed), but it can also contain motivational content (i.e., how their performance compares to other people). Varying feedback content to influence motivation and target the dopaminergic neural networks may benefit movement restoration and skill learning. Current research does not fully elucidate how variations in the motivational aspect of feedback might alter both behavioral outcomes and specific neural networks. Therefore, research is needed to understand how feedback variations might impact motor performance and target the dopaminergic neural networks to benefit motor skill learning.

The OPTIMAL (Optimizing Performance Through Intrinsic Motivation and Attention for Learning) theory of motor learning is a theoretical approach that states that motivational and attentional factors influence motor performance and learning by coupling goals to actions (Wulf & Lewthwaite, 2016). According to

this theory, practice conditions that enhance a learner's expectancies about future performance lead to goal-action coupling and optimized motor learning (Fig. 1.1). Enhanced expectancies refer to a learner's anticipatory cognitions about future events based on previous experiences or outcomes. Expectancies include the learners' perceived competence about their ability to perform the task, task related self-efficacy, expectations about task outcome (success or failure), and predictions of extrinsic reward related to performance. Positive social comparative feedback, which indicates to the learner that they are better than others, is one way to enhance a learner's expectancies. While positive social comparative feedback supports motor skill learning and enhances expectancies in some motor tasks (Lewthwaite & Wulf, 2010; Pascua et al., 2015; Wulf et al., 2012, 2014), this type of feedback has not been applied to a motor sequence learning task.

Motor sequence learning can occur through both explicit processes, with knowledge of the sequence, and implicit processes, without explicit knowledge or awareness of the sequence (L. R. Squire, 1992; Larry R. Squire, 1987). Implicitly learned motor skills have been shown to be robust and durable (Lam et al., 2009; Liao & Masters, 2001; Masters et al., 2008; Verburgh et al., 2016), resilient to deficits resulting from aging or injury (Kal et al., 2016; Verneau et al., 2014), and unrelated to intelligence (Maybery et al., 1995). For these reasons, training movement sequences in an implicit manner may be effective for robust motor skill learning in many applications, but especially in the context of skilled sport training and rehabilitation. In addition, implicit sequence learning tasks allow for

detailed investigation of many aspects of motor learning. By embedding random and repeated sequence types into the sequence learning task, this task provides insight into general sensorimotor learning (random sequence type) and implicit sequence learning (repeated sequence type). This task also allows for tracking of spatial and temporal aspects of performance across motor practice. Improvements in overall performance over practice can be achieved through changes in both spatial (i.e. hand path distance) and temporal (i.e. peak velocity) components of movement (J. Baird & Stewart, 2018). These variables could be sensitive to social comparative feedback; however, they have not been investigated in previous studies, and the effect of social comparative feedback on implicit motor sequence learning (including spatial and temporal variables) and performance expectancies remains unclear.

Other gaps in the literature exist, including an understanding of the neural mechanism that supports optimized learning under practice conditions that enhance expectancies. The OPTIMAL Theory predicts that conditions that enhance expectancies trigger a dopaminergic response in the brain ((Wulf & Lewthwaite, 2016). Dopamine is a neurotransmitter involved in many physiologic processes including reward, motivation, and motor function. Dopamine is released from the ventral tegmental area (VTA) and substantia nigra (SN) in anticipation of and response to rewarding stimuli (Hahn et al., 2021; Schott et al., 2008). Dopamine can exert influence on behaviors through several pathways in the brain (Fig. 1.2). These neural pathways include the mesolimbic, mesocortical, and nigrostriatal pathways (Haber & Knutson, 2010; Ikemoto, 2007;

Wise, 2004). The mesolimbic pathway refers to dopamine projections from VTA to the nucleus accumbens (NAcc), while the mesocortical pathway includes dopamine projections from VTA directly to regions in the prefrontal cortex, like the orbitofrontal cortex (OFC) (often referred to collectively as the mesocorticolimbic pathway) (Coenen et al., 2018; MacNiven et al., 2020). The nigrostriatal pathway consists of dopamine projections from SN to the caudate and putamen (i.e., the dorsal striatum) which functions to influence movement (Luo & Huang, 2016). While the mesocorticolimbic pathway has been the focus of previous research in this area, both the mesocorticolimbic pathway and nigrostriatal pathway play a role in reward processing and motivation (Ikemoto et al., 2015; Wise, 2004).

Similar brain regions are engaged when people are provided social rewards and monetary rewards, which include regions along both the mesocorticolimbic and nigrostriatal pathways (Gu et al., 2019). The mesocorticolimbic pathway is responsive to a variety of social rewards including smiling faces and feelings of love (Aharon et al., 2001; Bartels & Zeki, 2004; A. Lin et al., 2012; Rademacher et al., 2010). The nigrostriatal pathway has also been implicated in reward and motivational processing in animal models (Ikemoto et al., 2015), and the caudate and putamen, regions along the nigrostriatal pathways, are active in processing of social rewards in human fMRI studies (Gu et al., 2019; Izuma et al., 2008; Wake & Izuma, 2017). Given the overlap between dopaminergic pathways and the neural pathways implicated in reward and motivation, positive social comparative feedback during practice

could trigger dopaminergic signaling between regions along the mesocorticolimbic and/or nigrostriatal pathways. However, no studies have investigated this question by using neuroimaging techniques to measure changes in brain connectivity along these pathways related to feedback with positive social comparison.

Further evidence that anticipation of positive experiences (i.e. enhanced expectancies) triggers a dopamine response comes from research on the placebo effect. The placebo effect refers to improvements in behavior or symptomology in the absence of active intervention which can only be attributed to the individual's expectancy of improvement or a positive outcome. The expectancy of a positive outcome, or placebo effect, results in dopamine release in the ventral striatum/NAcc as measured by positron emissions topography (PET) scanning (Boileau et al., 2007; Lidstone et al., 2010), which supports the idea of expectancy-dependent dopamine release. Taken together, expectancies can trigger a dopamine response in the brain, supporting the prediction asserted in the OPTIMAL theory. However, no studies have investigated whether positive social comparative feedback engages dopaminergic pathways using neuroimaging techniques.

Connectivity between pairs of brain regions, examined by resting state functional magnetic resonance imaging (rsfMRI), reflects the activation of brain regions required to support task performance. rsfMRI measures the low-frequency activity in the brain during rest, which identifies coherent patterns of brain activity (Fox & Raichle, 2007). rsfMRI generates connectivity patterns

similar to the networks that are involved during active performance of the task (Biswal et al., 1995; Cao et al., 2014; Fox & Raichle, 2007; Shehzad et al., 2009; Smith et al., 2009). In addition, rsfMRI has unique advantages by allowing motor practice to occur outside the confines of the MRI scanner while minimizing the confounds of online movement (i.e. motor performance, head motion) (Carter et al., 2012; Grefkes & Fink, 2011). In this way, resting state connectivity can be measured before and after practice, reflecting the networks underlying the motor learning process. Finally, resting state connectivity has been shown to change with short-term practice of motor skills (Albert et al., 2009; C. H. Lin et al., 2018; Steel et al., 2019). Therefore, rsfMRI provides the opportunity to determine whether social comparative feedback engages the mesocorticolimbic and/or nigrostriatal dopaminergic neural networks during motor learning with social comparative feedback, addressing a significant gap in the literature.

The purpose of this dissertation was to determine the effects of social comparative feedback during motor practice on motor sequence learning, performance expectancies, and functional connectivity of the dopaminergic neural network. The current approach was innovative in that we combined neuroimaging techniques with a skilled motor task to investigate the mechanism through which social comparative feedback shapes both motor behavior and brain connectivity. The joystick-based sequence task required precise temporal and spatial demands, providing motor challenge to the learner, and allowed for detailed measurement of spatial and temporal aspects of performance, beyond simple response time. This study addresses a critical hurdle in the field of

rehabilitation, which is how to optimize motor practice to promote learning, enhance expectancies, and support motivation. Understanding the neural mechanism through which practice conditions optimize learning is important for matching and targeting interventions, especially in populations with neurologic damage.

Aim 1 (Chapter 2): Determine the effect of positive social comparative feedback during practice on the learning of and performance expectancies for a joystick-based motor sequence task

Hypothesis 1A: All groups will demonstrate learning (faster response times) of the motor task. However, the group receiving positive social comparative feedback will show faster response times over acquisition and at retention testing than groups that do not receive positive social comparative feedback.

Hypothesis 1B: All groups will demonstrate increases in performance expectancies after practice. However, the group receiving positive social comparative feedback will show greater increases in performance expectancies at the end of acquisition and at retention than the groups who do not receive positive social comparative feedback.

Aim 2 (Chapter 3): Determine the effect of positive social comparative feedback during practice of a joystick-based motor sequence task on the resting state connectivity of the dopaminergic neural network

Hypothesis 2: The group that receives positive social comparative feedback will show engagement of the reward network through increased functional connectivity after motor practice while the group that does not receive positive social comparative feedback will not.

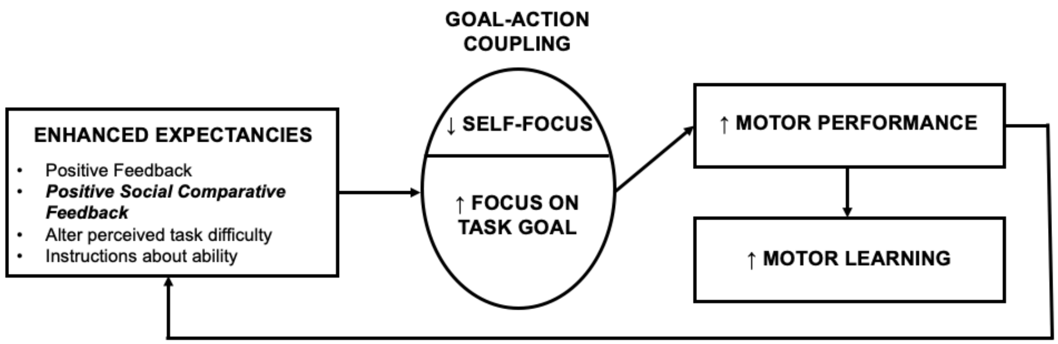

Figure 1.1: Conceptualization of the enhanced expectancy component of the OPTIMAL theory. Adapted from Wulf & Lewthwaite (2016).

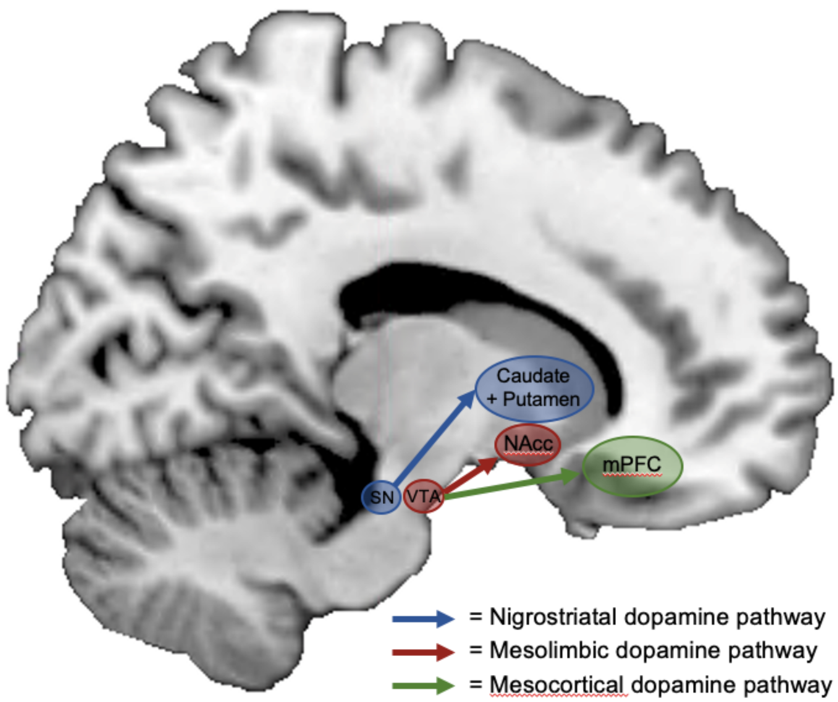

Figure 1.2: Dopaminergic pathways. SN = substantia nigra; VTA = ventral tegmental area; NAcc = nucleus accumbens; mPFC = medial prefrontal cortex

CHAPTER 2

EFFECTS OF POSTIVE SOCIAL COMPARATIVE FEEDBACK DURING PRACTICE ON MOTOR SEQUENCE LEARNING AND PERFORMANCE EXPECTANCIES

1. Introduction

Behavioral practice is the foundation of restorative motor rehabilitation and motor skill learning. According to the OPTIMAL (Optimizing Performance Through Intrinsic Motivation and Attention for Learning) theory, positive social comparative feedback during practice (i.e., feedback that indicates to the learner that they are performing better than others) enhances a learner's expectancies about their performance, thereby benefitting motor performance and learning (Wulf & Lewthwaite, 2016). Expectancies include the learners' perceived competence, expectations about task outcome (success or failure), and predictions of extrinsic reward (Wulf & Lewthwaite, 2016). In previous research, positive social comparative feedback enhanced learners' expectancies via improvements in measures of perceived competence, self-efficacy, positive affect, and overall intrinsic motivation towards the motor task (Ávila et al., 2012; Stoate et al., 2012; Wulf et al., 2012, 2014). In addition, learners who received positive social comparative feedback during practice showed better performance and learning at retention testing compared to learners who received performance

feedback without positive social comparison (Lewthwaite & Wulf, 2010; Pascua et al., 2015; Wulf et al., 2012, 2014).

While positive social comparative feedback appears to support motor skill learning and confidence in some motor tasks, this type of feedback has not been applied to a motor sequence learning task. Motor sequence learning can occur through both explicit processes, with knowledge of the sequence, and implicit processes, without explicit knowledge or awareness of the sequence (L. R. Squire, 1992). Implicitly learned motor skills have been shown to be more robust and durable in sport situations when a second task or a stressor is introduced (Lam et al., 2009; Liao & Masters, 2001; Masters et al., 2008; Verburgh et al., 2016). Further, implicit learning ability is resilient to deficits resulting from aging or injury (Kal et al., 2016; Verneau et al., 2014) and is unrelated to intelligence (Maybery et al., 1995). For these reasons, training movement sequences in an implicit manner may be effective for robust motor skill learning in many applications, but especially in the context of skilled sport training and rehabilitation. The effect of social comparative feedback on implicit motor sequence learning and expectancies remains unclear.

Serial target tasks (STTs) have been utilized to study motor learning including for the examination of implicit motor sequence learning. By embedding random and repeated sequence types into the STT, this task can provide insight into general sensorimotor learning (random sequence type) and implicit sequence learning (repeated sequence type). Further, STTs can allow for tracking of spatial and temporal aspects of performance across motor practice.

With practice of an STT, improvements in overall performance can be achieved through changes in both spatial (i.e. hand path distance) and temporal (i.e. peak velocity) components of movement (J. Baird & Stewart, 2018). These variables could be sensitive to social comparative feedback; however, they have not been investigated in previous studies.

Therefore, the purpose of this study was to determine the effects of positive social comparative feedback on the learning of a joystick-based implicit motor sequence task and related performance expectancies. It was hypothesized that the group who received positive social comparative feedback would show greater improvements in performance (faster response times) and greater increases in task-related confidence, reflecting enhanced expectancies, at retention testing than groups that did not receive positive social comparative feedback. A secondary aim of this study was to determine the effect of social comparative feedback on spatial and temporal components of motor performance, such as hand path distance and peak velocity, in order to better characterize how performance changed over practice as a result of feedback type.

2. Methods

2.1 Participants

Fifty-four non-disabled adults between age 18 and 40 years were recruited from the university and local community. Individuals were included in the study if they were right-hand dominant as measured by the Edinburgh Handedness

Questionnaire (Oldfield, 1971) and denied pain or other limitation affecting their ability to move their right arm and hand. Since dopamine plays a major role in learning and motivation (Wise, 2004), individuals were excluded if they were taking medication that impacts dopamine transmission (i.e. dopamine reuptake inhibitors) or were diagnosed by a physician with a disorder affecting dopamine transmission (i.e. Parkinson's disease). Five individuals were on medications that might impact dopamine transmission and one individual did not return for Session 2; these individuals were not included, leaving 48 participants for final data analysis. All participants provided written informed consent prior to enrollment in the study. The university's Institutional Review Board approved all procedures. Participants were provided a $10 cash card at the end of each session.

2.2 Experimental Design

Participants completed two experimental sessions on consecutive days (Day 1 and Day 2). In each session, participants completed a series of questionnaires and practiced a serial target task (STT) with the right arm and hand. Participants were block randomized into one of three experimental feedback conditions, such that each experimental group had equal numbers of males and females. The three experimental groups received different feedback about their task performance and included a control group (CONTROL), a response time feedback group (RT ONLY), and a response time plus positive

feedback group (RT+POS). Participants were tested on their explicit awareness of the repeated sequence at the end of Day 2.

2.3 Serial Target Task

The serial target task (STT) was modified from previous studies (J. Baird & Stewart, 2018; Mang et al., 2014) such that the present task allowed the joystick to act as the cursor, had no central target, and had a greater number of potential target positions. The central target was removed since the spring in the joystick automatically positions the joystick to center which would not require a goal-directed movement for target capture. Participants sat facing a laptop where the STT was displayed on the screen and held a joystick with the right, dominant hand. Participants used their right arm and hand to move the joystick, which moved a pointer-shaped cursor on the screen in proportion to the joystick movement. Circular targets (20-millimeter diameter) appeared one at a time in one of twelve distinct locations (Fig. 2.1). Before beginning task practice, participants were provided verbal and written instructions about the task goal (i.e., to hit the target as fast as possible). The task required the participant to move the joystick "cursor" to the center of each target until it disappeared, and the next target would appear. The target was considered "hit" and disappeared when the position of the cursor was within 7 millimeters of the center of the target for 500 milliseconds. Targets were presented in alternating random and repeated 8-target sequences; the random sequences were included to help ensure the repeated sequence remained implicit. In addition, the two sequence

types allowed for distinction between changes in performance related to more general sensorimotor learning (random sequences) and changes related to sequence-specific motor learning (repeated sequences).

The two sequence types were matched for difficulty based on Fitts' Law, which considers the distance between the targets and the diameter of the target (Fitts & Peterson, 1964). In this task, the target diameter was the same for all targets; therefore, the repeated sequence and all random sequences were matched on their total straight-line inter-target distance. Individual movements between two targets were assigned a difficulty ID based on Fitts' Law (difficulty IDs = 2.14, 3.10, 3.61, 3.90, 4.05, and 4.10) where higher ID numbers indicate greater difficulty and longer inter-target distance. The Fitts' ID numbers were then assigned a rank order for simplicity (e.g., target pairs with ID 2.14=1, target pairs with ID 3.10=2, etc). The repeated sequence contained one target each at IDs 1, 2, 5, and 6 and two targets each at IDs 3 and 4 (repeated sequence: 11-10-5-9-7-3-6-12). Each random sequence contained the same number of targets at each ID level as the repeated sequence. Participants were not made aware of the presence of any sequences.

Participants completed the STT in blocks that contained 41 targets (a "start" target plus five 8-target sequences per block) and sequence types alternated within a block. Movement to the first target was not included in data analysis, as this target served to initiate movement away from the joystick's automatic center before beginning the sequenced movements. At the beginning of Day 1, participants completed an exposure block that included 5 random

sequences but no feedback to ensure understanding of the task and to provide a baseline measure of performance. After the exposure block, participants completed 28 blocks of practice for a total of 70 repeated sequence repetitions and 70 random sequence repetitions. Group-specific feedback (see below) was provided in written format on the laptop screen after each of the 28 blocks practice. Participants returned for the second session on the following day (Day 2), which measured retention performance (i.e., motor learning) of the STT, and completed 12 blocks of motor practice. These blocks of retention testing were structured the same as the Day 1 practice blocks but did not include any feedback.

Position data from joystick was collected at a rate of 60 Hz using E-Prime 2.0 (Psychology Software Tools, Inc., Sharpsburg, PA). Position data was used for calculation of response time, path distance, and peak velocity. The primary measure of STT performance was response time (time to complete one 8-target sequence). Path distance, a spatial measure of performance, was defined as the total distance travelled to complete all 8 targets in a sequence, where shorter distances indicated straighter hand paths. Peak velocity, a temporal measure of performance, was defined as the peak of velocity for each movement between two targets which was then averaged across all movements in each 8-target sequence. Performance data were separated by sequence type (repeated or random) and averaged across five trials of the same sequence type for statistical analysis.

2.4 Feedback

During practice on Day 1, all participants received feedback after each block. The control group (CONTROL) received feedback that they completed the block (e.g., “You have completed the block. Take a rest”). The response time only group (RT ONLY) received feedback on their response time to complete all of the targets in the block (e.g., “You completed this block in 86.1 seconds”) where the feedback provided their actual response time to “hit” all 41 targets in the block. The response time plus positive feedback group (RT+POS) received feedback about their response time with the additional information that their response time was faster than others (e.g., “Your response time was 86.1 seconds. You were 17.2 seconds faster than the average”). The social comparative difference (e.g., “You were 17.2 seconds faster than the average”) was a set percentage of the individual participant’s response time on that block (Wulf et al., 2014). The percentage varied between 14% and 20% for 24 blocks and was reduced to 5% for four randomly selected blocks.

2.5 Explicit Awareness Testing

At the end of Session 2, participants were tested to evaluate awareness of the repeated sequence pattern. Subjective awareness was determined by asking participants if they noticed anything about the motor task. Subjective awareness was defined as the ability to explicitly state that there was a pattern or repeated combinations in the targets. Participants with subjective awareness were tested on their recall awareness whereby the participant was asked to

reproduce the sequence by tracing the repeated pattern on a printed paper with the 12-target layout (Fig. 2.1). Participants who did not report subjective awareness where not tested on recall awareness.

All participants were then tested for recognition awareness of the repeated sequence. Participants were first informed of the presence of a repeating pattern and then asked to complete six recognition tests. Each test required participants to view three 8-target sequences play on the laptop, where targets were displayed one at a time. At the end of each test, the participants were asked whether the repeated sequence was present at the "beginning," "middle," "end," or "not at all." Recognition awareness was defined as the ability to correctly identify two out of three positive tests and correctly reject two out of three negative tests (J. Baird & Stewart, 2018).

2.6 Surveys and Questionnaires

All surveys were collected by subject direct input into RedCap. Prior to STT practice on Day 1, participants completed the Rosenberg Self-Esteem Scale (RSES) (Rosenberg, 1965) and the State Trait Anxiety Index (Spielberger et al., 1983; Thomas & Cassady, 2021) to provide additional information about baseline self-esteem and anxiety, respectively. To assess changes in psychosocial factors over practice, participants completed surveys which measured task-specific self-efficacy (Task-Specific Self Efficacy Scale), perceived competence in task performance and interest/enjoyment in the task (subscales of the Intrinsic

Motivation Inventory), and general positive affect (Positive and Negative Affect Scale) before and after practice on Day 1 and before retention testing on Day 2.

After the exposure block, participants completed three surveys. The Task-Specific Self-Efficacy Scale (TSSE) measured participants' self-efficacy related to STT performance (Bandura, 2006; Saemi et al., 2012). The scale asked participants to rate their perceived ability to perform the task on a scale from 0 ("cannot do it at all") to 100 ("completely certain I can do it") in intervals of 10 second response times (e.g. How confident are you in your ability to complete the task in 100-109 s?). The scale contained 10 items at 10-second intervals, and ratings were summed to create an overall self-efficacy score for analyses with higher scores indicating higher self-efficacy with a maximum score of 1000.

A modified version of the Intrinsic Motivation Inventory (IMI) was utilized to survey perceived competence and task interest/enjoyment (Deci & Ryan, 1985; Ryan, 1982). The modified version was adapted for task evaluation and contains four subscales for interest/enjoyment, perceived competence, perceived choice, and pressure/tension. Only the perceived competence and interest/enjoyment subscales were measured due to their relationship to intrinsic motivation which was expected to be sensitive to positive social comparative feedback (Wulf & Lewthwaite, 2016). The perceived competence subscale contains 5 items, each rated on a scale from 1 to 7, and is theorized to be a positive predictor of intrinsic motivation. The interest/enjoyment subscale contains 7 items, each rated on a scale from 1 to 7, and is considered a measure of intrinsic motivation. The items

in each subscale were summed where higher scores indicate higher levels of perceived competence or interest/enjoyment.

The Positive and Negative Affect Scale (PANAS-X) was used to measure positive affect (Watson et al., 1988). This assessment tool is composed of words (i.e. cheerful) or phrases (i.e. dissatisfied with self) that describe different feelings or emotions. Participants were asked to indicate the extent to which they felt this way at the current time on a scale where 1= very slightly or not at all, 2 = a little, 3 = moderately, 4 = quite a bit, and 5 = extremely. The General Positive Affect subscore was the primary score of interest with a maximum score of 50 (higher scores indicate higher positive affect).

2.7 Data Analysis

All analyses were conducted in SPSS version 27 (IBM Corp., Armonk, NY). To examine differences between groups at baseline, a one-way analysis of variance (ANOVA) was run on age, state anxiety scores, trait anxiety scores, self-esteem scores, baseline psychosocial measure scores (task-specific self-efficacy, perceived competence, interest/enjoyment, positive affect) and baseline performance measures from the exposure block (response time, path distance, and peak velocity).

To examine motor skill acquisition over Day 1, a univariate generalized linear model (GLM) with fixed factors for group (CONTROL, RT ONLY, RT+POS), sequence type (repeated and random), and block of practice (first block on Day 1 to last block on Day 1) was used for all performance variables

(response time, path distance, peak velocity). To examine retention performance on Day 2 (i.e. motor skill learning), a univariate GLM with fixed factors for group (CONTROL, RT ONLY, RT+POS), sequence type (repeated and random), and block of practice (first block on Day 1; first block on Day 2) was used for all performance variables. A repeated measures ANOVA with between-subject factors for group (CONTROL, RT ONLY, RT+POS) and a within-subject variable for time (pre-practice, post-practice, and retention) was used to examine task-specific self-efficacy, perceived competence, interest/enjoyment, and general positive affect. Partial eta squared (η_p^2) estimated the effect size where a value 0.01-0.059 indicates a small effect, 0.06-0.139 indicates a medium effect, and $\geq$ 0.14 indicates a large effect (Cohen 1988). Post hoc analyses were performed to further assess significant main effects using pairwise comparisons and Bonferroni corrections for multiple comparisons. For significant interactions, post hoc testing was performed in each group using a repeated measures ANOVA with a factor for time.

3. Results

3.1 Participants

Participants were on average 25.4 ± 5.2 years old with 11 females and 5 males in each group. There was no significant difference between groups in age, Rosenberg Self-Esteem scores, or State Trait Anxiety Scale scores (Table 2.1). In addition, there was no significant difference between groups in any psychosocial variable at baseline (pre-practice scores for task-specific self-

efficacy, perceived competence, interest/enjoyment, and positive affect) (Table 2.2) or in any performance variable at baseline (response time, path distance, and peak velocity) as measured during the exposure block (Table 2.1).

3.2 Motor Task Performance and Learning - Acquisition

Response times decreased for both sequence types over task practice on Day 1 (Fig. 2.2 A-B; main effect of time $F_{(13,1260)} = 39.94$, $p < 0.001$, $\eta_p^2 = 0.29$) demonstrating improved task performance across groups. Additionally, response times were lower for the repeated sequence compared to the random sequence (main effect of sequence $F_{(1,1260)} = 244.90$, $p < 0.001$, $\eta_p^2 = 0.16$). However, the type of feedback participants received impacted response times (main effect of group $F_{(2,1260)} = 30.01$, $p < 0.001$, $\eta_p^2 = 0.05$), where the CONTROL group ($p<0.001$) and RT+POS group ($p<0.001$) showed lower response times for completing a sequence than the RT ONLY group. There was no significant difference between the CONTROL and RT+POS groups.

Path distance decreased over practice on Day 1 (Fig. 2.2 C-D; main effect of time $F_{(13,1260)} = 27.71$, $p < 0.001$, $\eta_p^2 = 0.22$), and path distance was shorter for the repeated sequence than the random sequence (main effect of sequence type $F_{(1,1260)} = 192.12$, $p < 0.001$, $\eta_p^2 = 0.13$). The type of feedback participants received impacted path distance (main effect of group $F_{(2,1260)} = 21.88$, $p < 0.001$, $\eta_p^2 = 0.03$), where the CONTROL group showed shorter path distances than both the RT ONLY ($p = 0.003$) and the RT+POS group ($p < 0.001$). There was

no significant difference between the RT ONLY and RT+POS group for path distance.

Peak velocity increased over practice on Day 1 for both sequence types (Fig. 2.2 E-F; main effect of time $F_{(13,1260)} = 5.76$, $p < 0.001$, $\eta_p^2 = 0.06$); there was no difference in peak velocity between sequence types (no main effect of sequence type $F_{(1,1260)} = 2.80$, $p = 0.094$). The type of feedback participants received impacted peak velocity (main effect of group $F_{(2,1260)} = 41.85$, $p < 0.001$, $\eta_p^2 = 0.06$), where the RT+POS group showed higher peak velocities than both the CONTROL ($p < 0.001$) and RT ONLY group ($p < 0.001$). There was no significant difference between the CONTROL and RT ONLY group for peak velocity.

3.3 Motor Task Performance and Learning - Learning

The results for retention were similar to the results from acquisition for all performance variables. Response times decreased from the start of Day 1 to the start of Day 2 (main effect of time $F_{(1,180)} = 147.73$, $p < 0.001$, $\eta_p^2 = 0.45$), and response times were lower for the repeated sequence versus the random sequence (main effect of sequence $F_{(1,180)} = 33.73$, $p < 0.001$, $\eta_p^2 = 0.16$). The type of feedback participants received impacted response times (main effect of group $F_{(2,180)} = 6.59$, $p = 0.002$, $\eta_p^2 = 0.07$), where the CONTROL group ($p = 0.002$) and RT+POS group ($p = 0.017$) showed lower response times than the RT ONLY group (Fig. 2.2 A-B). There was no significant difference between the CONTROL and RT+POS group for response time.

Similarly, path distances got shorter from the start of Day 1 to the start of Day 2 (main effect of time $F_{(1,180)} = 71.42$, $p < 0.001$, $\eta_p^2 = 0.28$), and path distances were shorter for the repeated sequence type (main effect of sequence type $F_{(1,180)} = 30.46$, $p < 0.001$, $\eta_p^2 = 0.15$). The type of feedback participants received impacted path distance (main effect of group $F_{(2,180)} = 3.38$, $p = 0.036$, $\eta_p^2 = 0.04$), where the CONTROL group showed shorter path distances than the RT+POS group ($p = 0.038$) (Fig. 2.2 C-D). There was no significant difference between the RT ONLY group and either of the other two groups for path distance.

Finally, peak velocity was higher at retention (main effect of time $F_{(1,180)} = 17.52$; $p < 0.001$, $\eta_p^2 = 0.09$). There was no difference in peak velocity between sequence types (no main effect of sequence type $F_{(1,180)} = 0.01$, $p = 0.935$). The type of feedback participants received impacted peak velocity (main effect of group $F_{(2,180)} = 9.93$, $p < 0.001$, $\eta_p^2 = 0.10$), where the RT+POS group showed higher peak velocities than the CONTROL ($p = 0.020$) and RT ONLY group ($p < 0.001$) (Fig. 2.2 E-F). There was no significant difference between the CONTROL and RT ONLY group for peak velocity.

3.4 Explicit Awareness

Ten participants recognized a pattern during practice (subjective awareness), however, seven could not reproduce any part of the repeated sequence. Two participants from the CONTROL group and one participant from the RT+POS were able to reproduce part of the repeated sequence in the correct

sequential order. None were able to reproduce the whole sequence. Nine participants were identified as having recognition awareness of the repeated sequence (two from CONTROL, three from RT ONLY, and four from RT+POS). Only two participants had recognition awareness and were able to recall part of the repeated sequence in the correct sequential order (one each from CONTROL and RT+POS group). The similar distribution of explicit awareness across groups suggests that the provision of performance related feedback did not impact explicit awareness of the repeated sequence.

3.5 Performance Expectancies

Task-Specific Self-Efficacy scores for each group were assessed at pre-practice, post-practice and retention (Table 2.2, Fig. 2.3A). One participant from the CONTROL group was missing retention data for the TSSE due to a technical difficulty. This person was dropped from this analysis only. As expected, task-specific self-efficacy scores increased with task practice (main effect of time $F_{(1.35,59.59)} = 28.18$, $p < 0.001$, $\eta_p^2 = 0.39$). However, the type of feedback provided did not impact task-specific self-efficacy ratings (no main effect of group, $p = 0.62$).

Perceived competence was assessed for each group at pre-practice, post-practice and retention (Table 2.2, Fig. 2.3B). The groups' perceived competence scores changed differently over time, as indicated by a significant GROUP X TIME interaction ($F_{(2.75,61.76)} = 4.21$; $p = 0.011$, $\eta_p^2 = 0.16$). The CONTROL group (main effect of time $F_{(1.48,22.25)} = 19.42$, $p < 0.001$, $\eta_p^2 = 0.56$) and RT+POS (main

effect of time $F_{(1.48,22.25)} = 29.89$, $p < 0.001$, $\eta_p^2 = 0.67$) group showed a significant increase in perceived competence over time while the RT ONLY group (no main effect of time, $p = 0.121$) did not. The CONTROL group increased perceived competence by 3.5 ± 3.4 points at the end of practice and 4.6 ± 3.6 points at retention. The RT+POS group increased perceived competence by 6.1 ± 4.0 at the end of practice and 5.6 ± 4.2 at retention.

The type of feedback provided had no impact on positive affect, as measured with the General Positive Affect score from the PANAS-X, or task interest/enjoyment, as measured with the interest/enjoyment subscale of the IMI (Table 2.2). Interest/enjoyment (no main effect of time, $p = 0.463$) and positive affect decreased (no main effect of time, $p = 0.071$) did not change over time. Positive affect scores (max score = 50) decreased by 0.48 ± 4.40 points from pre-practice to post-practice and 1.58 ± 5.07 points from pre-practice to retention.

4. Discussion

This study examined the effect of positive social comparative feedback on the learning of a joystick-based motor sequence task. For all three feedback groups (CONTROL, RT ONLY, and RT+POS), overall performance improved over practice and at retention as seen by faster response times. However, the type of feedback provided during practice influenced acquisition and retention performance with small to medium effect sizes. Overall, performance was better in the groups that received positive social comparative feedback (RT+POS) and no feedback (CONTROL) than the group that received performance feedback

without comparison (RT ONLY). In addition, the type of feedback provided during practice resulted in the learner utilizing a different kinematic approach to improving performance. The group who received positive social comparative showed higher movement speeds between targets, while the group who received no performance feedback showed straighter movements between targets. Therefore, feedback may be leveraged to bias motor practice towards higher movement speeds versus spatial accuracy along the movement path, depending on the goal of the training. To our knowledge, we are the first to identify how positive social comparative feedback content may differentially impact implicit motor sequence learning and the spatial and temporal aspects of motor performance and learning. Based on these results, clinicians and trainers might consider feedback content as a useful tool for optimizing training outcomes or to target a specific motor control pattern (e.g. movement speed versus spatial control).

The primary measure to assess motor skill acquisition and learning was response time to complete a sequence. Our results regarding response time partially confirmed our hypothesis and the OPTIMAL theory perspective that positive social comparative feedback optimizes motor learning given that the RT+POS group showed better performance (lower response times) than the RT ONLY group over practice and at retention. However, we did not find differences in response times between the CONTROL group and the RT+POS group. Previous literature on positive social comparative feedback included groups comparable to the RT ONLY and RT+POS group, but not a group comparable to

the CONTROL group (Ávila et al., 2012; Chua et al., 2018; Lewthwaite & Wulf, 2010). We included a CONTROL group to mirror traditional implicit sequence learning task paradigms, where performance feedback is generally not provided (Nissen & Bullemer, 1987). By combining two separate lines of motor learning research (positive social comparative feedback and implicit motor sequence learning), our findings contribute novel information to both areas of research. Overall, our findings indicate that there may be specific task domains (e.g. implicit motor sequence) where expectancy enhancing feedback is not necessarily better for learning than no feedback. Additionally, providing performance feedback with social comparison resulted in similar response times and similar explicit awareness of the repeated sequence as the traditional approach of not providing performance feedback. This indicates that positive social comparative feedback does not interfere with implicit sequence learning processes or increase explicit awareness of the repeated sequence.

In contrast, response time feedback without social context (RT ONLY) appears to be detrimental for motor sequence learning compared to no feedback (CONTROL) and positive social comparative feedback (RT+POS). A possible explanation for this effect is that the RT ONLY group was given performance information without a means for assessing whether their performance was good or bad. Knowledge of results feedback, such as response time, encourages learning through cognitive processes rather than conditioning responses (Maier et al., 2019; Salmoni et al., 1984). Therefore, response time feedback during an implicit sequence learning task may not be helpful to the learner without relevant

context for evaluating the performance information. According to the OPTIMAL theory, feedback that enhances expectancies helps the learner to reduce focus on the self and increase focus on the task goal, which then supports motor skill acquisition and learning (Wulf & Lewthwaite, 2016). Feedback about performance without immediate context might result in increased internal focus, whereby the learner is attending to their response time without information to determine whether their performance is good or bad. This idea is supported in the perceived competence data. The RT ONLY group did not show an increase in perceived confidence despite the fact that their performance improved over time. This disconnect between actual performance improvements and perceptions of competence could be attributed to increased self-focus on their response time with an inability to determine whether they are meaningfully improving performance or not. Future studies should aim to determine how performance feedback without accessible context during novel skill practice influences attentional and cognitive aspects of learning.

The CONTROL and RT+POS groups achieved similar response times over practice and at retention. However, these two groups used different kinematic approaches to support and improve their performance providing evidence that feedback can impact a learner's motor control pattern. Hand path distance and peak velocity are kinematic variables that contribute to the resulting response time (J. Baird & Stewart, 2018; Moisello et al., 2009). Shorter hand paths indicate greater spatial accuracy along the movement trajectory which leads to reduced response times, while higher peak velocities indicate faster

reach speeds which leads to reduced response times. A learner may improve their response time by utilizing straighter/shorter hand paths (spatial control pattern), higher peak velocities (temporal control pattern), or a combination of both. Prior work suggests that variations in motor practice conditions can alter whether the learner utilizes a spatial or temporal approach to improve performance (J. F. Baird et al., 2018). Our results suggest that feedback content can influence a learner's approach to improving their performance as the CONTROL group showed shorter and straighter paths than RT+POS group (small effect size) while the RT+POS group showed higher peak velocities than either of the other two groups (medium effect size). This finding aligns with the OPTIMAL theory perspective that positive social comparative feedback aligns the learner's actions to the task goal (Wulf & Lewthwaite, 2016), since the task goal was to move fast and the RT+POS showed higher peak velocities. Future work should aim to determine if positive social comparative feedback consistently leads to changes in the component of performance that is stated as the task goal or if this type of feedback always encourages a temporal approach to improving performance.

For performance expectancies, the feedback provided impacted some measures of expectancies (perceived competence) but not others (task-specific self-efficacy, task interest/enjoyment, positive affect). All groups showed gains in task-specific self-efficacy, which was expected given that all groups improved performance over practice and previous performance level predicts self-efficacy (Moritz et al., 2000; Wulf et al., 2014). However, the hypothesized group effect,

where the RT+POS would show the greatest gains, was not present. This could be attributable to the TSSE scale, which includes a range of response time windows; the time windows selected may not have been optimal for detecting differences between groups. In addition, other expectancy-related measure (task interest/enjoyment and positive affect) were not different by group. The absence of change in task interest and enjoyment has been noted previously (Lewthwaite & Wulf, 2010), and may be explained by a global characteristic of the task practice (i.e., highly repetitive simple lab task) and not the feedback. On the other hand, the feedback provided impacted self-assessments of perceived competence, where the CONTROL and RT+POS group showed increased perceived competence and the RT ONLY group did not. These results suggest no feedback is better for supporting self-assessed perceived competence than performance feedback without social context. If providing performance related feedback during practice, comparative context may be necessary for supporting perceptions of competence and enhancing expectancies.

The joystick-based motor sequence task allowed the investigation of the spatial and temporal aspects of motor performance as well as examination of general sensorimotor learning and implicit sequence learning. However, this task does not represent all types of motor skill learning, and our results may be specific to this task paradigm. In addition, positive social comparative feedback is a type of feedback manipulation intended to enhance the learners' expectancies; however, there are many potential feedback manipulations that might enhance a learners' expectancies and benefit motor learning

(Chiviacowsky et al., 2012; Saemi et al., 2012; Wulf et al., 2012). Finally, the feedback approach in the current study was based on prior research (Wulf et al., 2014), but the best parameters for providing expectancy enhancing feedback have not been established. As such, the parameters of the social comparative feedback provided in this study may not have been the most effective approach for enhancing performance and expectancies in the RT+POS group. The feedback manipulation involved nonveridical comparative values in order to maintain tight control of feedback delivery in a task that lacked age-matched normative values. While this is valid approach for scientific investigation, nonveridical feedback may not be a feasible clinical intervention. In addition, some participants may not have believed the positive social comparative feedback. However, group differences in expectancies and performance were still present despite this. Future studies could include assessment of feedback believability to determine whether believability influences performance or expectancy improvements.

5. Conclusion

Positive social comparative feedback indicates to the learner that they are performing better than others. This type of feedback resulted in better overall performance (i.e. lower response times) over acquisition and at retention and higher perceived confidence than response time feedback without social comparison, but similar overall performance and confidence to a control condition without feedback. Response time only feedback was detrimental motor

performance and learning as compared to no feedback or feedback with social context. In addition, positive social comparative feedback resulted in higher peak velocities, a temporal aspect of performance, than no feedback or response time only feedback, while no feedback resulted in shorter path distances, a spatial aspect of performance, than feedback with positive social comparison. Our results suggest that the motivation content of feedback can impact the acquisition and learning of a motor sequence task and the motor control approach taken to improve performance (temporal versus spatial). These results have implications for how clinicians may provide feedback during motor practice in sport and rehabilitation settings to promote motor learning, the utilization of a specific motor control pattern, and/or optimally enhance expectancies.

Table 2.1. Group demographics and baseline characteristics

	Group 1 CONTROL	Group 2 RT ONLY	Group 3 RT+POS
n	16	16	16
Sex	11F/5M	11F/5M	11F/5M
Age (y)	24.8 (3.7)	26.8 (6.1)	24.8 (5.6)
RSE Score	35.1 (4.1)	35.0 (3.1)	35.4 (4.1)
State Anxiety Score	29.5 (3.7)	27.9 (6.8)	28.8 (6.2)
Trait Anxiety Score	33.1 (6.3)	33.1 (6.5)	32.8 (8.8)
Response Time (s)	13.8 (1.4)	14.3 (0.7)	13.7 (1.3)
Path Distance (cm)	151.3 (12.4)	154.2 (11.4)	154.9 (16.3)
Peak Velocity (cm/s)	54.3 (7.3)	51.0 (3.7)	56.2 (8.0)
Feedback	"You completed the block. Take a rest."	"You completed the block in 87.2 seconds."	"You completed the block in 87.2 seconds. Your time was 17.5 seconds faster than the average of others on this block."

Mean values (standard deviation); F=Female; M=Male; y=years; RSE Score = Rosenberg Self-Esteem Score; no significant differences between groups on any measure

Table 2.2: Scores from expectancy measures over practice and at retention

		CONTROL	RT ONLY	RT+POS
Task-Specific Self-Efficacy	*Pre*	484.0 (85.0)*	477.5 (74.4)*	520.0 (125.9)*
	Post	568.7 (98.2)*	574.4 (86.4)*	582.5 (77.4)*
	Retention	555.5 (111.3)*	586.2 (76.7)*	585.6 (71.4)*
Perceived Competence	*Pre*	18.6 (6.3) †	18.6 (4.8)	20.3 (5.6) †
	Post	22.1 (6.3) †	20.1 (3.3)	26.3 (5.1) †
	Retention	23.2 (5.5) †	20.4 (3.5)	26.0 (4.9) †
Interest/Enjoyment	*Pre*	24.6 (7.2)	23.5 (6.3)	26.1 (6.6)
	Post	25.9 (8.3)	23.5 (7.1)	26.8 (6.2)
	Retention	26.1 (8.1)	22.6 (7.4)	26.1 (7.4)
Positive Affect	*Pre*	31.7 (5.5)*	28.8 (5.6)*	33.1 (8.9)*
	Post	30.8 (8.4)*	29.8 (8.2)*	31.5 (9.4)*
	Retention	29.9 (7.6)*	28.3 (9.0)*	30.6 (11.3)*

Mean values (standard deviation); Pre = scores from before practice on Day 1; Post = scores after practice on Day 1; Retention = scores from before Retention testing on Day 2; * = significant main effect of time in repeated measures ANOVA at $p < 0.05$; † = significant main effect of time within the group upon post hoc testing of significant GROUP X TIME at $p < 0.05$

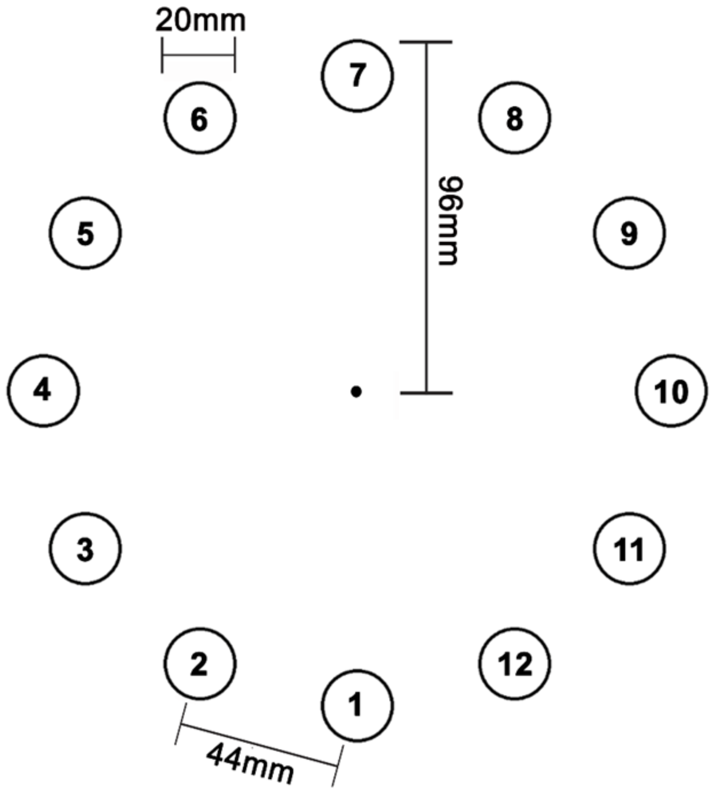

Figure 2.1: Schematic of the spatial locations of the twelve targets. Each target was 20 mm in diameter with a tangential distance of 44 mm between any adjacent target. The radius of the circular array was 96 mm. The repeated sequence consisted of targets 11, 10, 5, 9, 7, 3, 6, and 12.

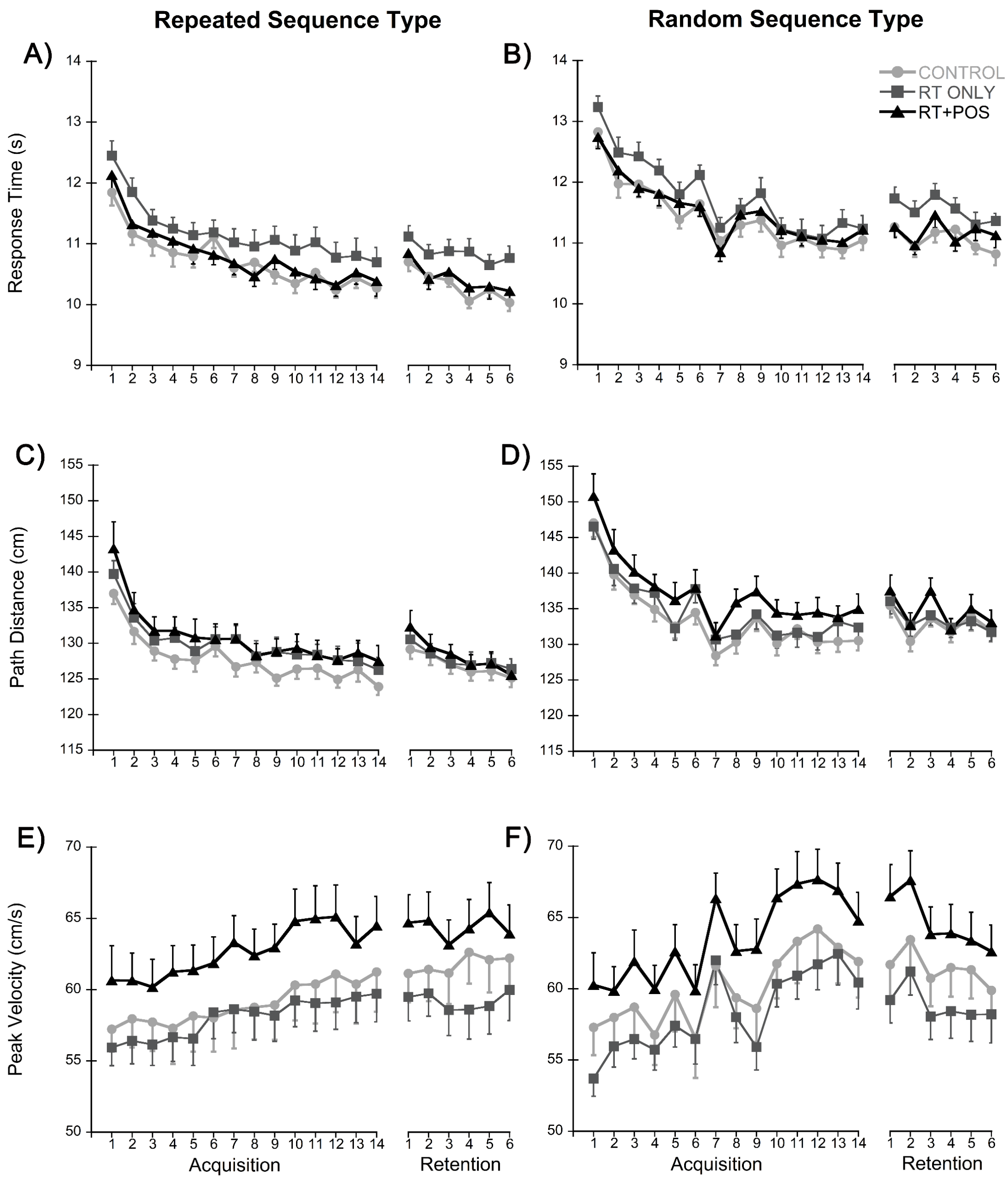

Figure 2.2: Motor performance over acquisition and at retention. Each data point is the average ± standard error of 5 sequence trials. **A)** Response time for the repeated sequence; **B)** Response time for the random sequence; **C)** Path distance for the repeated sequence; **D)** Path distance for the random sequence; **E)** Peak velocity for the repeated sequence; **F)** Peak velocity for the random sequence.

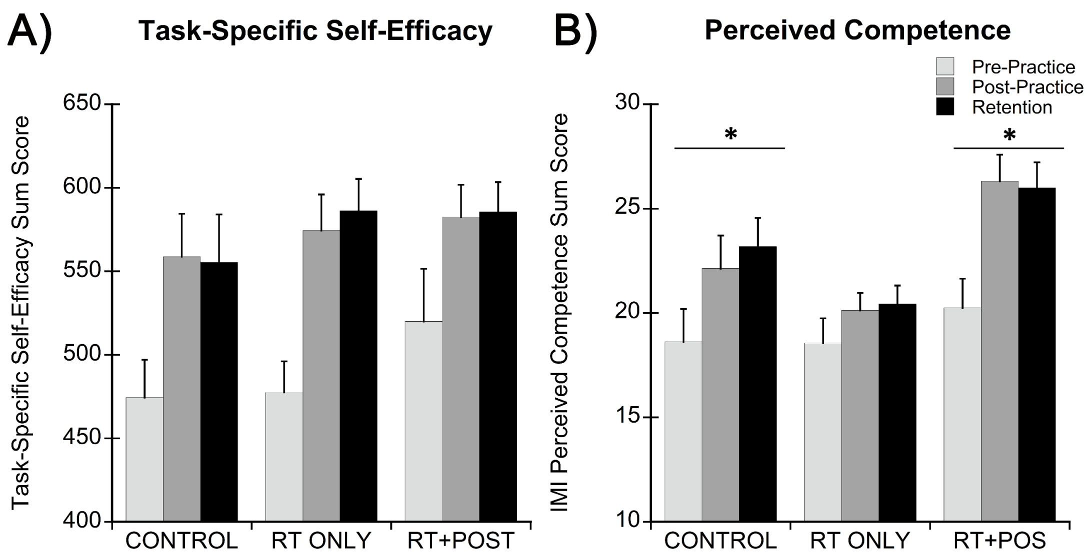

Figure 2.3: Performance expectancies. **A)** Task-Specific Self-Efficacy Scores ± standard deviation for each group at pre-practice, post-practice, and retention**. B)** Intrinsic Motivation Inventory (IMI) Perceived Competence subscale sum scores ± standard error for each group at pre-practice, post-practice, and retention. Maximum scores for the IMI Perceived Competence subscale is 35. * = significant main effect of time within group.

CHAPTER 3

EFFECTS OF POSITIVE SOCIAL COMPARATIVE FEEDBACK ON THE RESTING STATE CONNECTIVITY OF DOPAMINERGIC NEURAL PATHWAYS

1. Introduction

The OPTIMAL (Optimizing Performance Through Intrinsic Motivation and Attention for Learning) theory of motor learning states that motivational and attentional factors influence motor performance and learning (Wulf & Lewthwaite, 2016). According to this theory, motor practice conditions that enhance a learner's expectancies about future performance lead to optimized motor learning. Expectancies include the learners' perceived competence about their ability to perform the task, task-related self-efficacy, expectations about task outcome (success or failure), and predictions of extrinsic reward related to performance. Positive social comparative feedback, which indicates to the learner that they are performing better than others, is one way to enhance a learner's expectancies. While positive social comparative feedback during motor practice supports motor skill learning and enhances expectancies (Lewthwaite & Wulf, 2010; Pascua et al., 2015; Wulf et al., 2012, 2014), the neural mechanism through which this effect occurs is unknown.

The OPTIMAL theory hypothesizes that a dopaminergic response occurs in the brain as a result of enhanced expectancies, which in turn supports motor

skill learning (Wulf & Lewthwaite, 2016). Dopamine is a neurotransmitter that subserves many physiologic processes including reward, motivation, and motor function (Suzanne N. Haber & Knutson, 2010; Ikemoto et al., 2015; Wise, 2004). Dopamine serves to promote learning of and motivation towards actions that result in the rewarding experience (Schultz, 2016). Because dopamine supports learning and motivation, the field of motor learning and rehabilitation has begun to consider how this system might be leveraged to maximize motor skill learning to promote recovery after injury (Johnson & Cohen, 2022; Widmer et al., 2022).

Dopamine is released from the ventral tegmental area (VTA) and substantia nigra (SN) in anticipation of and response to rewarding stimuli (Hahn et al., 2021; Schott et al., 2008). Dopamine can exert influence on behaviors through several pathways in the brain. These neural pathways include the mesolimbic, mesocortical, and nigrostriatal pathways (Suzanne N. Haber & Knutson, 2010; Ikemoto, 2007; Wise, 2004). The mesolimbic pathway refers to dopamine projections from VTA to the nucleus accumbens (NAcc), while the mesocortical pathway includes dopamine projections from VTA directly to regions in the prefrontal cortex, like the orbitofrontal cortex (OFC) (often referred to collectively as the mesocorticolimbic pathway) (Coenen et al., 2018; MacNiven et al., 2020). The nigrostriatal pathway consists of dopamine projections from SN to the caudate and putamen (i.e., the dorsal striatum) which functions to influence movement (Luo & Huang, 2016). While the mesocorticolimbic pathway has been the focus of previous research in this area, both the mesocorticolimbic

pathway and nigrostriatal pathway play a role in reward processing and motivation (Ikemoto et al., 2015; Wise, 2004).

Similar brain regions are engaged when people are provided social rewards and monetary rewards, which include regions along both the mesocorticolimbic and nigrostriatal pathways (Gu et al., 2019). The mesocorticolimbic pathway is responsive to a variety of social rewards including smiling faces and feelings of love (Aharon et al., 2001; Bartels & Zeki, 2004; A. Lin et al., 2012; Rademacher et al., 2010). The nigrostriatal pathway has also been implicated in reward and motivational processing in animal models (Ikemoto et al., 2015), and the caudate and putamen, regions along the nigrostriatal pathways, are active in processing of social rewards in human fMRI studies (Gu et al., 2019; Izuma et al., 2008; Wake & Izuma, 2017). Given the overlap between dopaminergic pathways and the neural pathways implicated in reward and motivation, positive social comparative feedback during practice could trigger dopaminergic signaling between regions along the mesocorticolimbic and/or nigrostriatal pathways. However, no studies have investigated this question by using neuroimaging techniques to measure changes in brain connectivity along these pathways related to feedback with positive social comparison.

Connectivity between pairs of brain regions, examined by resting state functional magnetic resonance imaging (rsfMRI), reflects the activation of brain regions required to support task performance. rsfMRI measures the low-frequency activity in the brain during rest, which identifies coherent patterns of

brain activity (Fox & Raichle, 2007). rsfMRI generates connectivity patterns similar to the networks that are involved during active performance of the task (Biswal et al., 1995; Cao et al., 2014; Fox & Raichle, 2007; Shehzad et al., 2009; Smith et al., 2009). In addition, rsfMRI has unique advantages that can be leveraged to examine the neural networks involved in the learning of a motor task. rsfMRI can be applied to a variety of motor tasks that cannot be studied using task-based fMRI, since motor practice can occur outside the confines of the MRI scanner. Further, rsfMRI is collected at rest, which minimizes the confounds of online movement (i.e. motor performance, head motion) (Carter et al., 2012; Grefkes & Fink, 2011). In this way, resting state connectivity can be measured before and after practice, reflecting the networks underlying the motor learning process. Finally, resting state connectivity has been shown to change with short-term practice of motor skills (Albert et al., 2009; C. H. Lin et al., 2018; Steel et al., 2019). Therefore, rsfMRI provides the opportunity to determine whether social comparative feedback engages the mesocorticolimbic and/or nigrostriatal dopaminergic neural networks during motor learning with social comparative feedback, addressing a significant gap in the literature.

The purpose of this preliminary study was to examine the effect of positive social comparative feedback on resting state functional connectivity of the mesocorticolimbic and nigrostriatal neural pathways. We hypothesized that rsfMRI connectivity would increase along dopaminergic neural pathways in the group that received positive social comparative feedback but not in the group that received performance feedback without positive social comparison. Motor

performance, motor learning, and expectancies were also investigated to allow for interpretation of the brain data in context with the behavioral data, and to allow comparison with results from Chapter 2. In addition, exploratory analyses examining alternative neural pathways and brain-behavior relationships were conducted to inform and guide future studies.

2. Methods

2.1 Participants

Thirty-two non-disabled adults were recruited from the local community. To be included in the study, participants had to be age 18-40 years, right hand dominant as indicated by the Edinburgh Handedness Questionnaire (Oldfield, 1971), and able to move their right arm and hand without pain or limitation. Since the purpose of the study was to investigate resting state connectivity between dopamine synthesizing brain regions using MRI, individuals were excluded from the study if they were taking medications that might impact dopamine transmission, if they had a current medical diagnosis affecting dopamine transmission, or if MRI was contraindicated (e.g., metal implants). Thirty individuals were included in the final data analysis; two individuals with incidental findings on structural imaging were excluded in final data analysis. The study was approved by the University of South Carolina's Institutional Review Board. All participants provided written informed consent before beginning the research study protocol.

2.2 Experimental Design

Participants were randomized into an experimental feedback group: the response time only feedback group (RT ONLY) or the response time plus positive social comparison group (RT+POS). Participants completed two sessions on consecutive days. In both sessions, participants completed questionnaires and practiced the joystick-based motor sequence task. On Day 1, participants received their group specific feedback during practice and underwent MRI before and after the motor practice. On Day 2, participants returned for retention testing of the motor task. An honorarium was provided to participants at the end of each session ($10/session).

2.3 Serial Target Task

The serial target task (STT) was adapted from previous studies (J. Baird & Stewart, 2018; Mang et al., 2014) and implemented using E-Prime 2.0 (Psychology Software Tools, Inc., Sharpsburg, PA). The task has been fully described in the methods in Chapter 2. Briefly, participants sat facing a laptop screen with their right hand on a joystick. Movement of the joystick corresponded with proportional movement of a pointer-shaped cursor on the laptop screen. Circular targets appeared one at a time in one of twelve spatially distinct locations (Fig. 3.1). The task required the participant to move the cursor inside of the circular target for 500 milliseconds before the target would disappear and the next target would appear. However, the task did not require participants to return to the center between targets. The targets were arranged

in two types of 8-target sequences: a random sequence type and a repeated sequence type. The sequences were matched for difficulty according to Fitts' Law (Fitts & Peterson, 1964).

On Day 1, participants first completed an exposure block of 5 random sequences to ensure understanding of the task and to provide a baseline measure of performance. After exposure, participants completed 28 blocks of practice where each block contained 5 sequences that alternated between repeated and random for a total of 70 repetitions of each sequence type. The repeated sequence allowed for investigation of implicit, sequence-specific learning since participants were not made aware of the presence of repeated pattern. For both feedback groups, the learner received feedback in text on the laptop screen at the end of each block of practice. The RT ONLY group received feedback about their response time to complete the block (e.g., "You completed this block in 86.1 seconds"). The RT+POS group received feedback about their response time plus positive social comparison indicating they were faster than others (e.g., "You completed this block in 86.1 seconds. You were 17.2 seconds faster than the average"). The social comparative difference (e.g., "You were 17.2 seconds faster than the average") was a set percentage of the individual participant's response time on that block (Wulf et al., 2014). The percentage varied between 14% and 20% for 24 blocks and was reduced to 5% for four randomly selected blocks.

On Day 2, participants returned for retention testing of the motor sequence task, which included 12 blocks of motor practice. The structure of a motor

practice block was identical to Day 1 except that no feedback was provided. At the end of Day 2, participants were tested for explicit awareness of the repeated sequence. Sequences can be learned by either explicit processes, with awareness of the sequential pattern, or implicit processes, without awareness of the sequential pattern. The intent of this task paradigm was to limit explicit awareness and keep the sequence implicit. In the explicit awareness testing, participants were assessed on their subjective awareness of the presence of a pattern, recall awareness requiring tracing of the sequence in the correct order, and recognition awareness requiring identification of the repeated pattern from a series of targets visually displayed one at a time (details of these procedures are outlined in Chapter 2). Finally, participants were asked to rate the believability of the feedback from 0 to 10, where 0 indicated that the feedback was not believable up to 10 indicating the feedback was extremely believable.

Position data from the joystick was collected at 60 hertz and used to calculate response time, path distance, and peak velocity for each 8-target sequence. The primary measure for overall performance and learning was response time to complete an 8-target sequence. Path distance, a spatial measure of performance, was defined as the total distance traveled to complete all 8 targets in a sequence. Peak velocity, a temporal measure of performance, was defined as the highest velocity achieved between two targets and averaged across all targets in a sequence. Performance data were separated by sequence type (repeated or random) and averaged across five trials of the same sequence type for statistical analysis.

2.4 Performance Expectancies

Participants answered surveys and questionnaires by direct input into RedCap. The Rosenberg Self-Esteem Scale (Rosenberg, 1965) and the State Trait Anxiety Index (Spielberger et al., 1983) were completed before motor practice on Day 1 to provide baseline information about the participants self-esteem and anxiety, respectively. To assess changes in performance expectancies over practice, the Task-Specific Self-Efficacy Scale (TSSE), Intrinsic Motivation Inventory (IMI) perceived competence subscale, and IMI interest/enjoyment subscale were completed at three timepoints: after Exposure but before motor practice on Day 1, after motor practice on Day 1, and before retention testing on Day 2. The TSSE measured participants' self-efficacy related to STT performance (Bandura, 2006; Saemi et al., 2012). The scale asked participants to rate their perceived ability to perform the task on a scale from 0 ("cannot do it at all") to 100 ("completely certain I can do it") in intervals of 10 second response times (e.g., How confident are you in your ability to complete the task in 100-109 s?). The scale contained 10 items at 10-second intervals, and ratings were summed to create an overall self-efficacy score for analyses with higher scores indicating higher self-efficacy with a maximum score of 1000. The IMI Perceived Competence subscale scores range from 5 to 35, where higher scores indicate higher perceived competence related to the task (Deci & Ryan, 1985; Ryan, 1982). The IMI Interest/Enjoyment subscale scores

range from 7 to 49, where higher scores indicate greater interest or enjoyment of the task.

2.5 Magnetic Resonance Imaging

Participants underwent MRI before and after practice on Day 1 at the McCausland Center for Brain Imaging on a Siemens 3.0 Tesla MRI scanner using a 20-channel head coil. In each session, 12 minutes of resting state functional data was acquired with a 3D EPI sequence (TR = 1650 ms, TE = 35 ms, flip angle = 72 , 2.4mm × 2.4mm × 2.0mm voxel dimension, FOV 215mm × 215mm × 128mm, 50 slices, 2mm slice thickness). During the resting state scan, participants were instructed to keep their eyes closed, relax, think of nothing in particular, and not fall asleep. At the end of each resting state scan, participants were asked if they stayed awake and kept their eyes closed in order to verify that instructions were followed. A T1 weighted image was acquired with an MGH multiecho MPRAGE sequence (T1 = 1100 ms, TR = 2530 ms, flip angle = 8, 1mm × 1mm × 1mm voxel size, FOV 256mm × 256mm × 192mm, 192 slices, 1 mm slice thickness) for normalization of functional images.

The fMRI data were preprocessed using the CONN toolbox in SPM12 (CONN v19.c, Functional Connectivity SPM toolbox, McGovern Institute of Brain Research, Massachusetts Institute of Technology; www.nitrc.org/projects/conn) using the default preprocessing pipeline for volume-based analyses (Nieto-Castanon, 2020; Whitfield-Gabrieli & Nieto-Castanon, 2012). The functional images were corrected for subject motion using realign and unwarp functions

(Andersson et al., 2001). Images were then corrected for inter-slice differences in acquisition time via slice-timing correction (Henson et al., 1999). Outlier volumes were identified using ART-based identification (Power et al., 2014) based on conservative settings, where images that exceeded 0.5 mm of motion or global-signal z-value threshold of 3 were scrubbed and excluded from further analysis. Structural and functional images were segmented and normalized to MNI space with a structural image target resolution of 1mm and functional target resolution of 2mm (Ashburner & Friston, 2005). Functional images were smoothed with Gaussian kernel (FMWH = 4mm). Functional data were then preprocessed through the default denoising pipeline in CONN. The denoising pipeline uses linear regression to regress out potential confounding effects in the BOLD signal as well has temporal band-pass filtering. Noise regressors included signal components from white matter and CSF (Behzadi Y et al., 2007), estimated subject-motion parameters (Friston et al., 1996), noise from scrubbed outlier volumes (Power et al., 2014), and session/task effects (Whitfield-Gabrieli & Nieto-Castanon, 2012). For band-pass filtering, temporal frequencies below 0.008 Hz or above 0.09 Hz were removed from the BOLD signal (Hallquist et al., 2013).

Next, seed-based connectivity measures between pairs of ROIs were assessed on the individual subject level. ROIs were selected a priori and included regions along the mesocorticolimbic dopamine pathway (VTA-L NAcc, VTA-R NAcc, VTA-L OFC, VTA-R OFC) and along the nigrostriatal dopamine pathway (L SN-L Caudate, L SN-L Putamen). In addition, an exploratory

analysis investigated pathways that could play a role in interfacing motivational signals with motor behaviors (S N Haber et al., 2000; Hosp et al., 2019; MacNiven et al., 2020), including pathways between VTA and motor-related regions (VTA-L M1, VTA-L Putamen, VTA-L Caudate). Several of these ROIs were available in CONN via the Harvard-Oxford probabilistic atlas (left caudate, left putamen, and left and right OFC) (Desikan et al., 2006). Additional ROIs were identified and downloaded from published, publicly available atlases, and manually added as binarized masks during initial preprocessing steps. These ROIs included VTA, left SN, right SN (Murty et al., 2014), and the human motor area template for the left primary motor cortex (M1) (Mayka et al., 2006). Seed-based connectivity analysis were run to generate a functional connectivity correlation matrix of Fisher's Z transformed correlation coefficients for connections between a priori ROIs.

2.5 Statistical Analysis

All statistical analyses were conducted in SPSS version 28. Independent samples t-tests were run on baseline data to determine between group differences in demographics, psychosocial assessments, motor task performance, and resting state connectivity (pre-practice Z-scores). This analysis was intended to aid in interpretation of how similar the two groups were at baseline.

Performance changes were investigated separately for within session practice effects (first block of Day 1 to the last Block of Day 1) and for learning

(first block of Day 1; first block of Day 2). For acquisition performance, a generalized linear model (GLM) with fixed factors for group (RT ONLY, RT+POS), sequence type (random, repeated), and block (first block on Day 1 to last block on Day 1) was utilized. For motor learning at retention, a similar GLM was utilized with factors for group, sequence, and block (first block of Day 1; first block of Day 2).

To examine the effect of feedback on expectancies (TSSE and IMI scores), a repeated-measures ANOVA with between-subject factor for group and within-subject factor for time (pre-practice, post-practice, and retention) was utilized. Partial eta squared estimated effect sizes for GLM and ANOVA analyses, and effect sizes were classified according to the following criteria: 0.01-0.059 = small, 0.06-0.139 = medium, and $\geq$ 0.14 = large (Cohen, 1988).

For resting state connectivity, Z-scores for each pair of brain regions for each subject were moved forward into SPSS for group analyses. Paired t-tests within group compared pre-practice and post-practice Z-scores. Paired t-tests within each group were selected over between group comparisons due to the preliminary nature of the study and the size of the groups. Cohen's d estimated effect sizes, and effect sizes were classified according to the following criteria: 0.2 = small, 0.5 = medium, and 0.8 = large (Cohen, 1988). Significance was set at a corrected $p < 0.008$ (0.05 divided by the 6 pairs of brain regions) for the primary networks of interest (mesocorticolimbic and nigrostriatal). For the exploratory pathway, significance was set at a corrected $p < 0.017$ (0.05 divided by the 3 pairs of brain regions). Z-scores were converted to correlation

coefficients for data presentation in figures to aid in interpretation of the data. However, all statistical analyses were performed on Z-scores. In order examine how feedback believability impacted the response to feedback in the RT+POS group, nonparametric Spearman's correlations between believability rating and change in performance expectancies, change in performance, and change in connectivity were computed.

Linear regression models were analyzed to explore relationships between brain connectivity and change in performance. The dependent variable in these models was change in performance. Change over acquisition was calculated by subtracting performance on the first block of Day 1 from the last block of Day 1. Change at retention was calculated by subtracting performance on the first block of Day 1 from the first block of Day 2. Two sets of models were analyzed, where Model 1 included group, baseline connectivity, and the interaction between group and baseline connectivity as independent variables. Model 2 included the same variables plus baseline performance. The same process was repeated with change in connectivity in place of baseline connectivity. All continuous variables were mean centered before being entered into the model. Given the exploratory nature of these analyses and the sample size, significance was set $p < 0.05$. Significant interactions between group and baseline connectivity in Model 1 were further analyzed with correlations separately by group. Significant interactions between group and change in connectivity in Model 1 were further analyzed with partial correlations, controlling for baseline performance, separately by group.

3. Results

3.1 Participants

Participants were mostly female (RT ONLY 10 females; RT+POS 11 females) and on average 25.62 ± 4.28 years old. The two groups did not differ in age, Rosenberg Self-Esteem score, or Trait Anxiety Score or State Anxiety Score (Table 3.1). Further, the groups were not different on baseline motor performance (response time, path distance, peak velocity), baseline expectancy variables (task-specific self-efficacy, perceived competence, and interest/enjoyment in the task) (Table 3.2), or baseline connectivity between pairs of brain regions in any pathway (Table 3.3).

3.2 Motor Performance, Learning, and Explicit Awareness

3.2.1 Acquisition

Response time, path distance, and peak velocity improved over practice on Day 1 for both sequence types (main effect of block on response time $F_{(13,784)} = 24.85$, $p < 0.001$, $\eta_p^2 = 0.29$; path distance $F_{(13,839)} = 16.93$, $p < 0.001$, $\eta_p^2 = 0.22$; peak velocities $F_{(13,784)} = 2.55$, $p = 0.002$, $\eta_p^2 = 0.04$) (Fig. 3.2 A-F), regardless of group. For both groups, response time was faster, path distance was shorter, and peak velocity was higher for the repeated sequence versus the random sequence (main effect of sequence type on response time $F_{(1,784)} = 73.68$, $p < 0.001$ $\eta_p^2 = 0.09$; path distance $F_{(1,784)} = 72.32$, $p < 0.001$, $\eta_p^2 = 0.08$; peak velocities $F_{(1,784)} = 6.81$, $p = 0.009$, $\eta_p^2 = 0.01$). The RT+POS group showed faster response times and higher peak velocities than the RT ONLY

group on Day 1 (main effect of group on response time $F_{(1,784)} = 39.77$, $p < 0.001$, $\eta_p^2 = 0.05$; peak velocity $F_{(1,784)} = 80.94$, $p < 0.001$, $\eta_p^2 = 0.09$). There were no significant differences between groups in path distance on Day 1 (no main effect of group $F_{(1,784)} = 0.01$, $p = 0.93$, $\eta_p^2 < 0.001$).

3.2.2 Learning

Regardless of group, response time, path distance, and peak velocity improved for both sequence types at retention testing on Day 2 (main effect of block on response time $F_{(1,112)} = 66.90$, $p < 0.001$, $\eta_p^2 = 0.37$; path distance $F_{(1,112)} = 41.73$, $p < 0.001$, $\eta_p^2 = 0.27$; peak velocity $F_{(1,112)} = 11.39$, $p = 0.001$, $\eta_p^2 = 0.09$) (Fig. 3.2 A-F). Response time was faster and path distance was shorter for the repeated sequence over the random sequence; however, there was no effect of sequence on peak velocity (main effect of sequence on response time $F_{(1,112)} = 5.39$, $p = 0.022$, $\eta_p^2 = 0.05$; path distance $F_{(1,112)} = 6.64$, $p = 0.01$, $\eta_p^2 = 0.06$; peak velocity $F_{(1,112)} = 0.80$, $p = 0.373$, $\eta_p^2 = 0.01$). The RT+POS group showed higher peak velocities than the RT ONLY group ($F_{(1,112)} = 8.89$, $p = 0.004$, $\eta_p^2 = 0.07$). However, there was no effect of group on response time or path distance (no main effect of group on response time $F_{(1,112)} = 2.90$, $p = 0.091$, $\eta_p^2 = 0.03$; path distance $F_{(1,112)} = 0.01$, $p = 0.937$, $\eta_p^2 < 0.001$).

3.2.3 Explicit Awareness and Believability

Seven participants reported subjective awareness by stating that they recognized a repeating pattern. Of these seven, five participants could not

reproduce any part of the repeated sequence. One participant from the RT ONLY group and one participant from the RT+POS were able to reproduce all or most of the repeated sequence. Six participants were identified as having recognition awareness of the repeated sequence (two of these were also able to recall all or most of the sequence). The six with recognition awareness were divided equally between the groups with three in each group.

For believability of the feedback, the average was 8.73 ± 1.28 for the RT ONLY group and 5.53 ± 2.64 for RT+POS group. Correlations between believability and change in performance expectancies (task-specific self-efficacy), change in performance (response time), and change in connectivity (VTA-L NAcc) were analyzed for the RT+POS group and were not significant.

3.3 Performance Expectancies

As expected, both groups showed improvements in task-specific self-efficacy (main effect of time $F_{(1.22,34.15)} = 39.50$, $p < 0.001$, $\eta_p^2 = 0.59$) and perceived competence (main effect of time $F_{(1.22,34.28)} = 26.70$, $p < 0.001$, $\eta_p^2 = 0.49$) over practice (Table 3.2). However, the improvements in task-specific self-efficacy and perceived competence were not different by group (no main effect of group on TSSE $F_{(1,28)} = 1.79$, $p = 0.192$, $\eta_p^2 = 0.06$ or IMI Perceived Competence $F_{(1,28)} = 0.06$, $p = 0.807$, $\eta_p^2 < 0.01$). Task interest/enjoyment did not change over time regardless of group (no effect of time $F_{(1,28)} = 3.24$, $p = 0.06$, $\eta_p^2 = 0.10$; no effect of group $F_{(1,28)} = 0.02$, $p = 0.89$, $\eta_p^2 < 0.01$). Interactions between group and time were not significant for any of the expectancy measures.

3.4 Resting State Functional Connectivity

For the RT ONLY group, mesocorticolimbic and nigrostriatal connectivity did not change from before to after practice (Table 3.3; Fig. 3.3 and 3.4). For the mesocorticolimbic pathway, VTA-L NAcc connectivity ($p = 0.281$, $d = 0.29$), VTA-R NAcc connectivity ($p = 0.155$, $d = 0.39$), VTA-L OFC connectivity ($p = 0.774$, $d = 0.08$), and VTA-R OFC connectivity ($p = 0.383$, $d = 0.23$) did not change significantly. For the nigrostriatal pathway, L SN-L Caudate ($p = 0.212$, $d = 0.34$) and L SN-L Putamen connectivity ($p = 0.720$, $d = 0.09$) did not change significantly from before to after practice

For the RT+POS group, VTA-L NAcc connectivity (mesocorticolimbic pathway) increased from before to after practice ($p = 0.001$, $d = 1.03$) (Table 3.3; Fig. 3.3C) but not for the RT ONLY group (see above). L SN-L Caudate connectivity (nigrostriatal pathways) increased from before to after practice but this increase did not exceed the corrected statistical level ($p = 0.021$, $d = 0.67$) (Fig. 3.4C). Connectivity did not change from before to after practice for any other pairs of brain regions (Fig. 3.3 and 3.4) including VTA-R NAcc ($p = 0.837$, $d = 0.05$), VTA- L OFC ($p = 0.947$, $d = 0.02$), VTA-R OFC ($p = 0.805$, $d = 0.07$), and L SN-L Putamen ($p = 0.459$, $d = 0.20$).

3.5 Exploratory Analyses

3.5.1 Exploratory Pathway Connectivity

For the RT ONLY group, VTA-L Caudate ($p = 0.099$, $d = 0.46$) and VTA-L Putamen ($p = 0.105$, $d = 0.45$) did not increase from before to after practice while

VTA-L M1 connectivity did ($p < 0.001$; $d = 1.09$) (Fig. 3.5). Pre-practice VTA-L M1 connectivity was lower for the RT ONLY group ($Z = -0.11 \pm 0.07$) than the RT+POS group ($Z = 0.00 \pm 15$), but this baseline difference was not statistically significant ($p = 0.018$) at the corrected p-value of 0.017. For the RT+POS group, connectivity between pairs of brain regions along the exploratory pathways did not significantly change from before to after practice (VTA-L M1 $p = 0.476$, $d = 0.19$; VTA-L Caudate $p = 0.029$, $d = 0.63$; VTA-L Putamen $p = 0.091$, $d = 0.47$) (Fig. 3.5).

3.5.2 Brain Behavior Relationships

Linear regressions models were utilized to explore relationships between connectivity and change in motor performance, with specific interest in whether these relationships differed by group. These analyses focused on change in response time and peak velocity as the dependent variables because group effects were identified in these performance measures. The VTA-L NAcc connectivity was selected as the independent variable representing brain function since this was the only pair of brain regions that showed a significant change from before to after practice.

The first set of models explored relationships between change in performance and baseline VTA-L NAcc connectivity (Table A.1; Fig. 3.6). For Model 1, the group by connectivity interaction term was significant for response time at acquisition (interaction $\beta = -0.60$, $p = 0.005$), response time at retention (interaction $\beta = -0.42$, $p = 0.049$), and peak velocity at retention (interaction $\beta = 0.43$, $p = 0.042$). Post-hoc correlations showed that, for the RT+POS group only,

higher baseline VTA-L NAcc connectivity was related to greater improvements in performance including faster response times at acquisition (RT ONLY r = 0.41, p = 0.128; RT+POS r = -0.60, p = 0.017), faster response times at retention (RT ONLY r = -0.07, p = 0.794; RT+POS r = -0.66, p = 0.007), and higher peak velocities at retention (RT ONLY r = -0.17, p = 0.550; RT+POS r = 0.67, p = 0.006) (Fig. 3.6). When baseline performance was added to the model (Model 2), these significant interactions were no longer present. In Model 2, baseline performance was the only significant predictor of change in response time at acquisition (baseline RT β = -0.56, p = 0.001), response time at retention (baseline RT β = -0.45, p = 0.016), and peak velocity at acquisition (baseline peak velocity β = -0.40, p = 0.025). For peak velocity change at retention, group was the only significant predictor (group β = 0.37, p = 0.032). Change in peak velocity at retention was greater for the RT+ POS group (7.92 ± 5.93 cm/s) than the RT ONLY group (2.44 ± 8.97 cm/s).

The second set of models explored relationships between change in performance and change in connectivity (Table A.2; Fig. 3.7). Model 1 (group, change in connectivity, and group by change in connectivity) was not significant for any of the change in performance variables at any time point ($p < 0.05$). In Model 2, the only significant relationship was between baseline performance and change in performance (change in response time at acquisition (baseline RT β = -0.63, p = 0.001), change in response time at retention (baseline RT β = -0.53, p = 0.003), and change in peak velocity at acquisition (baseline peak velocity β = -0.46, p = 0.010)). For change in peak velocity at retention, the interaction term

was significant (interaction β = -0.47, p = 0.031). Post-hoc partial correlations showed that greater increases in connectivity were not related to greater improvements in performance for either group. Instead, greater increases in connectivity were related to less improvement in peak velocity for the RT+POS group only (RT ONLY r = 0.08, p = 0.780; RT+POS r = -0.67, p = 0.009) (Fig. 3.7 D).

4. Discussion

The current study investigated the effects positive social comparative feedback on resting state connectivity of dopaminergic neural pathways, as well as its effects on motor learning and performance expectancies. Only the group that received positive social comparative feedback showed increased connectivity from before to after practice between the ventral tegmental area (VTA) and the left nucleus accumbens (L NAcc), suggesting positive social comparative feedback engages part of the mesocorticolimbic dopaminergic pathway during motor practice. To our knowledge, the current study is the first to investigate how social comparative feedback might engage dopaminergic neural networks. In addition, positive social comparative feedback during practice supported better overall performance (response times) than response time only feedback on Day 1 (acquisition) but not at Day 2 (retention). Consistent with Chapter 2, positive social comparative feedback resulted in higher peak velocities than response time only feedback, which adds to existing evidence that the spatial and temporal components of performance are distinctly sensitive to

the structure of motor practice (J. F. Baird et al., 2018) including feedback content (Chapter 2).

Increased connectivity along the mesolimbic pathway (VTA-L NAcc) was found after practice in the positive social comparative group but not the response time only group. This result supports the prediction of the OPTIMAL theory that positive social comparative feedback may trigger a dopaminergic response in the brain (Wulf & Lewthwaite, 2016). The idea of expectancy-dependent dopamine release from VTA to NAcc is supported by prior research. For example, the expectancy of a positive outcome from placebo resulted in dopamine release in the ventral striatum/NAcc as measured by positron emissions topography (PET) scanning (Boileau et al., 2007; Lidstone et al., 2010). While the current study did not directly measure dopamine binding, changes in rsfMRI informs what brain regions are active during task practice (Biswal et al., 1995; Cao et al., 2014; Fox & Raichle, 2007; Shehzad et al., 2009; Smith et al., 2009). The increase in connectivity between VTA and NAcc suggests that these regions along the mesolimbic pathway were active together during task practice with positive social comparative feedback.

Positive social comparative feedback resulted in increased connectivity along the mesolimbic pathway but not the nigrostriatal pathway. These results are partially consistent with previous studies that examined dopamine release in response to expectancies (placebo). In this previous work, expectancy-dependent dopamine release occurred in the ventral striatum/NAcc (i.e. the mesolimbic pathway) (Boileau et al., 2007) or in the ventral striatum/NAcc as well

as the putamen (Lidstone et al., 2010). Increased connectivity with the putamen (i.e. the nigrostriatal pathway) was not identified in the current study, suggesting that this pathway was not engaged during practice with positive social comparative feedback. While previous studies showed that the nigrostriatal pathway is engaged with social rewards (Gu et al., 2019; Izuma et al., 2008), such as smiling faces, the current study suggests that the nigrostriatal pathway may not be sensitive to expectancy enhancing feedback in the same way that it is sensitive to feedback that implies social approval, like smiling faces.

Positive social comparative feedback did not result in increased connectivity along the exploratory pathways (VTA-L Putamen, VTA-L Caudate, or VTA-L M1). However, the RT ONLY group demonstrated an increase in connectivity between VTA and L M1 from before to after practice. VTA-L M1 connectivity increased from a negative value to approximately zero in the RT ONLY group and stayed around zero for the RT+POS group. This suggests that VTA and L M1 were not functionally connected post-practice for either group. Further, neither group showed increases in connectivity between VTA and the dorsal striatum (caudate and putamen). This suggests that these pairs of brain regions were not activating together during motor practice to process feedback or to support motor performance or learning.

Overall performance on the motor task improved on acquisition and retention for both groups. As expected, RT+POS group showed faster response times at acquisition than the RT ONLY group. However, the two feedback groups did not differ in response time at retention or in performance

expectancies, which is in contrast to our findings in Chapter 2. The lack of group differences at retention may be attributed to the current study's design and protocol. Due to the primary aim of the current study, an MRI scan was completed immediately after motor practice, where participants were asked to "think of nothing in particular," a standard instruction during resting state scans. This instruction may have interfered with off-line processing that occurs during the consolidation phase of motor learning, the phase between the end of practice and retention testing where the memory representation of the motor skill is strengthened (Kantak & Winstein, 2012). This interference effect could be especially problematic in the RT+POS group, since this kind of feedback is meant to enhance the learner's perceptions of success, and perceptions of success may positively affect retention performance through modulation of the consolidation phase (Trempe et al., 2012). In addition, the MRI scan was performed before post-practice ratings of expectancies, and therefore, the potential interference effect from the MRI scan could have attenuated the individual's perceptions of success and impacted ratings of task-specific self-efficacy and perceived competence,

Consistent with previous work using the same joystick-based motor sequence task (Chapter 2), the group that received social comparative feedback showed higher peak velocities at acquisition and retention compared to the group that did not receive positive social comparative feedback. In this task, a learner may improve overall performance (response time) by utilizing a spatial approach (straighter movements along the trajectory between targets) and/or a temporal

approach (higher movement speeds between targets). The current results support our previous finding that positive social comparative feedback drives movements speeds, which has applications to sport and rehabilitation. Clinicians and trainers may leverage positive social comparative feedback to promote movement speed during motor practice, depending on the goal of the motor practice.

Exploratory analyses identified possible interactions between the type of feedback received and brain-behavior relationships. The significant interactions between feedback and baseline VTA-L NAcc connectivity suggested that higher baseline connectivity might be important to produce improvements in performance RT+POS feedback. When baseline performance was added to the models, these interactions were no longer significant. This demonstrated that baseline performance was a stronger predictor of improvements in performance than feedback group or connectivity. One interaction term (group by change in connectivity for change in peak velocity at retention) was still significant when baseline performance was added to the model (Fig. 3.6 D). For the RT+POS group only, greater increases in VTA-L NAcc connectivity were related to less improvement in peak velocity, indicating that increased connectivity along this pathway may not be contributing to peak velocity improvements in this small sample size. Overall, the exploratory regression results suggest that positive social comparative feedback may modulate relationships between dopaminergic pathway connectivity and change in performance, and that these complex relationships warrant further investigation with larger sample sizes.

The current study did not have the power to complete a whole brain analysis. The regions of interest included in our analysis were selected based on prior research on reward (Diekhof et al., 2012; Gu et al., 2019). Other brain regions that might play a role in motivation or motor learning may have also changed over practice. Additionally, while resting state analyses have some advantages, resting state connectivity does not allow for direct measurement of dopamine response in the brain. Mouse models suggest that the VTA contains neurons that signal via other neurotransmitters besides dopamine, like glutamate, and that these signals may also correspond with rewarding stimuli (Yoo et al., 2016). However, while the VTA glutamate neurons receive similar input to dopamine neurons, dopamine neurons appear to be more connected with ventral striatal neurons in mice (Faget et al., 2016), making the VTA-ventral striatum pathway more specific to dopamine. Yet, we are unable to rule out that increased connectivity along this pathway could be due to signaling from other neurotransmitters. Additionally, due to the preliminary nature of the current study, changes in connectivity between groups were not compared. The findings of the current study suggest additional studies with the power to directly compare changes between groups are warranted. Finally, the feedback was nonveridical and not all participants in the RT+POS group fully believed the feedback. Despite this fact, the response to feedback (change in performance, expectancies, and connectivity) did not vary based on believability rating.

5. Conclusion

The results of this study indicate that positive social comparative feedback supports motor performance and learning by driving higher peak velocities. Motor practice with positive social comparative feedback resulted in increased connectivity between the ventral tegmental area and the nucleus accumbens, regions along the mesolimbic dopamine pathway that are involved in motivation and reward processing. The increase in connectivity from before to after practice was not present in the group that received performance feedback without social context. This suggests that positive social comparative feedback may operate to support motor performance and learning by triggering a dopaminergic response in the brain, as predicted in the OPTIMAL theory. Overall, this study provides a framework for future studies on the neural effects of positive social comparative feedback on motor skill learning and motor rehabilitation in individuals with and without neural damage.

Table 3.1. Group demographics and baseline characteristics

	Group 1 RT ONLY	**Group 2 RT+POS**
n	15	15
Sex	10F/5M	11F/4M
Age (y)	26.2 (4.9)	25.1 (3.6)
RSE Score	35.1 (3.8)	35.8 (3.7)
State Anxiety Score	27.9 (10.4)	25.7 (4.3)
Trait Anxiety Score	30.3 (7.9)	29.3 (6.0)
Response Time (s)	16.0 (1.9)	15.5 (2.0)
Path Distance (cm)	176.4 (25.0)	169.6 (21.7)
Peak Velocity (cm/s)	55.4 (5.3)	56.3 (7.5)
Feedback	"You completed the block in 87.2 seconds."	"You completed the block in 87.2 seconds. Your time was 17.5 seconds faster than the average of others on this block."

Mean values (standard deviation); F=Female; M=Male; y=years; RSE Score = Rosenberg Self-Esteem Score. There were no significant differences between groups on any variable.

Table 3.2. Scores from expectancy measures over practice and at retention

		RT ONLY	RT+POS
Task-Specific Self-Efficacy	*Pre*	411.3 (86.5)	439.3 (102.4)
	Post	553.3 (48.2)	586.0 (111.7)
	Retention	542.7 (48.2)	573.3 (88.5)
Perceived Competence	*Pre*	19.7 (6.9)	17.9 (5.4)
	Post	23.2 (4.9)	23.7 (6.6)
	Retention	23.5 (5.1)	23.2 (6.2)
Interest/Enjoyment	*Pre*	24.3 (9.4)	22.3 (4.6)
	Post	24.5 (8.7)	25.1 (8.0)
	Retention	24.7 (9.0)	25.1 (6.4)

Mean values (standard deviation); Pre = scores from before practice on Day 1; Post = scores after practice on Day 1; Retention = scores from before Retention testing on Day 2

Table 3.3. Fisher's Z values representing connectivity between each pair of brain regions

Pathway	ROI	RT ONLY		RT +POS	
		Pre	**Post**	**Pre**	**Post**
Mesocortico-limbic	*VTA-L OFC*	0.06 (0.10)	0.04 (0.11)	0.05 (0.08)	0.05 (0.16)
	VTA-R OFC	0.10 (0.10)	0.07 (0.12)	0.10 (0.10)	0.11 (0.18)
	VTA-L NAcc	0.10 (0.14)	0.14 (0.10)	**0.10 (0.09)***	**0.20 (0.08)***
	VTA-R NAcc	0.12 (0.12)	0.16 (0.09)	0.14 (0.08)	0.14 (0.11)
Nigrostriatal	*L SN-L Caud*	0.11 (0.11)	0.06 (0.12)	0.03 (0.09)	0.10 (0.08)
	L SN-L Put	0.08 (0.14)	0.10 (0.12)	0.07 (0.12)	0.11 (0.13)
Other Exploratory	*VTA-L M1*	**-0.11 (0.07)** †	**0.02 (0.09)** †	0.00 (0.15)	-0.04 (0.17)
	VTA-L Put	0.07 (0.15)	0.14 (0.14)	0.09 (0.14)	0.17 (0.11)
	VTA-L Caud	0.12 (0.13)	0.18 (0.12)	0.09 (0.13)	0.17 (0.11)

Mean Fisher's Z values (standard deviation); ROI = region of interest; Pre = values from before practice on Day 1; Post = values from after practice on Day 1; VTA = ventral tegmental area; L = Left; OFC = orbitofrontal cortex; R = right; NAcc = nucleus accumbens; SN = substanta nigra; Caud = caudate; Put = putamen; * = significant difference from pre to post practice at $p < 0.008$; † = significant difference from pre to post practice at $p < 0.17$

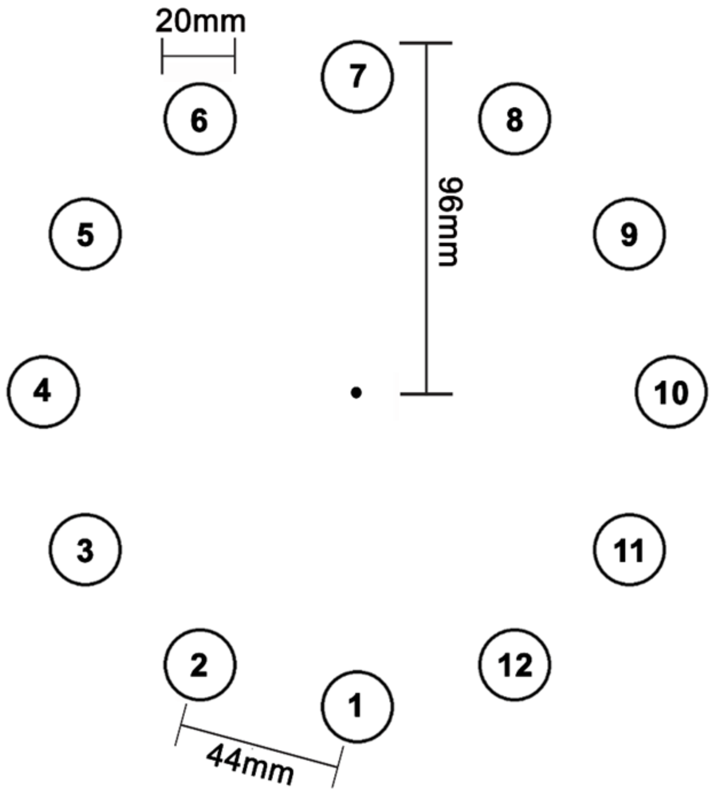

Figure 3.1: Schematic of the spatial locations of the twelve targets. Each target was 20 mm in diameter with a tangential distance of 44 mm between any adjacent target. The radius of the circular array was 96 mm. The repeated sequence consisted of targets 11, 10, 5, 9, 7, 3, 6, and 12.

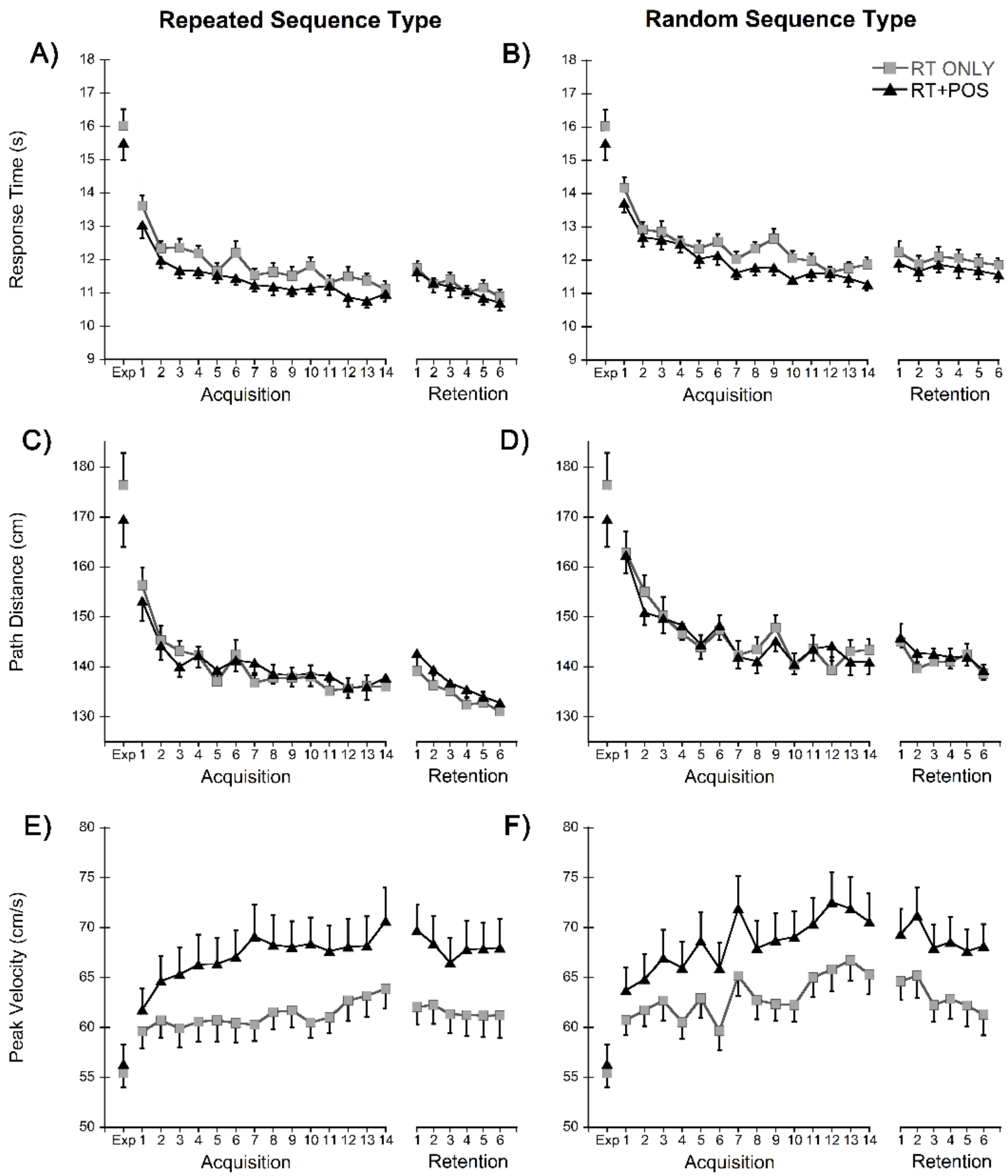

Figure 3.2: Motor performance during acquisition and retention. Each data point is the average ± standard error of 5 sequence trials. **A)** Response time for the repeated sequence; **B)** Response time for the random sequence; **C)** Path distance for the repeated sequence; **D)** Path distance for the random sequence; **E)** Peak velocity for the repeated sequence; **F)** Peak velocity for the random sequence

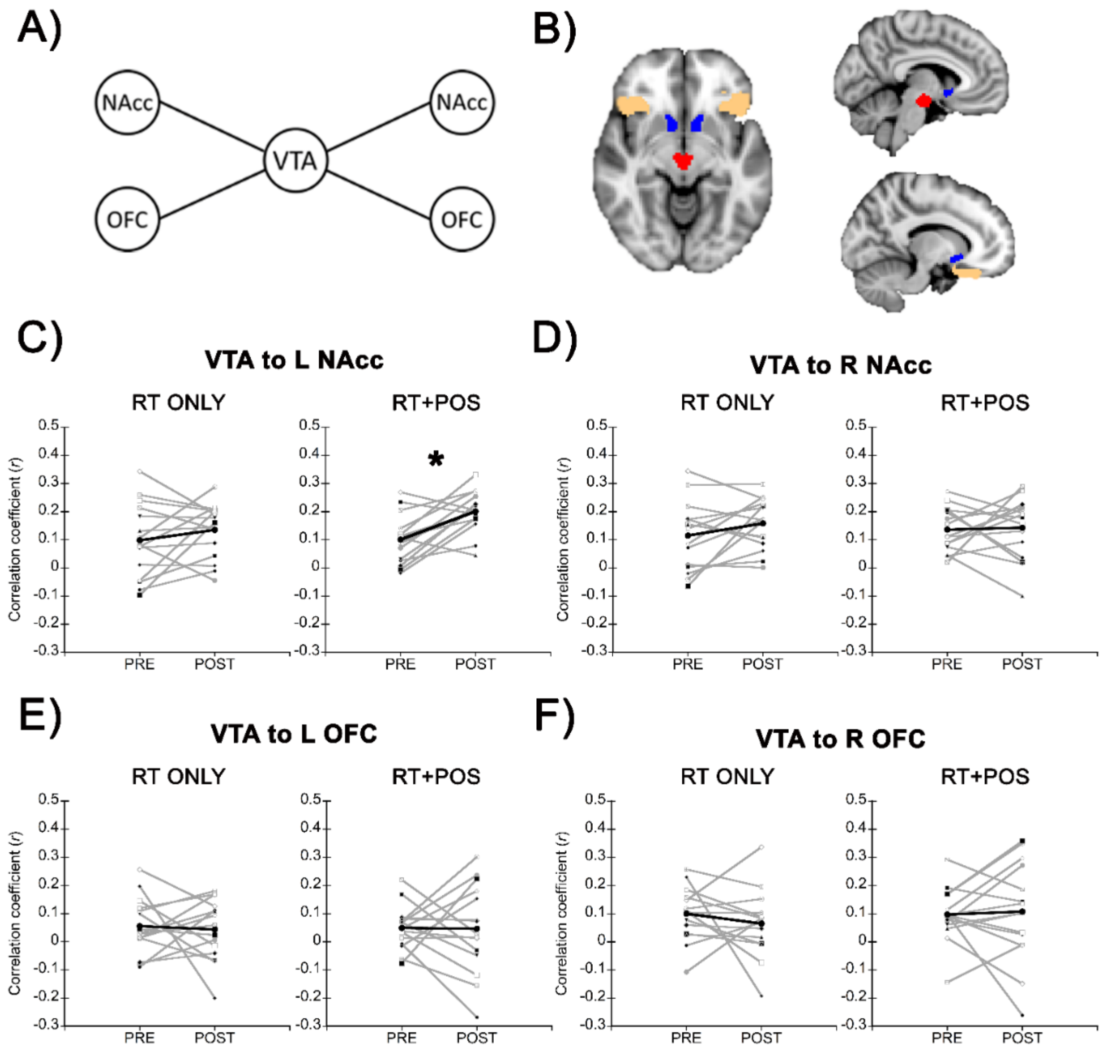

Figure 3.3: The mesocorticolimbic pathway and resting state connectivity from before to after practice. Light gray lines in C-F represent an individual participant and black lines represent the group mean. **A)** Conceptual diagram of ventral tegmental area (VTA) connections in the mesocorticolimbic pathway including the nucleus accumbens (NAcc) and orbitofrontal cortex (OFC). **B)** Regions of interest utilized in resting state connectivity analysis including VTA (red), NAcc (blue), and OFC (copper). Pre-practice and post-practice resting state connectivity between **C)** VTA and left NAcc; **D)** VTA and right NAcc; **E)** VTA and left OFC; and **F)** VTA and right OFC. L = Left; R = Right; * = significant difference between pre and post practice connectivity

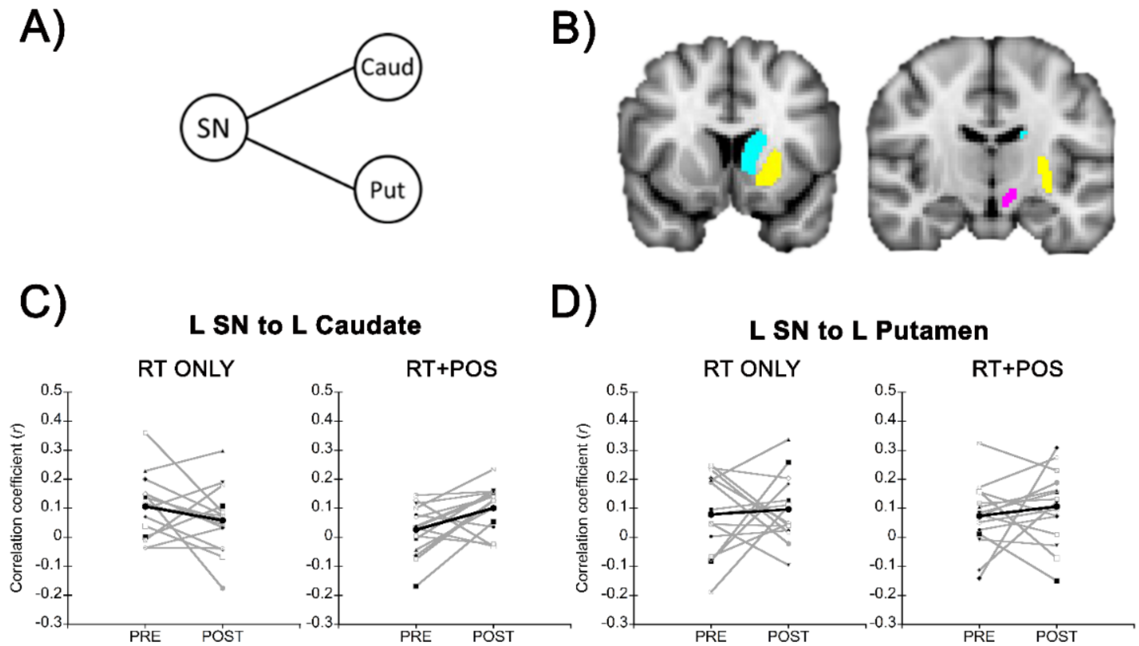

Figure 3.4: The nigrostriatal pathway and resting state connectivity from before to after practice. Light gray lines in C and D represent an individual participant and black lines represent the group mean. **A)** Conceptual diagram of substantia nigra (SN) connections in the nigrostriatal pathway including the caudate (Caud) and putamen (Put). **B)** Regions of interest utilized in resting state connectivity analysis including SN (pink), caudate (turquoise), and putamen (yellow). Pre-practice and post-practice resting state connectivity between **C)** left SN and left caudate; **D)** left SN and left putamen. L = Left; R = Right

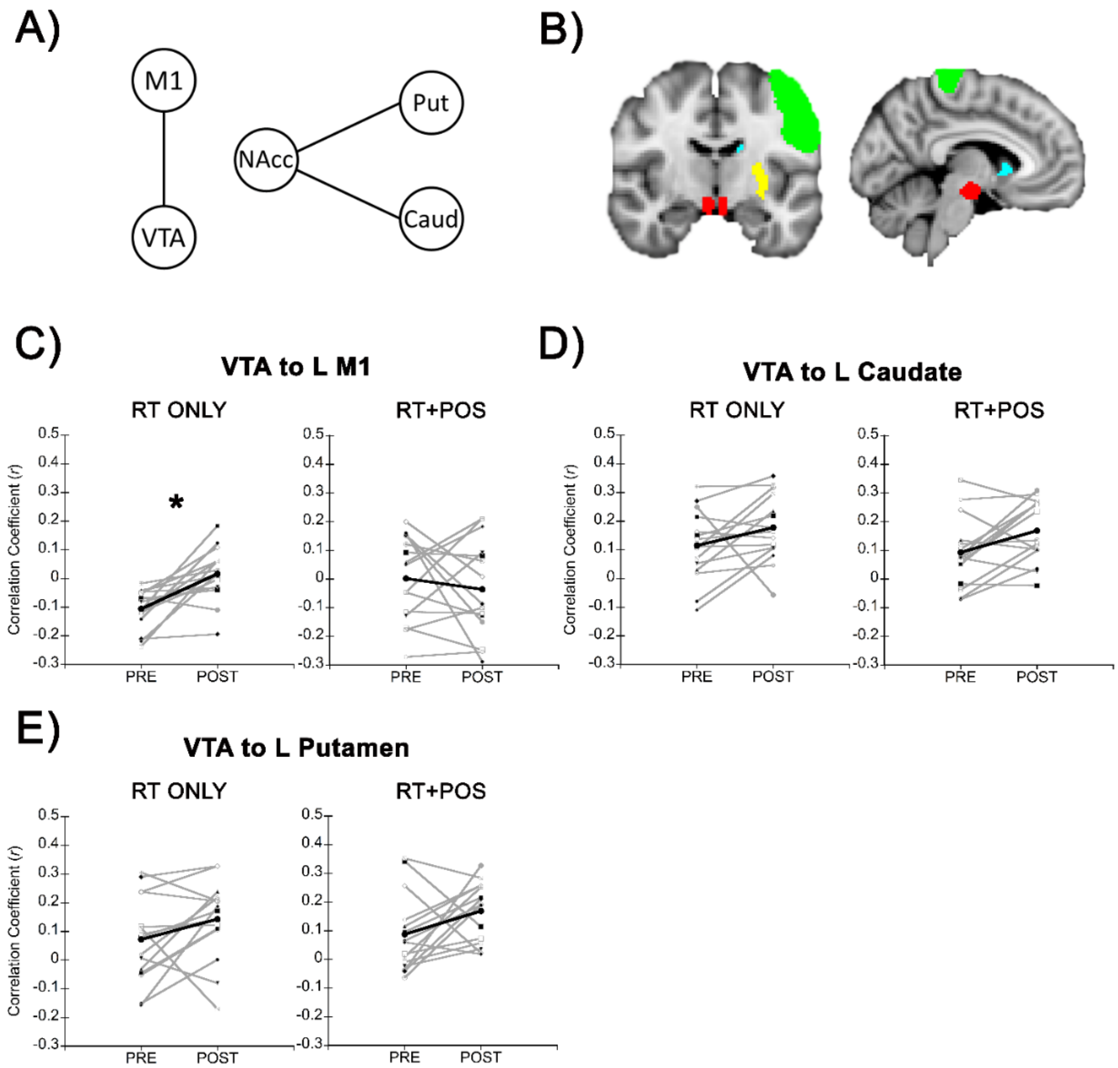

Figure 3.5: The exploratory pathways and resting state connectivity from before to after practice. Light gray lines in C-E represent an individual participant and black lines represent the group mean. **A)** Conceptual diagram of ventral tegmental (VTA) connections to motor-related regions including primary motor cortex (M1), caudate (Caud), and putamen (Put). **B)** Regions of interest utilized in resting state connectivity analysis including VTA (red), M1 (green), caudate (turquoise), and putamen (yellow). Pre-practice and post-practice resting state connectivity between **C)** VTA and left M1; **D)** VTA and left caudate; and **E)** VTA to left putamen. L = Left; R = Right; * = significant difference between pre and post practice connectivity

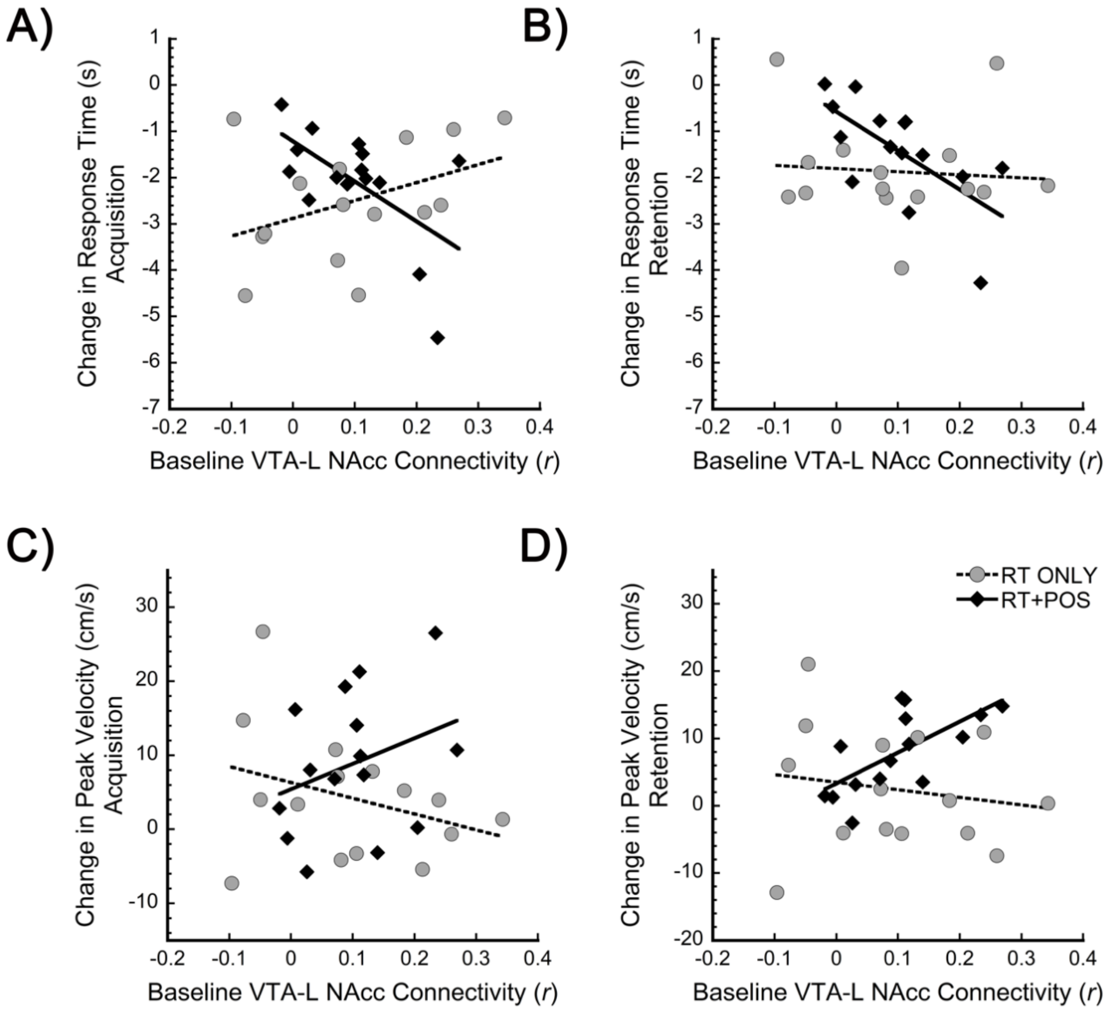

Figure 3.6: Relationships between baseline connectivity and change in performance. The linear regression interaction term “Feedback Group X Baseline VTA-L NAcc Connectivity” was significant for **A)** response time change over acquisition, **B)** response time change at retention, and **D)** peak velocity change at retention, but only before baseline performance was included in the regression model. The interaction term was not significant for **C)** peak velocity change over acquisition. RT ONLY = response time only feedback group; RT+POS = response time plus positive social comparison feedback group; VTA = ventral tegmental area; L NAcc = left nucleus accumbens; r = correlation coefficient

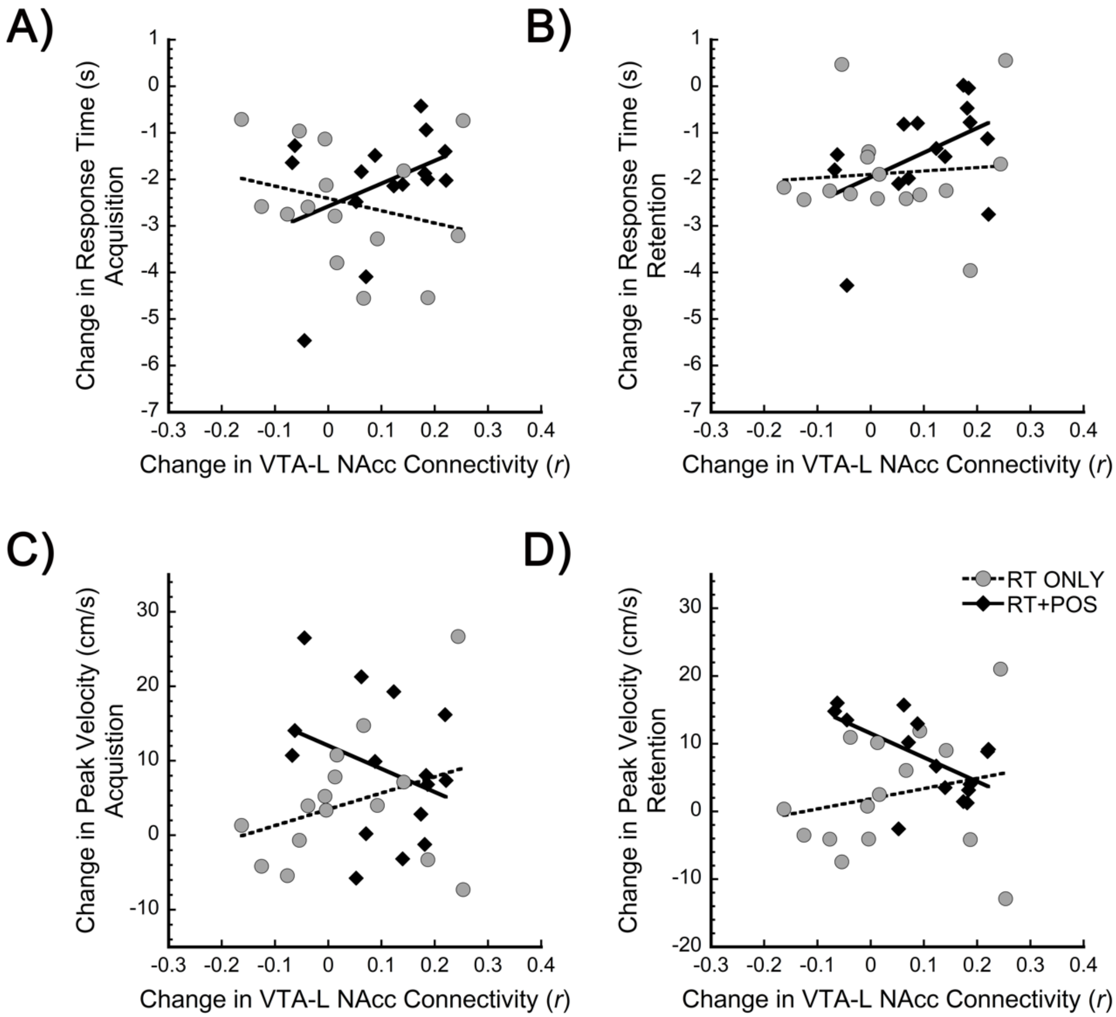

Figure 3.7: Relationships between change in connectivity and change in performance. The regression interaction term “Feedback Group X Change in VTA-L NAcc Connectivity” was not significant for **A)** response time change over acquisition, **B)** response time change at retention, or **C)** peak velocity change over acquisition. The interaction term was significant at $p < 0.05$ for **D)** peak velocity change at retention after baseline performance was added to the regression model. RT ONLY = response time only feedback group; RT+POS = response time plus positive social comparison feedback group; VTA = ventral tegmental area; L NAcc = left nucleus accumbens; r = correlation coefficient

CHAPTER 4

CONCLUSIONS AND DISCUSSION

The aim of this dissertation was to determine the effect of positive social comparative feedback during motor practice on motor sequence learning, performance expectancies, and resting state connectivity of dopaminergic neural pathways. The current studies directly addressed gaps in the literature as no previous studies applied positive social comparative feedback to a motor sequence learning task, and no previous studies directly investigated whether expectancy enhancing feedback impacts dopaminergic neural pathways using neuroimaging. The results showed that positive social comparative feedback supported motor sequence learning and performance expectancies similar to no feedback. However, performance feedback without comparative context was detrimental to acquisition, learning, and perceived competence.

The results of the current work showed that spatial and temporal components of performance are sensitive to feedback. Learners who were not provided any performance feedback used a spatial approach to improve performance (straighter hand paths), while learners that received performance feedback with positive social comparison used a temporal approach to improve performance (higher movement speeds). With regards to connectivity, positive social comparative feedback results in increased connectivity along the

mesolimbic dopamine pathways (VTA to left nucleus accumbens), while performance feedback without social comparison did not, supporting the prediction of the OPTIMAL theory that positive social comparative feedback may trigger a dopaminergic response in the brain. Overall, the methods utilized in the current dissertation addressed the aims, and the results partially confirmed the hypotheses.

According to the OPTIMAL theory, conditions of practice that enhance the learner's expectancies support motor learning and motivation towards the task (Wulf & Lewthwaite, 2016). Positive social comparative feedback is one way to enhance a learner's expectancies. Previous work showed that positive social comparative feedback supported motor learning more than performance feedback alone (Lewthwaite & Wulf, 2010; Pascua et al., 2015; Wulf et al., 2012, 2014). However, this prior work did not include a group that received no performance-related feedback. By including a no feedback group, the current study showed that performance feedback without comparative context is less effective at supporting learning and expectancies than no feedback at all. This finding contributes novel insights to the current evidence and suggests that clinicians and trainers should consider shifting away from providing performance feedback without any comparative context.

Feedback can provide a learner with knowledge of the results of their performance (i.e., accuracy or speed), but it can also contain motivational content (i.e., how their performance compares to other people). In the field of motor learning and rehabilitation, the motivational aspects of feedback are

understudied compared with other components of performance feedback such as feedback timing and scheduling. The results of the current study expose the importance of considering the motivational aspects of feedback as useful tools for promoting motor skill performance and learning. For example, performance feedback had differential effects on performance. Positive social comparative feedback led to higher peak velocities. In contrast, the absence of feedback led to learners' utilizing straighter movements along the trajectory between targets. Therefore, feedback may be leveraged to drive movement speeds (positive social comparative feedback) or spatial accuracy (no feedback) during motor skill practice. These findings have applications to sport and rehabilitation in that clinicians and trainers may leverage feedback to promote movement speed or spatial accuracy during motor practice. This highlights the importance of considering feedback as a tool to affect performance via its' motivational characteristics, rather than viewing feedback as a purely informational and motivationally neutral tool.

In general, performance expectancies improved over practice and at retention as reflected by increases in task-specific self-efficacy and perceived competence. However, the positive social comparative feedback group did not always show significantly greater improvements in expectancies than the other feedback groups. One potential reason for this finding is that the subjective expectancy measures were not sensitive enough to identify between group differences. Instead, the higher peak velocities may be a more sensitive marker of the learner's motivation toward the task. This is supported by the idea that

movement vigor, including movement velocity, reflects the learner's valuation of the expected outcome (Shadmehr et al., 2019). For example, in monkeys, the peak velocity of eye movements (saccades) increased as the probability of reward increased (Seideman et al., 2018). In humans, reaches were faster towards rewarded versus nonrewarded targets (Summerside et al., 2018). Taken together, this suggests that, when a reward is possible, animals will move with greater speed to achieve it. In this way, the control of movements may reflect our valuation of subjective goodness or "utility" of an option, where higher speed reflects higher valuation (Shadmehr et al., 2019). While self-reported expectancies may not have shown greater increases for the positive social comparative group, the higher peak velocities in this group may reflect the learner's higher subjective value of the task when positive social comparative feedback is provided during practice.

A relevant component of the OPTIMAL theory is the idea of goal-action coupling. According to the OPTIMAL theory, practice conditions that enhance a learner's expectancies lead to an alignment between the learner's actions and the task goal (Wulf & Lewthwaite, 2016). The goal of the joystick-based motor sequence task was to hit the targets as fast as possible. Therefore, under the goal-action coupling concept from the OPTIMAL theory, positive social comparative feedback would promote actions that resulted in faster movements and/or quicker response times versus straighter hand paths or greater spatial accuracy. Taking this into consideration, the higher peak velocities seen in the RT+POS group could be due to the aligning of learner's actions to the stated task

goal, rather than a function of the feedback driving greater perceived utility or intrinsic motivation towards the task. Given this possibility, future research is necessary to distinguish whether positive social comparative feedback always drives peak velocities OR works to align the learner's actions to the perceived goal of the task. For example, would learners in the RT+POS group show straighter hand paths if the state goal of the task and the focus of the feedback was on path distance? Additionally, the positive social comparative feedback was centered on response time; therefore, the effect of feedback centered on a spatial variable, like path distance, is unknown. Identifying the effects of variations of positive social comparative feedback will allow this kind of feedback to be applied with greater precision toward the intended movement or learning outcome.

Positive social comparative feedback led to an increase in resting state connectivity between brain regions along the dopaminergic mesolimbic pathway, as predicted in the OPTIMAL theory. These results provide preliminary evidence that positive social comparative feedback might be leveraged to target dopaminergic pathways. This finding is novel and may be meaningful for fields that utilize motor practice to drive learning, such as rehabilitation. Because dopamine promotes motivation towards actions and supports motor learning, interventions that target dopamine pathways may be especially useful for learning of motor skills in sport or rehabilitation settings. The field of motor learning and rehabilitation has begun to consider how the dopamine system

might be leveraged to maximize motor skill learning to promote recovery after injury (Johnson & Cohen, 2022; Widmer et al., 2022).

Monetary reward can facilitate motor skill learning (Abe et al., 2011); however, less is known about how reward might facilitate motor recovery after injury. A recent study showed that monetary reward during motor skill practice facilitated improvements in motor function after stroke (Widmer et al., 2022). Since monetary reward and positive social comparative feedback might target the same dopaminergic neural pathway (Chapter 3, Diekhof et al., 2012; Gu et al., 2019), it is possible expectancy-enhancing feedback could be applied to clinical populations to promote recovery in a similar manner as money. Expectancy-enhancing feedback is more feasible than monetary reward in a clinical setting and could be paired with virtually all current interventions for promoting motor recovery after stroke including task-oriented training, therapeutic exercise, and brain stimulation with behavior training. As such, expectancy-enhancing feedback has the potential to impact clinical care by serving as a no cost and easily accessible tool for clinicians and trainers to apply during motor practice sessions.

In conclusion, results from the first study showed that response time only feedback may be detrimental to motor sequence learning and performance expectancies, while positive social comparative feedback and no feedback supported learning and performance expectancies similarly. Both studies showed that positive social comparative feedback led to higher movement velocities, highlighting the importance of considering the motivational aspects of

feedback as tools for influencing motor performance and learning. The results of our second study showed increased connectivity between regions along the mesolimbic dopamine pathway for the positive social comparative group only. These findings support the predication of the OPTIMAL theory that positive social comparative feedback may trigger a dopaminergic response in the brain. Overall, this study provides a framework for future studies on the neural effects of positive social comparative feedback on motor skill learning and motor rehabilitation in individuals with and without neural damage. Future studies are needed to better understand the impact of expectancy-enhancing feedback on neural networks by examining between group comparisons and performing whole brain analyses. Finally, further investigation is necessary to identify potential neural pathways through with motivational and reward signals are integrated to affect motor actions. Understanding these mechanisms are important for future applications in individuals with neurologic damage.

REFERENCES

Abe, M., Schambra, H., Wassermann, E. M., Luckenbaugh, D., Schweighofer, N., & Cohen, L. G. (2011). Reward improves long-term retention of a motor memory through induction of offline memory gains. *Current Biology*, *21*(7), 557–562. https://doi.org/10.1016/j.cub.2011.02.030

Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. (2001). Beautiful Faces Have Variable Reward Value: fMRI and Behavioral Evidence. *Neuron*, *32*, 537–551. https://doi.org/10.1026//0012-1924.48.1.55

Albert, N. B., Robertson, E. M., & Miall, R. C. (2009). The Resting Human Brain and Motor Learning. *Current Biology*, *19*(12), 1023–1027. https://doi.org/10.1016/j.cub.2009.04.028

Andersson, J. L. R., Hutton, C., Ashburner, J., Turner, R., & Friston, K. (2001). Modeling geometric deformations in EPI time series. *NeuroImage*, *13*(5), 903–919. https://doi.org/10.1006/nimg.2001.0746

Ashburner, J., & Friston, K. J. (2005). Unified segmentation. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2005.02.018

Ávila, L. T. G., Chiviacowsky, S., Wulf, G., & Lewthwaite, R. (2012). Positive social-comparative feedback enhances motor learning in children. *Psychology of Sport and Exercise*, *13*(6), 849–853. https://doi.org/10.1016/j.psychsport.2012.07.001

Baird, J. F., Gaughan, M. E., Saffer, H. M., Sarzynski, M. A., Herter, T. M., Fritz, S. L., den Ouden, D. B., & Stewart, J. C. (2018). The effect of energy-matched exercise intensity on brain-derived neurotrophic factor and motor learning. *Neurobiology of Learning and Memory*, *156*, 33–44. https://doi.org/10.1016/j.nlm.2018.10.008

Baird, J., & Stewart, J. C. (2018). Sequence-specific implicit motor learning using whole-arm three-dimensional reach movements. *Experimental Brain Research*, *236*(1), 59–67. https://doi.org/10.1007/s00221-017-5107-0

Bandura, A. (2006). Guide for constructing self-efficacy scales (revised). In F. Pajares & T. Urdan (Eds.), *Self-Efficacy Beliefs of Adolescents.* (pp. 307–337). Information Age Publishing.

Bartels, A., & Zeki, S. (2004). The neural correlates of maternal and romantic love. *NeuroImage*, *21*(3), 1155–1166. https://doi.org/10.1016/j.neuroimage.2003.11.003

Behzadi Y, Restom K, Liau J, & Liu TT. (2007). A component based noise correction method (CompCor) for BOLD and perfusion based fMRI. *NeuroImage*, *37*(1), 90–101. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2214855/pdf/nihms-27952.pdf

Biswal, B., Zerrin Yetkin, F., Haughton, V. M., & Hyde, J. S. (1995). Functional connectivity in the motor cortex of resting human brain using echo-planar mri. *Magnetic Resonance in Medicine*, *34*(4), 537–541. https://doi.org/10.1002/mrm.1910340409

Boileau, I., Dagher, A., Leyton, M., Welfeld, K., Booij, L., Diksic, M., & Benkelfat, C. (2007). Conditioned dopamine release in humans: A positron emission tomography [11C]raclopride study with amphetamine. *Journal of Neuroscience*, *27*(15), 3998–4003. https://doi.org/10.1523/JNEUROSCI.4370-06.2007

Cao, H., Plichta, M. M., Schäfer, A., Haddad, L., Grimm, O., Schneider, M., Esslinger, C., Kirsch, P., Meyer-Lindenberg, A., & Tost, H. (2014). Test-retest reliability of fMRI-based graph theoretical properties during working memory, emotion processing, and resting state. *NeuroImage*, *84*, 888–900. https://doi.org/10.1016/j.neuroimage.2013.09.013

Carter, A. R., Shulman, G. L., & Corbetta, M. (2012). Why use a connectivity-based approach to study stroke and recovery of function? In *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2012.02.070

Chiviacowsky, S., Wulf, G., & Lewthwaite, R. (2012). Self-controlled learning: The importance of protecting perceptions of competence. *Frontiers in Psychology*, *3*(NOV). https://doi.org/10.3389/fpsyg.2012.00458

Chua, L. K., Wulf, G., & Lewthwaite, R. (2018). Onward and upward: Optimizing motor performance. *Human Movement Science*, *60*, 107–114. https://doi.org/10.1016/j.humov.2018.05.006

Coenen, V. A., Schumacher, L. V., Kaller, C., Schlaepfer, T. E., Reinacher, P. C., Egger, K., Urbach, H., & Reisert, M. (2018). The anatomy of the human medial forebrain bundle: Ventral tegmental area connections to reward-associated subcortical and frontal lobe regions. *NeuroImage: Clinical*, *18*(January), 770–783. https://doi.org/10.1016/j.nicl.2018.03.019

Cohen, J. (1988). *Statistical Power Analysis for the Behavioral Sciences* (2nd ed.). Routledge. https://doi.org/https://doi.org/10.4324/9780203771587

Deci, E. L., & Ryan, R. M. (1985). Conceptualizations of Intrinsic Motivation and Self-Determination. In *Intrinsic Motivation and Self-Determination in Human Behavior* (pp. 11–40). https://doi.org/10.1007/978-1-4899-2271-7_2

Desikan, R. S., Ségonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., Buckner, R. L., Dale, A. M., Maguire, R. P., Hyman, B. T., Albert, M. S., & Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NeuroImage*, *31*(3), 968–980. https://doi.org/10.1016/j.neuroimage.2006.01.021

Diekhof, E. K., Kaps, L., Falkai, P., & Gruber, O. (2012). The role of the human ventral striatum and the medial orbitofrontal cortex in the representation of reward magnitude - An activation likelihood estimation meta-analysis of neuroimaging studies of passive reward expectancy and outcome processing. *Neuropsychologia*, *50*(7), 1252–1266. https://doi.org/10.1016/j.neuropsychologia.2012.02.007

Faget, L., Osakada, F., Duan, J., Ressler, R., Johnson, A. B., Proudfoot, J. A., Yoo, J. H., Callaway, E. M., & Hnasko, T. S. (2016). Afferent inputs to neurotransmitter-defined cell types in the ventral tegmental area. *Cell Rep.*, *15*(12), 2796–2808. https://doi.org/10.1016/j.celrep.2016.05.057.Afferent

Fitts, P., & Peterson, J. (1964). Information capacity of discrete motor responses. *J Exp Psychol*, *67*(2), 103–112.

Fox, M. D., & Raichle, M. E. (2007). Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nature Reviews Neuroscience*, *8*(9), 700–711. https://doi.org/10.1038/nrn2201

Friston, K. J., Williams, S., Howard, R., Frackowiak, R. S. J., & Turner, R. (1996). Movement-related effects in fMRI time-series. *Magnetic Resonance in Medicine*, *35*(3), 346–355. https://doi.org/10.1002/mrm.1910350312

Grefkes, C., & Fink, G. R. (2011). Reorganization of cerebral networks after stroke: New insights from neuroimaging with connectivity approaches. *Brain*, *134*(5), 1264–1276. https://doi.org/10.1093/brain/awr033

Gu, R., Huang, W., Camilleri, J., Xu, P., Wei, P., Eickhoff, S. B., & Feng, C. (2019). Love is analogous to money in human brain: Coordinate-based and functional connectivity meta-analyses of social and monetary reward anticipation. *Neuroscience and Biobehavioral Reviews*, *100*(October 2018), 108–128. https://doi.org/10.1016/j.neubiorev.2019.02.017

Haber, S N, Fudge, J. L., & McFarland, N. R. (2000). Striatonigrostriatal pathways in primates form an ascending spiral from the shell to the dorsolateral striatum. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *20*(6), 2369–2382. http://www.ncbi.nlm.nih.gov/pubmed/10704511

Haber, Suzanne N., & Knutson, B. (2010). The reward circuit: Linking primate anatomy and human imaging. *Neuropsychopharmacology*, *35*(1), 4–26. https://doi.org/10.1038/npp.2009.129

Hahn, A., Reed, M. B., Pichler, V., Michenthaler, P., Rischka, L., Godbersen, G. M., Wadsak, W., Hacker, M., & Lanzenberger, R. (2021). Functional dynamics of dopamine synthesis during monetary reward and punishment processing. *Journal of Cerebral Blood Flow and Metabolism*, *41*(11), 2973–2985. https://doi.org/10.1177/0271678X211019827

Hallquist, M. N., Hwang, K., & Luna, B. (2013). The nuisance of nuisance regression: Spectral misspecification in a common approach to resting-state fMRI preprocessing reintroduces noise and obscures functional connectivity. *NeuroImage*, *82*, 208–225. https://doi.org/10.1016/j.neuroimage.2013.05.116

Henson, R., Büchel, C., Josephs, O., & Fristen, K. (1999). The slice-timing problem in event-related fMRI. *NeuroImage*, *9*(6 PART II), 1998.

Hosp, J. A., Coenen, V. A., Rijntjes, M., Egger, K., Urbach, H., Weiller, C., & Reisert, M. (2019). Ventral tegmental area connections to motor and sensory cortical fields in humans. *Brain Structure and Function*, *224*(8), 2839–2855. https://doi.org/10.1007/s00429-019-01939-0

Ikemoto, S. (2007). Dopamine reward circuitry: Two projection systems from the ventral midbrain to the nucleus accumbens-olfactory tubercle complex. In *Brain Research Reviews* (Vol. 56, Issue 1, pp. 27–78). https://doi.org/10.1016/j.brainresrev.2007.05.004

Ikemoto, S., Yang, C., & Tan, A. (2015). Basal ganglia circuit loops, dopamine and motivation: A review and enquiry. *Behavioural Brain Research*, *290*, 17–31. https://doi.org/10.1016/j.bbr.2015.04.018

Izuma, K., Saito, D. N., & Sadato, N. (2008). Processing of Social and Monetary Rewards in the Human Striatum. *Neuron*, *58*(2), 284–294. https://doi.org/10.1016/j.neuron.2008.03.020

Johnson, B., & Cohen, L. G. (2022). Reward and plasticity: Implications for neurorehabilitation. *Handbook of Clinical Neurology*, *184*, 331–340.

Kal, E., Winters, M., Van Kamp, J. Der, Houdijk, H., Groet, E., Bennekom, C., & Scherder, E. (2016). Is implicit motor learning preserved after stroke? A systematic review with meta-analysis. *PLoS ONE*, *11*(12), 1–23. https://doi.org/10.1371/journal.pone.0166376

Kantak, S. S., & Winstein, C. J. (2012). Learning-performance distinction and memory processes for motor skills: A focused review and perspective. In *Behavioural Brain Research*. https://doi.org/10.1016/j.bbr.2011.11.028

Lam, W. K., Maxwell, J. P., & Masters, R. (2009). Analogy Learning and the Performance of Motor Skills Under Pressure The Pressure-Performance Relationship. *Health (San Francisco)*, 337–357.

Lewthwaite, R., & Wulf, G. (2010). Social-comparative feedback affects motor skill learning. *Quarterly Journal of Experimental Psychology*, *63*(4), 738–749. https://doi.org/10.1080/17470210903111839

Liao, C. M., & Masters, R. S. W. (2001). Analogy learning: A means to implicit motor learning. *Journal of Sports Sciences*, *19*(5), 307–319. https://doi.org/10.1080/02640410152006081

Lidstone, S., Schulzer, D., Dinelle, K., Mak, E., Sossi, V., Ruth, T., De La Fuente-Fernandez, R., & Phillips, A. (2010). Effects of expectation on placebo-induced dopamine release in Parkinson disease. *Archives of General Psychiatry*, *67*(8), 857–865. https://doi.org/http://dx.doi.org/10.1001/archgenpsychiatry.2010.88

Lin, A., Adolphs, R., & Rangel, A. (2012). Social and monetary reward learning engage overlapping neural substrates. *Social Cognitive and Affective Neuroscience*, *7*(3), 274–281. https://doi.org/10.1093/scan/nsr006

Lin, C. H., Yang, H. C., Knowlton, B. J., Wu, A. D., Iacoboni, M., Ye, Y. L., Huang, S. L., & Chiang, M. C. (2018). Contextual interference enhances motor learning through increased resting brain connectivity during memory consolidation. *NeuroImage*, *181*, 1–15. https://doi.org/10.1016/j.neuroimage.2018.06.081

Luo, S. X., & Huang, E. J. (2016). Dopaminergic neurons and brain reward pathways: From neurogenesis to circuit assembly. *American Journal of Pathology*, *186*(3), 478–488. https://doi.org/10.1016/j.ajpath.2015.09.023

MacNiven, K. H., Leong, J. K., & Knutson, B. (2020). Medial forebrain bundle structure is linked to human impulsivity. *Science Advances*, *6*(38), 1–8. https://doi.org/10.1126/sciadv.aba4788

Maier, M., Ballester, B. R., & Verschure, P. F. M. J. (2019). Principles of Neurorehabilitation After Stroke Based on Motor Learning and Brain Plasticity Mechanisms. *Frontiers in Systems Neuroscience*, *13*(December), 1–18. https://doi.org/10.3389/fnsys.2019.00074

Mang, C. S., Snow, N. J., Campbell, K. L., Ross, C. J. D., & Boyd, L. A. (2014). A single bout of high-intensity aerobic exercise facilitates response to paired associative stimulation and promotes sequence-specific implicit motor learning. *J Appl Physiol*, *117*, 1325–1336. https://doi.org/10.1152/japplphysiol.00498.2014.-The

Masters, R. S. W., Poolton, J. M., & Maxwell, J. P. (2008). Stable implicit motor processes despite aerobic locomotor fatigue. *Consciousness and Cognition*, *17*(1), 335–338. https://doi.org/10.1016/j.concog.2007.03.009

Maybery, M., Taylor, M., & O'brien-Malone, A. (1995). Implicit learning: Sensitive to age but not IQ. *Australian Journal of Psychology*.

https://doi.org/10.1080/00049539508258763

Mayka, M. A., Corcos, D. M., Leurgans, S. E., & Vaillancourt, D. E. (2006). Three-dimensional locations and boundaries of motor and premotor cortices as defined by functional brain imaging: A meta-analysis. *NeuroImage*, *31*(4), 1453–1474. https://doi.org/10.1016/j.neuroimage.2006.02.004

Moisello, C., Crupi, D., Tunik, E., Quaratarone, A., Bove, M., Tononi, G., & Ghilardi, M. F. (2009). The Serial Reaction Time Task revisited: A study on motor sequence learning with an arm-reaching task. *Experimental Brain Research*, *194*(1), 143–155. https://doi.org/10.1055/s-0029-1231437

Moritz, S. E., Feltz, D. L., Fahrbach, K. R., & Mack, D. E. (2000). The relation of self-efficacy measures to sport performance: A meta-analytic review. *Research Quarterly for Exercise and Sport*, *71*(3), 280–294. https://doi.org/10.1080/02701367.2000.10608908

Murty, V. P., Shermohammed, M., Smith, D. V., Carter, R. M. K., Huettel, S. A., & Adcock, R. A. (2014). Resting state networks distinguish human ventral tegmental area from substantia nigra. *NeuroImage*, *100*, 580–589. https://doi.org/10.1016/j.neuroimage.2014.06.047

Nieto-Castanon, A. (2020). *Handbook of functional connectivity Magnetic Resonance Imaging methods in CONN.* Hilber Press.

Nissen, M. J., & Bullemer, P. (1987). Attention Requirements of Learning Evidence from Performance Measures. *Cognitive Psychology*, *19*, 1–32. https://ac.els-cdn.com/0010028587900028/1-s2.0-0010028587900028-main.pdf?_tid=bec66475-4a81-467d-852a-1417270cd733&acdnat=1543287406_5f864c76f3d75cceef7b9aa67f51ada2

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Pascua, L. A. M. M., Wulf, G., & Lewthwaite, R. (2015). Additive benefits of external focus and enhanced performance expectancy for motor learning. *Journal of Sports Sciences*, *33*(1), 58–66. https://doi.org/10.1080/02640414.2014.922693

Power, J. D., Mitra, A., Laumann, T. O., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2014). Methods to detect, characterize, and remove motion artifact in resting state fMRI. *NeuroImage*, *84*, 320–341. https://doi.org/10.1016/j.neuroimage.2005.05.058

Rademacher, L., Krach, S., Kohls, G., Irmak, A., Gründer, G., & Spreckelmeyer, K. N. (2010). Dissociation of neural networks for anticipation and consumption of monetary and social rewards. *NeuroImage*, *49*(4), 3276–3285. https://doi.org/10.1016/j.neuroimage.2009.10.089

Rosenberg, M. (1965). *Society and the Adolescent Self-Image.* Princeton University Press. https://doi.org/10.1126/science.148.3671.804

Ryan, R. M. (1982). Control and information in the intrapersonal sphere: An extension of cognitive evaluation theory. *Journal of Personality and Social Psychology*. https://doi.org/10.1037/0022-3514.43.3.450

Saemi, E., Porter, J. M., Ghotbi-Varzaneh, A., Zarghami, M., & Maleki, F. (2012). Knowledge of results after relatively good trials enhances self-efficacy and motor learning. *Psychology of Sport and Exercise*, *13*(4), 378–382. https://doi.org/10.1016/j.psychsport.2011.12.008

Sainburg, R. L., & Schaefer, S. Y. (2004). Interlimb differences in control of movement extent. *Journal of Neurophysiology*, *92*(3), 1374–1383. https://doi.org/10.1152/jn.00181.2004

Salmoni, A. W., Schmidt, R. A., & Walter, C. B. (1984). Knowledge of results and motor learning: A review and critical reappraisal. *Psychological Bulletin*. https://doi.org/10.1037/0033-2909.95.3.355

Schmidt, R. A., & Lee, T. D. (2011). Motor control and learning: A behavioral emphasis. In *Human Kinetics* (5th ed., Vol. 3). Human Kinetics. https://doi.org/10.1016/0021-9290(88)90286-2

Schott, B. H., Minuzzi, L., Krebs, R. M., Elmenhorst, D., Lang, M., Winz, O. H., Seidenbecher, C. I., Coenen, H. H., Heinze, H. J., Zilles, K., Düzel, E., & Bauer, A. (2008). Mesolimbic functional magnetic resonance imaging activations during reward anticipation correlate with reward-related ventral striatal dopamine release. *Journal of Neuroscience*, *28*(52), 14311–14319. https://doi.org/10.1523/JNEUROSCI.2058-08.2008

Schultz, W. (2016). Reward functions of the basal ganglia. *Journal of Neural Transmission*, *123*(7), 679–693. https://doi.org/10.1007/s00702-016-1510-0

Seideman, J. A., Stanford, T. R., & Salinas, E. (2018). Saccade metrics reflect decision-making dynamics during urgent choices. *Nature Communications*, *9*(1). https://doi.org/10.1038/s41467-018-05319-w

Shadmehr, R., Reppert, T. R., Summerside, E. M., Yoon, T., & Ahmed, A. A. (2019). Movement Vigor as a Reflection of Subjective Economic Utility. *Trends in Neurosciences*, *42*(5), 323–336. https://doi.org/10.1016/j.tins.2019.02.003

Shehzad, Z., Kelly, A. M. C., Reiss, P. T., Gee, D. G., Gotimer, K., Uddin, L. Q., Lee, S. H., Margulies, D. S., Roy, A. K., Biswal, B. B., Petkova, E., Castellanos, F. X., & Milham, M. P. (2009). The resting brain: Unconstrained yet reliable. *Cerebral Cortex*, *19*, 2209–2229. https://doi.org/10.1093/cercor/bhn256

Smith, S. M., Fox, P. T., Miller, K. L., Glahn, D. C., Fox, P. M., Mackay, C. E., Filippini, N., Watkins, K. E., Toro, R., Laird, A. R., & Beckmann, C. F. (2009). Correspondence of the brain’s functional architecture during activation and rest. *Proceedings of the National Academy of Sciences*, *106*(31), 13040–13045. https://doi.org/10.1073/pnas.0905267106

Spielberger, C., Gorsuch, R., Lushene, R., Vagg, P., & Jacobs, G. (1983). *Manual for the State-Trait Anxiety Inventory for Adults*. Consulting Psychologists Press.

Squire, L. R. (1992). Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. *Journal of Cognitive Neuroscience*, *4*(3), 232–243. https://doi.org/10.1162/jocn.1992.4.3.232

Squire, Larry R. (1987). *Memory and Brain*. Oxford University Press. https://doi.org/10.1523/JNEUROSCI.3575-09.2009

Steel, A., Silson, E. H., Stagg, C. J., & Baker, C. I. (2019). Differential impact of reward and punishment on functional connectivity after skill learning. *NeuroImage*, *189*, 95–105. https://doi.org/10.1016/j.neuroimage.2019.01.009

Stoate, I., Wulf, G., & Lewthwaite, R. (2012). Enhanced expectancies improve movement efficiency in runners. *Journal of Sports Sciences*, *30*(8), 815–823. https://doi.org/10.1080/02640414.2012.671533

Summerside, E. M., Shadmehr, R., & Ahmed, A. A. (2018). Vigor of reaching movements: Reward discounts the cost of effort. *Journal of Neurophysiology*, *119*(6), 2347–2357. https://doi.org/10.1152/JN.00872.2017

Thomas, C. L., & Cassady, J. C. (2021). Validation of the State Version of the State-Trait Anxiety Inventory in a University Sample. *SAGE Open*. https://doi.org/10.1177/21582440211031900

Trempe, M., Sabourin, M., & Proteau, L. (2012). Success modulates consolidation of a visuomotor adaptation task. *Journal of Experimental Psychology: Learning Memory and Cognition*, *38*(1), 52–60. https://doi.org/10.1037/a0024883

Verburgh, L., Scherder, E. J. A., van Lange, P. A. M., & Oosterlaan, J. (2016). The key to success in elite athletes? Explicit and implicit motor learning in youth elite and non-elite soccer players. *Journal of Sports Sciences*, *34*(18), 1782–1790. https://doi.org/10.1080/02640414.2015.1137344

Verneau, M., Van Der Kamp, J., Savelsbergh, G. J. P., & De Looze, M. P. (2014). Age and time effects on implicit and explicit learning. *Experimental Aging Research*, *40*(4), 477–511. https://doi.org/10.1080/0361073X.2014.926778

Wake, S. J., & Izuma, K. (2017). A common neural code for social and monetary rewards in the human striatum. *Social Cognitive and Affective Neuroscience*, *12*(10), 1558–1564. https://doi.org/10.1093/scan/nsx092

Watson, D., Clark, L. A., & Tellegen, A. (1988). Development and Validation of Brief Measures of Positive and Negative Affect: The PANAS Scales. *Journal of Personality and Social Psychology*. https://doi.org/10.1037/0022-3514.54.6.1063

Whitfield-Gabrieli, S., & Nieto-Castanon, A. (2012). Conn: A Functional Connectivity Toolbox for Correlated and Anticorrelated Brain Networks. *Brain Connectivity*, *2*(3), 125–141. https://doi.org/10.1089/brain.2012.0073

Widmer, M., Held, J. P. O., Wittmann, F., Valladares, B., Lambercy, O., Sturzenegger, C., Palla, A., Lutz, K., & Luft, A. R. (2022). Reward During Arm Training Improves Impairment and Activity After Stroke: A Randomized Controlled Trial. *Neurorehabilitation and Neural Repair*, *36*(2), 140–150. https://doi.org/10.1177/15459683211062898

Wise, R. A. (2004). Dopamine, learning and motivation. In *Nature Reviews Neuroscience* (Vol. 5, Issue 6, pp. 483–494). Nature Publishing Group. https://doi.org/10.1038/nrn1406

Wulf, G., Chiviacowsky, S., & Cardozo, P. L. (2014). Additive benefits of autonomy support and enhanced expectancies for motor learning. *Human Movement Science*, *37*(37), 12–20. https://doi.org/10.1016/j.humov.2014.06.004

Wulf, G., Chiviacowsky, S., & Lewthwaite, R. (2012). Altering mindset can enhance motor learning in older adults. *Psychology and Aging*, *27*(1), 14–21. https://doi.org/10.1037/a0025718

Wulf, G., & Lewthwaite, R. (2016). Optimizing performance through intrinsic motivation and attention for learning: The OPTIMAL theory of motor learning. *Psychonomic Bulletin & Review*, *23*(5), 1382–1414. https://doi.org/10.3758/s13423-015-0999-9

Wulf, G., Lewthwaite, R., Cardozo, P., & Chiviacowsky, S. (2017). Triple play: Additive contributions of enhanced expectancies, autonomy support, and external attentional focus to motor learning. *Quarterly Journal of Experimental Psychology*, *71*(4), 1–9. https://doi.org/10.1080/17470218.2016.1276204

Yoo, J. H., Zell, V., Gutierrez-Reed, N., Wu, J., Ressler, R., Shenasa, M. A., Johnson, A. B., Fife, K. H., Faget, L., & Hnasko, T. S. (2016). Ventral tegmental area glutamate neurons co-release GABA and promote positive reinforcement. *Nature Communications*, *7*(May), 1–13. https://doi.org/10.1038/ncomms13697

APPENDIX A

LINEAR REGRESSION TABLES

Table A.1. Linear regression analyses for motor performance, feedback group, and baseline VTA - L NAcc connectivity

Dep. Variable	Model	R^2	F statistic	p value	Independent Variable	β	p value
Δ RT – ACQ	*Model 1*	0.287	3.483	0.030*	Group	0.176	0.298
					Connectivity	0.345	0.092
					Group X Connectivity	-0.603	0.005*
	Model 2	0.535	7.188	0.001*	Group	0.099	0.478
					Connectivity	0.248	0.145
					Group X Connectivity	-0.320	0.088
					Baseline RT	-0.560	0.001*
Δ RT – RET	*Model 1*	0.249	2.868	0.056	Group	0.210	0.228
					Connectivity	-0.062	0.763
					Group X Connectivity	-0.418	0.049*
	Model 2	0.408	4.301	0.009*	Group	0.148	0.350
					Connectivity	-0.139	0.460
					Group X Connectivity	-0.191	0.356
					Baseline RT	-0.448	0.016*
Δ Peak Velocity – ACQ	*Model 1*	0.161	1.659	0.200	Group	0.252	0.172
					Connectivity	-0.255	0.243
					Group X Connectivity	0.364	0.101
	Model 2	0.315	2.880	0.043*	Group	0.283	0.101
					Connectivity	-0.252	0.213
					Group X Connectivity	0.304	0.139
					Baseline Peak Velocity	-0.399	0.025*
Δ Peak Velocity – RET	*Model 1*	0.259	3.022	0.048*	Group	0.347	0.050
					Connectivity	-0.156	0.445
					Group X Connectivity	0.430	0.042*
	Model 2	0.343	3.260	0.028*	Group	0.369	0.032*
					Connectivity	-0.154	0.434
					Group X Connectivity	0.386	0.058
					Baseline Peak Velocity	-0.294	0.086

VTA = ventral tegmental area; L NAcc = left nucleus accumbens; Dep. = Dependent; Δ = change in; RT = response time; ACQ = acquisition; RET = retention; * = significant at $p < 0.05$

Table A.2. Linear regression analyses for motor performance, feedback group, and change in VTA - L NAcc connectivity

Dep. Variable	Model	R^2	F statistic	p value	Independent Variable	β	p value
Δ RT – ACQ	*Model 1*	0.137	1.375	0.272	Group	0.143	0.458
					Δ Connectivity	-0.243	0.323
					Group X Δ Connectivity	0.425	0.085
	Model 2	0.487	5.940	0.002*	Group	0.068	0.655
					Δ Connectivity	-0.070	0.720
					Group X Δ Connectivity	0.177	0.375
					Baseline RT	-0.628	0.001*
Δ RT – RET	*Model 1*	0.151	1.542	0.227	Group	0.116	0.545
					Δ Connectivity	0.080	0.739
					Group X Δ Connectivity	0.285	0.238
	Model 2	0.403	4.224	0.010*	Group	0.052	0.750
					Δ Connectivity	0.227	0.289
					Group X Δ Connectivity	0.074	0.729
					Baseline RT	-0.533	0.003*
Δ Peak Velocity – ACQ	*Model 1*	0.161	1.663	0.199	Group	0.270	0.162
					Δ Connectivity	0.275	0.258
					Group X Δ Connectivity	-0.405	0.096
	Model 2	0.358	3.484	0.022*	Group	0.336	0.058
					Δ Connectivity	0.183	0.402
					Group X Δ Connectivity	-0.403	0.050
					Baseline Peak Velocity	-0.457	0.010*
Δ Peak Velocity – RET	*Model 1*	0.243	2.779	0.061	Group	0.392	0.037*
					Δ Connectivity	0.218	0.343
					Group X Δ Connectivity	-0.447	0.055
	Model 2	0.384	3.902	0.014*	Group	0.448	0.012*
					Δ Connectivity	0.140	0.510
					Group X Δ Connectivity	-0.469	0.031*
					Baseline Peak Velocity	-0.388	0.024*

VTA = ventral tegmental area; L NAcc = left nucleus accumbens; Dep. = Dependent; Δ = change in; RT = response time; ACQ = acquisition; RET = retention; * = significant at $p < 0.05$

APPENDIX B

EDINBURGH HANDEDNESS INVENTORY

For each of the activities listed below, please indicate your hand preference by selecting the most appropriate response. Some of the activities require the use of both hands. In these cases, the part of the task or object for which hand preference is wanted is indicated in brackets.

Which hand do you prefer when…

		Left	Right	No preference
1)	Writing	○	○	○
2)	Drawing	○	○	○
3)	Throwing	○	○	○
4)	Using scissors	○	○	○
5)	Using a toothbrush	○	○	○
6)	Using a knife (without a fork)	○	○	○
7)	Using a spoon	○	○	○
8)	Using a broom (upper hand)	○	○	○
9)	Striking a match	○	○	○
10)	Opening a box	○	○	○

APPENDIX C

ROSENBERG SELF-ESTEEM SCALE

Instructions

Below is a list of statements dealing with your general feelings about yourself. Please indicate how strongly you agree or disagree with each statement.

		Strongly Agree	Agree	Disagree	Strongly Disagree
1)	On the whole, I am satisfied with myself.				
2)	At times I think I am no good at all.				
3)	I feel that I have a number of good qualities.				
4)	I am able to do things as well as most other people.				
5)	I feel I do not have much to be proud of.				
6)	I certainly feel useless at times.				
7)	I feel that I'm a person of worth, at least on an equal plane with others.				
8)	I wish I could have more respect for myself.				
9)	All in all, I am inclined to feel that I am a failure.				
10)	I take a positive attitude toward myself.				

APPENDIX D

STATE TRAIT ANXIETY SCALE

The following questions are designed to understand how you feel about different aspects of your life. Read each statement and select the appropriate response to indicate how you feel RIGHT NOW, that is, at this very moment.

		Not at all	Somewhat	Moderately So	Very Much So
1)	I feel calm	○	○	○	○
2)	I feel secure	○	○	○	○
3)	I am tense	○	○	○	○
4)	I feel strained	○	○	○	○
5)	I feel at ease	○	○	○	○
6)	I feel upset	○	○	○	○
7)	I am presently worrying over possible misfortunes	○	○	○	○
8)	I feel satisfied	○	○	○	○
9)	I feel frightened	○	○	○	○
10)	I feel comfortable	○	○	○	○
11)	I feel self-confident	○	○	○	○
12)	I feel nervous	○	○	○	○
13)	I am jittery	○	○	○	○
14)	I feel indecisive	○	○	○	○
15)	I am relaxed	○	○	○	○
16)	I feel content	○	○	○	○
17)	I am worried	○	○	○	○
18)	I feel confused	○	○	○	○
19)	I feel steady	○	○	○	○
20)	I feel pleasant	○	○	○	○

Read each statement and select how you feel about life IN GENERAL.	Almost Never	Sometimes	Often	Almost Always
22) I feel pleasant	O	O	O	O
23) I feel nervous and restless	O	O	O	O
24) I feel satisfied with myself	O	O	O	O
25) I wish I could be as happy as the others seem to be	O	O	O	O
26)				
I feel like a failure	O	O	O	O
27) I feel rested	O	O	O	O
28) I am "calm, cool, and collected"	O	O	O	O
29) I feel that difficulties are piling up so that I cannot overcome them	O	O	O	O
30) I worry too much over something that really doesn't matter	O	O	O	O
31) I am happy	O	O	O	O
32) I have disturbing thoughts	O	O	O	O
33) I lack self-confidence	O	O	O	O
34) I feel secure	O	O	O	O
35) I make decision easily	O	O	O	O
36) I feel inadequate	O	O	O	O
37) I am content	O	O	O	O
38) Some unimportant thought runs through my mind and bothers me	O	O	O	O
39) I take disappointments so keenly that I can't put them out of my mind	O	O	O	O
40) I am a steady person	O	O	O	O
41) I get in a state of tension or turmoil as I think over my recent concerns and interest	O	O	O	O

APPENDIX E

POSITIVE AND NEGATIVE AFFECT SCALE

PANAS-X

This scale consists of a number of words and phrases that describe different feelings and emotions. Read each item and then mark the appropriate answer in the space next to that word. Indicate to what extent you feel this way RIGHT NOW at the present moment. Use the following scale to record your answers:

	Very slightly or not at all	A little	Moderately	Quite a bit	Extremely
1) Cheerful	○	○	○	○	○
2) Sad	○	○	○	○	○
3) Active	○	○	○	○	○
4) Angry at self	○	○	○	○	○
5) Disgusted	○	○	○	○	○
6) Calm	○	○	○	○	○
7) Guilty	○	○	○	○	○
8) Enthusiastic	○	○	○	○	○
9) Attentive	○	○	○	○	○
10) Afraid	○	○	○	○	○
11) Joyful	○	○	○	○	○
12) Downhearted	○	○	○	○	○
13) Bashful	○	○	○	○	○
14) Tired	○	○	○	○	○
15) Nervous	○	○	○	○	○
16) Sheepish	○	○	○	○	○
17) Sluggish	○	○	○	○	○
18) Amazed	○	○	○	○	○
19) Lonely	○	○	○	○	○
20) Distressed	○	○	○	○	○
21) Daring	○	○	○	○	○
22) Shaky	○	○	○	○	○
23) Sleepy	○	○	○	○	○
24) Blameworthy	○	○	○	○	○
25) Surprised	○	○	○	○	○
26) Happy	○	○	○	○	○
27) Excited	○	○	○	○	○
28) Determined	○	○	○	○	○
29) Strong	○	○	○	○	○
30) Timid	○	○	○	○	○
31)					

Hostile	○	○	○	○	○
32) Frightened	○	○	○	○	○
33) Scornful	○	○	○	○	○
34) Alone	○	○	○	○	○
35) Proud	○	○	○	○	○
36) Astonished	○	○	○	○	○
37) Relaxed	○	○	○	○	○
38) Alert	○	○	○	○	○
39) Jittery	○	○	○	○	○
40) Interested	○	○	○	○	○
41) Irritable	○	○	○	○	○
42) Upset	○	○	○	○	○
43) Lively	○	○	○	○	○
44) Loathing	○	○	○	○	○
45) Delighted	○	○	○	○	○
46) Angry	○	○	○	○	○
47) Ashamed	○	○	○	○	○
48) Confident	○	○	○	○	○
49) Inspired	○	○	○	○	○
50) Bold	○	○	○	○	○
51) At ease	○	○	○	○	○
52) Energetic	○	○	○	○	○
53) Fearless	○	○	○	○	○
54) Blue	○	○	○	○	○
55) Scared	○	○	○	○	○
56) Concentrating	○	○	○	○	○
57) Disgusted with self	○	○	○	○	○
58) Shy	○	○	○	○	○
59) Drowsy	○	○	○	○	○
60) Dissatisfied with self	○	○	○	○	○

APPENDIX F

TASK-SPECIFIC SELF-EFFICACY SCALE

Please rate your degree of confidence by selecting a number from 0 to 100 for each of the following questions using the scale given below.

Scale

0	10	20	30	40	50	60	70	80	90	100
Cannot do at all				Moderately can do				Highly certain can do		

		0	10	20	30	40	50	60	70	80	90	100
1)	How confident are you in your ability to complete the targets in 90-99 seconds?	○	○	○	○	○	○	○	○	○	○	○
2)	How confident are you in your ability to complete the targets in 80-89 seconds?	○	○	○	○	○	○	○	○	○	○	○
3)	How confident are you in your ability to complete the targets in 70-79 seconds?	○	○	○	○	○	○	○	○	○	○	○
4)	How confident are you in your ability to complete the targets in 60-69 seconds?	○	○	○	○	○	○	○	○	○	○	○
5)	How confident are you in your ability to complete the targets in 50-59 seconds?	○	○	○	○	○	○	○	○	○	○	○
6)	How confident are you in your ability to complete the targets in 40-49 seconds?	○	○	○	○	○	○	○	○	○	○	○
7)	How confident are you in your ability to complete the targets in 30-39 seconds?	○	○	○	○	○	○	○	○	○	○	○
8)	How confident are you in your ability to complete the targets in 20-29 seconds?	○	○	○	○	○	○	○	○	○	○	○
9)	How confident are you in your ability to complete the targets in 10-19 seconds?	○	○	○	○	○	○	○	○	○	○	○
10)	How confident are you in your ability to complete the targets in 0-9 seconds?	○	○	○	○	○	○	○	○	○	○	○

APPENDIX G

MODIFIED INTRINSIC MOTIVATION INVENTORY

For each of the following statements, please indicate how true it is for you using the following scale:

1	2	3	4	5	6	7
not at all true			somewhat true			very true

	Not true at all			Somewhat true			Very true
1) While I was working on the task, I was thinking about how much I enjoyed it.	O	O	O	O	O	O	O
2) I think I am pretty good at this task.	O	O	O	O	O	O	O
3) I found the task very interesting.	O	O	O	O	O	O	O
4) I think I did pretty well at this activity, compared to others.	O	O	O	O	O	O	O
5) Doing the task was fun.	O	O	O	O	O	O	O
6) I enjoyed doing the task very much.	O	O	O	O	O	O	O
7) I am satisfied with my performance at this task.	O	O	O	O	O	O	O
8) I thought the task was very boring.	O	O	O	O	O	O	O
9) I felt pretty skilled at this task.	O	O	O	O	O	O	O
10) I thought the task was very interesting.	O	O	O	O	O	O	O
11) I would describe the task as very enjoyable.	O	O	O	O	O	O	O
12) After working at this task for a while, I felt pretty competent.	O	O	O	O	O	O	O