Complimentary lower-level and higher-order systems underpin imitation learning

Matthew Andrew,[1] Simon J. Bennett,[1] Digby Elliott,[1, 2] Spencer J. Hayes[1*]

[1]Brain and Behaviour Laboratory,
Research Institute for Sport and Exercise Sciences,
Faculty of Science,
Liverpool John Moores University,
Liverpool,
UK

[2]Department of Kinesiology,
McMaster University,
Ontario,
Canada

[*]Corresponding author
Brain and Behaviour Laboratory, Faculty of Science, Liverpool John Moores University, Byrom Street, Liverpool, L3 3AF, UK
Tel: +44 (0) 151 904 6237, Fax: +44 (0) 151 904 6284
s.hayes@ljmu.ac.uk

Abstract

We examined whether the temporal representation developed during motor training with reduced-frequency knowledge of results (KR; feedback available on every other trial) was transferred to an imitation learning task. To this end, four groups first practised a three-segment motor sequence task with different KR protocols. Two experimental groups received reduced-frequency KR, one group received high-frequency KR (feedback available on every trial), and one received no-KR. Compared to the no-KR group, the groups that received KR learned the temporal goal of the movement sequence, as evidenced by increased accuracy and consistency across training. Next, all groups learned a single-segment movement that had the same temporal goal as the motor sequence task but required the imitation of biological and nonbiological motion kinematics. Kinematic data showed that while all groups imitated biological motion kinematics, the two experimental reduced-frequency KR groups were on average ~800ms more accurate at imitating movement time than the high-frequency KR and no-KR groups. The interplay between learning biological motion kinematics and the transfer of temporal representation indicates imitation involves distinct, but complementary lower-level sensorimotor and higher-level cognitive processing systems.

Key words: knowledge-of-results; motor training; imitation; transfer; biological motion

1.1 Introduction

Imitation learning (henceforth imitation) is a powerful mechanism for acquiring movements that are not present within an individual's sensorimotor repertoire. This process involves observing, and then imitating, a novel movement performed by human or non-human agents. Over repeated attempts, the goal(s) and biological movement kinematics displayed by an agent are encoded as a sensorimotor representation that acts as an internal model (efference copy) for comparison against incoming afferent (i.e., visual, proprioceptive) sensorimotor signals (Iacoboni, 2005; Wolpert, Doya, & Kawato, 2003). Any resulting discrepancies between expected and actual sensory consequences are then minimized by online adjustments to the ongoing motor response (Burke, Tobler, Baddeley, & Schultz, 2010; Carroll & Bandura, 1982; Kilner, Friston, & Frith, 2007) and offline adjustments for the next response.

Knowledge-of-results (KR) regarding a goal-directed movement response to a desired outcome goal (e.g., movement time) influences offline planning (i.e., error correction between trials) processes during practice (Debener et al., 2005; Miltner, Braun, & Coles, 1997). Although KR provided after every motor response significantly improves sensorimotor accuracy and variability, and motivation (Bilodeau, Bilodeau, & Schumsky, 1959), it can be detrimental to learning because performers become dependent on the guiding informational properties such that performance is degraded when KR is not available (Salmoni, Schmidt, & Walter, 1984). For example, KR frequency was examined during the acquisition (Schmidt, Young, Swinnen, & Shapiro, 1989; Winstein & Schmidt, 1990) and imitation (Badets & Blandin, 2004) of motor timing tasks where groups received KR every trial (100% KR) or across reduced-frequency conditions (e.g., 50% KR). As expected for 100% KR groups, timing accuracy improved with practice and KR, but reduced-frequency feedback led to significantly more accurate timing performances in retention tests. The retention effects are suggested to be underpinned by learning processes that are developed during no-KR trials (e.g., inter-trial processing) where performers operationalise (Salmoni, et al., 1984; Schmidt, et al., 1989; Winstein & Schmidt, 1990) self-generated, higher-order attention demanding processes associated with detecting, estimating, and correcting response produced errors.

Confirmation of inter-trial processing during motor learning is found by presenting KR instantaneously to learners after a motor response so that the temporal constraint limits the effective integration of afferent and efferent sensory information, and KR (Swinnen, Schmidt, Nicholson, & Shapiro, 1990). Secondary tasks have also been used to interfere with the primary task during motor learning to establish if error-detection and correction processing occurs between trials. Learners either engaged in self-generated processing during the inter-trial delay, or performed an interpolated activity to estimate their own, or an experimenter's, response produced error (Swinnen, 1990). Typical motor learning effects were found following self-generated processing, and the estimation of their own movement response. Whereas motor learning was attenuated when the interpolated activity was directed towards another person. The attenuation indicted the secondary task interfered with the primary task, and suggested learners were prevented from engaging in self-generated error-detection and correction processing associated with their own movement response. Therefore, processing, or being guided to estimate, self-generated movement responses leads to the development of a more refined sensorimotor representation and processes, that underpin independent production of a required outcome goal such as movement time in post or retention tests (Salmoni, et al., 1984; Swinnen, 1990; Swinnen, et al., 1990).

The contribution of higher-order (cognitive; attention; error detection) and lower-level (visuo-motor) processes, and the similar findings compared to motor training protocols, indicate imitation is underpinned by general purpose perceptual, motor, and attentional systems that interact based on the environmental/task requirements (Bird, Brindley, Leighton, & Heyes, 2007; Brass & Heyes, 2005; Hamilton, 2008; Heyes, Bird, Johnson, & Haggard, 2005; Wohlschlager, Gattis, & Bekkering, 2003). We examined the interaction between higher-order (attention) and lower-level (sensorimotor) processes during imitation using a novel protocol that required learners to acquire an atypical biological motion pattern that was not already represented in an existing sensorimotor repertoire (Hayes, Dutoy, Elliott, Gowen, & Bennett, 2016; Hayes, Roberts, Elliott, & Bennett, 2014). Because the novel movement pattern was atypical, imitation of biological motion was suggested to be underpinned predominantly via lower-level sensorimotor systems (Brass & Heyes, 2005; Hamilton, 2008), rather than higher-order semantic processes (Rumiati et al., 2005). We also enhanced imitation accuracy of atypical biological motion via selective attention (Hayes, et al., 2014), but importantly imitation fidelity was not attenuated by the presence of spatially distracting end-state goals (Hayes, et al., 2016). In these studies, however, we importantly reversed the performance effects of imitating atypical biological motion by attenuating the representation of associated temporal movement time goals. These specific modulatory effects suggest imitation of atypical biological motion is underpinned by higher-order cognitive and lower-level sensorimotor processes that operate as distinct, but complimentary systems.

It is precisely these systems, and the involvement of similar neural circuits (Buccino et al., 2004; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Prinz, 1997), that enable participants to exhibit positive transfer from imitation to subsequent motor performance (Hecht, Vogt, & Prinz, 2001). In the current study, we took a novel approach to examining the distinct, but similar, higher-order and lower-level processes underpinning motor training and imitation. A two-phase study determined whether a higher-order temporal representation (Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003) developed through prior motor training using reduced-frequency KR protocols transfers to subsequent imitation. Participants first engaged in motor training that required a three-segment motor timing movement to be acquired under different feedback conditions. Participants were randomly allocated to four groups, two of which acted as typical controls that received no-KR, or KR regarding movement time error following every (high-frequency) trial. To examine the development of self-generated error-detection and correction processes (Winstein & Schmidt, 1990), and thus a better representation of the temporal goal, we had two experimental groups that received reduced-frequency KR regarding movement time error on every other trial. One of these groups acted as an experimental-control group and received explicit instructions from an experimenter to estimate their own response produced movement time error on no-KR trials, and use this information to plan the next motor response. This condition is vital because it provides the experimental control needed to suggest any learning benefit following reduced-frequency KR in the group that did not receive explicit instructions to estimate is associated with self-generated error processing on no-KR trials (Swinnen, 1990).

Following motor training, participants transferred to an imitation phase where they imitated a non-human agent model moving through a single-segment with different biological (i.e., typical or atypical) motion (Hayes, et al., 2016). The non-human agent was used because it recruits lower-level sensorimotor (visuo-motor) processes (Press, Cook, Blakemore, & Kilner, 2011), and it enables us to present a constant velocity control stimulus (see below). The three models had the same overall movement time (1700 ms) as the movement learned during motor training, but displayed distinctly different amplitues and kinematics. This prevented participants from reparameterizing the three-segment movement learned during motor training in order to achieve accurate imitation. To examine biological motion specifically, an experimental model displayed novel atypical kinematics where peak velocity occurred at 18% of the trajectory. The atypical profile would not be part of an existing sensorimotor repertoire, and thus learners are required to represent the biological properties via lower-level sensorimotor processes in order to imitate the model. Two control (typical and constant velocity) models allowed us to show experimentally the movement reproduced after observing the atypical model was based on imitating biological motion kinematics, rather than recruiting and rescaling a pre-existing typical movement pattern. The typical biological motion control model displayed a profile where peak velocity occurred a 44% of the trajectory, which is consistent with most upper-limb aiming movements (Elliott, Helsen, & Chua, 2001). The constant velocity control model displayed the same overall movement time as the typical and atypical models (1700 ms), but the magnitude of velocity and direction remained constant, with no deviations in the perpendicular axis. KR was not provided in this phase in order to prevent it from modulating imitation learning.

We expected that if higher-order processes associated with representing movment time in the motor learning task transfer to the imitation task, the two groups provided with reduced-frequnecy KR should imitate with more accurate movement time than the high-frequency KR and no KR control groups. Based on the premise that higher-order cognitive and lower-level sensorimotor processes operate as distinct, but complimentary systems during imitation, we expected no such group difference in representing the observed biological motion kinematics. Specifically, all groups should represent the atypical biological motion kinematics because successful imitation in this context requires the engagement of lower-level sensorimotor processes (Brass, Bekkering, & Prinz, 2001; Brass & Heyes, 2005; Hayes, et al., 2014).

2.1 Methods

2.2Volunteers

Forty participants (aged between 18-21 years) volunteered for the study. Each participant was randomly allocated to either a high-frequency KR group that received KR on every trial (HF; n = 10), a control group that received no KR (CTL; n = 10), a reduced-frequency group that received KR on every other trial (RF; n = 10), or a reduced-frequency group that received KR on every other trial but were instructed to estimate the response outcome on no KR trials (RF+E; n = 10). All participants were right-hand dominant, had normal or corrected-to-normal vision and gave written informed consent. The experiment was designed in accordance with the 1964 Declaration of Helsinki and approved by the research ethics committee of the host university.

2.3 Procedure

2.3.1 Motor Training Task

Participants were informed the task procedure involved three phases: pre-test; practice; retention. Prior to the pre-test, participants were informed the to-be-learned motor task was a three-segment movement sequence, and were familiarised with the apparatus. Participants sat at a table, in front of a 21-inch CRT monitor (Iiyama Vision Master 505) that was operating with a resolution of 1280 x 1024 pixels, and a refresh rate of 85 Hz. The monitor was connected to a desktop computer (Dell Optiplex GX280), which also recorded motion of a hand-held stylus on graphics tablet (Wacom Intuos Pro XL), (Fig. A). In house routines programmed in MATLAB (The Mathworks, Inc.) controlled the experiment, and the visual stimulus, which was generated using Cogent 2000 toolbox (www.vislabucl.ac.uk/cogent.php).

During familiarisation, participants sat at a distance of ~555 mm from the centre of the monitor. Three red target circles (diameter = 12.50 mm) were displayed across the centre of the monitor with an equidistant horizontal extent of 18.75 mm. A white cursor (circle: diameter = 6.25 mm) was drawn on the monitor and represented the motion of the hand-held stylus. Participants started the movement sequence by moving the cursor, which was controlled by a hand-held stylus, so that it was first positioned in the left-hand start target. The movement sequence required the cursor to be moved horizontally to hit the centre target (segment 1), followed by a reversal movement back to the start target (segment 2), and finally another reversal to move the cursor back through the centre target and finally to stop in the right-hand end target (segment 3). Once participants confirmed they understood the sequence order, they were informed the goal of the task was to learn to perform the movement sequence with a criterion timing goal of 1700 ms. All participants were informed, and confirmed they understood the unit of milliseconds in relation to the more typical unit of seconds.

Participants performed 4 trials using the dominant right-arm in the pre-test. A trial commenced with the timing goal displayed ("Timing Goal = 1700 ms") on the monitor for 2000 ms, after which the goal display was replaced by the 3 red target circles. To begin a trial a participant moved the cursor to the start target. Once located, the targets turned green and the participant was free to move the cursor in order to complete the movement sequence as close to the timing goal as possible. To ensure participants performed the correct spatial dimensions of the movement sequence, an error message appeared on the monitor if the cursor did not pass through each target in the correct order (no error trials were recorded through the pre-test, practice or retention).

During the practice-phase participants performed 30 trials with the goal to meet the exact timing goal. To manipulate the processes developed during motor training, knowledge-of-results associated with each practice attempt was presented on the monitor (e.g., "Too Fast or Too Slow by 350 ms") following each trial (HF) or every other trial (RF). To confirm the RF group engaged in self-generated error detection and correction processing, an additional KR control group (RF+E) was instructed to estimate the response outcome on no KR trials. To do this, they provided a verbal statement to an experimenter as to whether the response movement time was shorter or longer than the timing goal, and consequently how to correct the error. There was no requirement to specify the exact duration of the absolute difference in milliseconds. Participants in the experimental groups were informed, and subsequently confirmed they understood how knowledge-of-results should be processed after practice trial *n* in order to adapt trial *n+1*. The control group performed an unrelated reading task for the time duration of the practice-phase. Following the practice-phase, a 10-minute retention test was performed in which participants from all groups completed four trials without the guiding presence of KR. The objective in retention was to perform a movement so that the exact 1700 ms timing goal was met, but this was completed by recalling what was learned during practice, rather than being guided by KR.

Insert Fig. A about here

2.3.2 Imitation Task

After completing the motor training task, participants performed the imitation task where they observed, and imitated, a movement displayed by a non-human agent model (a white cursor) on a 21-inch CRT monitor (Fig. B.1). The model had a horizontal trajectory that originated from a home position located on the left-hand side of the screen and ended at the right-hand ‘end’ position. The amplitude of the movement was 200 mm, and the total movement time was 1700 ms. To examine the imitation of movement kinematics, three non-human agent models were created that displayed typical, atypical or constant velocity profiles. The typical model was created by a human volunteer who practised the task by performing typical goal-directed aiming movements using a hand-held stylus on a graphics tablet until a white cursor, which represented the stylus, moved from the left-hand home-target to the right-hand end-target in 1700 ms. The displacement time-series data recorded from a successful practice trial was selected to create the typical velocity model. The model displayed a typical (Elliott, et al., 2001) bell-shaped velocity profile in which the peak occurred at 44% of movement time (dark grey trace; Fig. B.2). The atypical model was created by the same volunteer, but an atypical movement profile was practised until the 200 mm amplitude was performed in 1700 ms. A successful trial was selected to create the atypical velocity model, and had a velocity profile where the peak occurred at 18% of the movement time (black trace; Fig. B.2). The method of using a human volunteer to generate the atypical model was critical because it ensured the kinematics of the movement were biological in origin, and further that the movement was achievable by human participants. The model displaying constant velocity was created according to the amplitude (200 mm) and time (1700 ms) constraints associated with the task. The model displayed the exact movement time but with a constant velocity profile that also had no deviations in the perpendicular axis (light grey trace; Fig. B.2). The imitation task comprised 10 blocks of 6 trials (60 trials). A block contained the typical, atypical and constant velocity models each presented twice. Trial order within a block, as well as block order, was pseudo-randomised across participants. The randomised structure reduced predictability of an upcoming model(s) and thus promoted imitation on a trial-by-trial basis.

Prior to the experimental trials, all participants completed six familiarisation trials that replicated the conditions of the imitation task. Each trial commenced with the model being positioned in the left-hand 'home' position after which it moved to the 'end' position with a constant velocity and time of 1700 ms. A constant velocity trajectory was used to ensure construct validity by preventing participants from experiencing biological motion before the actual imitation trials. Participants were not informed about the duration of the movement. After observing a model, participants attempted to imitate the model by moving the stylus on the tablet so that the cursor moved to the 'end' position, as per the movement of the model. Participants confirmed they understood the model, the instruction to imitate a model, and the sensorimotor association between the stylus on a graphics tablet and the corresponding movement of cursor on the monitor.

Insert Fig. B about here

2.4 Data Reduction and Analysis

2.4.1 Motor Training Task

To quantify motor performance and learning of the timing goal, we extracted movement time for each participant across the 4 pre-test, 30 practice and 4 retention trials. To examine motor timing accuracy we calculated absolute constant error, which reflected the non-signed difference between movement time on each trial and the timing goal (e.g., 1900 ms – 1700 ms = 200 ms). To examine motor timing consistency we calculated variable error, which represented the trial-by-trial variability.

Individual-participant mean data during the practice-phase was calculated from successive blocks of 6 trials and submitted to separate 3 Group (HF, RF, RF+E) x 5 Block (1; 2; 3; 4; 5) mixed ANOVA. To examine changes in motor performance following practice, the 10-minute retention test data (absolute constant error; variable error) were submitted to one-factor analysis of covariance

(ANCOVA) involving all four groups. The pre-test scores served as the covariate. This approach has the advantage of minimizing the impact of any initial group differences performance due to random assignment and takes into account initial within-group variability in performance for our retention test comparisons of interest. Significant main and/or interactions effects involving more than two means were decomposed using Tukey HSD post-hoc procedure. Alpha was set at $p < 0.05$, and eta squared (η^2) expressed the size of the effect (Levine & Hullett, 2002).

2.4.2 Imitation Task

To quantify imitation performance, we extracted participant's movement kinematics exhibited on each imitation trial. The start of the movement was defined as the time the centre of the cursor moved beyond the perimeter of the 'home' position, and end was calculated when the participant clicked on the lower-button on the stylus. For each trial, the 2-dimensional displacement data sampled (85 Hz) from the graphics tablet were filtered using a low pass 4th order autoregressive filter with a 8 Hz cut-off. The filtered data were differentiated using a central difference algorithm to obtain velocity. A MATLAB routine extracted the primary movement occurring in the x-axis and then returned the following dependent variables: movement time, peak velocity, and percentage-time-to-peak-velocity. Individual-participant means of these data were submitted to separate 4 Group (HF, RF, RF+E, CTL) x 3 Model (atypical; typical; constant velocity) mixed ANOVA. Significant main and/or interactions effects involving more than two means were analysed using Tukey HSD post-hoc procedure. Alpha was set at $p < 0.05$, and eta squared (η^2) expressed the size of the effect.

3.1 Results

3.2 Motor Training Task

For absolute constant error, there was no main effect of Group [F(2, 27) = .92, $p > 0.05$, $\eta^2 = 0.06$] or Group x Block interaction [F(8, 108) = .68, $p > 0.05$, $\eta^2 = 0.03$] in the 3 x 5 ANOVA. A significant main effect of Block [F(4, 108) = 11.78, $p < 0.01$, $\eta^2 = 0.29$] showed participants in the experimental groups modified movement timing accuracy across the 5 blocks of practice (see Fig.

C1). Post-hoc tests showed accuracy improved from block 1 to block 2 by 245 ms ($p < 0.01$); from block 1 to block 3 by 307 ms ($p < 0.01$); from block 1 to block 4 by 332 ms ($p < 0.01$) and from block 1 to block 5 by 342 ms ($p < 0.01$). Also, from block 2 to block 3 by 62 ms ($p = 0.05$); from block 2 to block 4 by 87 ms ($p < 0.05$); and from block 2 to block 5 by 97 ms ($p < 0.05$). No significant changes occurred across blocks 3 to 5 (*ps* > 0.05).

For variability of error, there was no main effect of Group [F(2, 27) = 1.10, $p > 0.05$, $\eta^2 = 0.08$] or Group x Block interaction [F(8, 108) = .60, $p > 0.05$, $\eta^2 = 0.03$] in the 3 x 5 ANOVA. A main effect of Block [F(4, 108) = 17.40, $p < 0.01$, $\eta^2 = 0.38$] showed participants improved consistency across the 5 blocks of practice (Fig. C.2).). Post-hoc tests showed consistency improved from block 1 to block 2 by 201 ms ($p < 0.01$); from block 1 to block 3 by 212 ms ($p < 0.01$); from block 1 to block 4 by 230 ms ($p < 0.01$) and from block 1 to block 5 by 245 ms ($p < 0.01$). No significant changes occurred across blocks 2 to 5 (*ps* > 0.05).

When KR was removed in the retention test, the 4 group ANCOVA revealed that the experimental groups were significantly more accurate [F (3, 35) = 5.36, $p < 0.01$, $\eta^2 = 0.32$] and consistent [F (3, 35) = 5.71, $p < 0.01$, $\eta^2 = 0.31$] than the control group. Post-hoc testing showed that in comparison to the control group, accuracy was greater in the HF group by 598 ms, the RF group by 601 ms, and the RF+E group by 629 ms. For the variability, post-hoc testing showed that in comparison to the control group, consistency was greater in the HF group by 312 ms, the RF group by 269 ms, and the RF+E group by 300 ms.

Insert Fig. C about here

<u>3.3 Imitation Task</u>

As illustrated in Fig. D.1, the 4 Group x 3 Model ANOVA revealed a main effect of Group for movement time [F (3, 36) = 26.66, $p < 0.01$, $\eta^2 = 0.69$] that indicated the RF and RF+E groups imitated with significantly shorter movement times than HF and CTL groups (*ps* < 0.01). The RF group exhibited a movement time that was 774 ms and 826 ms more accurate, than the HF and CTL groups, respectively, and closer to the model movement time of 1700 ms (red dashed line; Fig. D.1).

The RF+E group showed similar performance with movement time being 826 ms and 878 ms more accurate than the HF and CTL groups. Independent of group, a main effect for Model [F(2, 72) = 83.23, $p < 0.01$, $\eta^2 = 0.63$] indicated shorter and more accurate movement times were imitated after observing the atypical (2057 ms) and typical (2153 ms) velocity models, compared to the constant (2591 ms) velocity model (*ps* < 0.01). These effects were associated with a main effect of Model [F (2, 72) = 128.92, $p < 0.01$, $\eta^2 = 0.76$] where the magnitude of peak velocity was significantly greater imitating atypical (0.26 mm/ms) compared to typical (0.19 mm/ms) and constant (0.15 mm/ms) velocity models (all *ps* < 0.01; Fig. D.2). A similar main effect of Model [F (2, 72) = 60.27, $p < 0.01$, $\eta^2 = 0.63$] was evident for percentage-time-to-peak-velocity, which revealed peak velocity occurred earlier in the movement trajectory when imitating atypical (29 %), compared to typical (42 %) and constant (48 %) velocity models (all *ps* < 0.01; Fig. D.3).

Insert Fig. D about here

4.1 Discussion

Similar higher-order and lower-level processes underpin performance and learning during motor training and imitation learning (Bird & Heyes, 2005; Buccino, et al., 2004; Cross, et al., 2009; Hayes, Elliott, & Bennett, 2010; Hecht, et al., 2001). These processes are part of general purpose perceptual, motor and attentional systems (Bird, et al., 2007; Brass & Heyes, 2005), and thereby facilitate positive transfer from imitation to subsequent motor performance (Hecht, et al., 2001). In the current study, we further examined whether higher-order processes developed using reduced-frequency feedback procedures in motor training transfer to imitation. The results from motor training indicated the experimental groups were more accurate and consistent at performing the timing goal than the control group. The finding of similar performance effects for the reduced-frequency and high-frequency KR groups is consistent with previous studies (Schmidt, et al., 1989; Swinnen, 1990; Winstein & Schmidt, 1990). Indeed, no difference between the groups in an immediate retention test would be expected because the beneficial effects of reduced frequency KR are not typically observed until performance is measured in a 24-hour delayed retention test (Schmidt, et al., 1989; Swinnen, 1990; Winstein & Schmidt, 1990). This does not mean that higher-order cognitive processes associated with representing movement time were not developed by the reduced-frequency KR protocols. Indeed, the main effect of group for movement time in the subsequent imitation phase showed the reduced frequency KR groups exhibited a performance advantage compared to the two other groups. Specifically, the reduced frequency KR groups outperformed the high-frequency KR and control groups by an average of ~800 ms, which resulted in movement times that were on average ~154 ms away from the model time goal of 1700 ms. The finding of such an advantage for both reduced-frequency KR groups, combined with evidence of similar performance in motor training, indicates the group that did not receive explicit instructions to perform error-detection and correction procedures on no KR trials must have done so via self-generation. The lack of difference between the high frequency KR and control groups indicates these higher-order cognitive processes were not effectively acquired, and subsequently transferred in imitation, when participants were able to rely on KR to correct their motor response between trials in motor training (Salmoni, et al., 1984; Swinnen, 1990).

As predicted, the frequency of KR received during motor training did not modulate or attenuate the imitation of biological motion kinematics with all groups exhibiting a higher magnitude of peak velocity, which occurred earlier in the movement trajectory, after imitating the atypical compared to typical and constant velocity models. These effects are consistent with our previous work that also showed accurate imitation of atypical biological motion was not attenuated by the presence of spatially distracting end-state goals (Hayes, et al., 2016). Given that atypical biological motion kinematics were not already part of an existing motor repertoire (Hayes, et al., 2016; Hayes, et al., 2014), the representation of these kinematics most likely involved lower-level sensorimotor processes (Brass, Bekkering, Wohlschlaeger, & Prinz, 2000; Heyes, 2001; Iacoboni, 2005; Kilner, Hamilton, & Blakemore, 2007; Prinz, 1997) as opposed to being imitated via a semantic coding route where the observed kinematics are recalled from memory (Rumiati, Carmo, & Corradi-Dell'Acqua, 2009). Whilst this supports the idea that visual features of an action are mapped directly to motor features (Heyes, 2001), it is important to bear in mind that the representation of biological movement kinematics was not achieved at the expense of performance outcome (i.e., both reduced-frequency groups exhibiting more accurate movement time). The implication is that although the interplay between lower-level and higher-order systems during imitation are distinct, the processes are complementary and regulated based on the action context and experience.

Complementarity in these processes is consistent with the suggestion that multiple routes underpin imitation (Bekkering, Wohlschlaeger, & Gattis, 2000; Buxbaum & Kalénine, 2010; Hamilton, 2008, 2014; Heyes, 2011; Rumiati, et al., 2009; Rumiati, Papeo, & Corradi-Dell'Acqua, 2010). An observed stimulus is represented in a hierarchical fashion based on rationality and social cues, goals, kinematics, and muscle activity (Hamilton, 2014). For example, the kinematic features (i.e., atypical biological motion in the present study) are suggested to be coded via visual areas (middle temporal gyrus; superior temporal sulcus) and inferior frontal gyrus (Hamilton & Grafton, 2007; Kilner, Neal, Weiskopf, Friston, & Frith, 2009) in the perception-action system, whereas the goal of an action (e.g., grasping an ear) is processed via a parietal (inferior parietal lobule; anterior intraparietal sulcus) network. We suggest that an area in the frontal cortex, which provides input and control to the perception-action system during imitation (Buccino, et al., 2004; Burke, et al., 2010; de Lange, Spronk, Willems, Toni, & Bekkering, 2008; Wang & Hamilton, 2014), could have underpinned the performance advantage observed here for the reduced-frequency KR groups. Specifically, dorsal lateral pre-frontal cortex, which is active between learning trials during imitation (Buccino, et al., 2004), and associated with response selection (Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000) and action-prediction error processing during imitation learning (Burke, et al., 2010), could have provided the means to transfer the temporal goal learned during motor training.

To conclude, we showed that the representation of movement time developed during motor training by reduced frequency KR protocols was transferred and facilitated subsequent imitation learning. Our findings support the notion that imitation is not a special purpose system endowed with processes that merely match observed visual properties to the motor system, but is rather a general system mediated by distinct, but complementary lower-level sensorimotor and higher-order cognitive processing systems developed through sensorimotor experience.

References

Badets, A., & Blandin, Y. (2004). The Role of Knowledge of Results Frequency in Learning Through Observation. *Journal of Motor Behavior, 36*(1), 62-70. doi: 10.3200/JMBR.36.1.62-70

Bekkering, H., Wohlschlaeger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *The Quarterly Journal of Experimental Psychology. , 53*(1), 153-164. doi: 10.1080/713755872

Bilodeau, E. A., Bilodeau, I. M., & Schumsky, D. A. (1959). Some effects of introducing and withdrawing knowledge of results early and late in practice. *Journal of Experimental Psychology, 58*(2), 142-144.

Bird, G., Brindley, R., Leighton, J., & Heyes, C. (2007). General processes, rather than "goals," explain imitation errors. *Journal of Experimental Psychology. Human Perception and Performance, 33*(5), 1158-1169. doi: 10.1037/0096-1523.33.5.1158

Bird, G., & Heyes, C. (2005). Effector-Dependent Learning by Observation of a Finger Movement Sequence. *Journal of Experimental Psychology: Human Perception and Performance, 31*(2), 262-275.

Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica, 106*(1-2), 3-22.

Brass, M., Bekkering, H., Wohlschlaeger, A., & Prinz, W. (2000). Compatibility between Observed and Executed Finger Movements: Comparing Symbolic, Spatial, and Imitative Cues. *Brain and Cognition, 44*(2), 124-143.

Brass, M., & Heyes, C. (2005). Imitation: is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences, 9*(10), 489-495. doi: 10.1016/j.tics.2005.08.007

Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron, 42*(2), 323-334. doi: Doi 10.1016/S0896-6273(04)00181-3

Burke, C. J., Tobler, P. N., Baddeley, M., & Schultz, W. (2010). Neural mechanisms of observational learning. *Proceedings of the National Academy of Sciences, 107*(32), 14431-14436. doi: 10.1073/pnas.1003111107

Buxbaum, L. J., & Kalénine, S. (2010). Action knowledge, visuomotor activation, and embodiment in the two action systems. *Annals of the New York Academy of Sciences, 1191*(1), 201-218. doi: 10.1111/j.1749-6632.2010.05447.x

Carroll, W. R., & Bandura, A. (1982). The role of visual monitoring in observational learning of action patterns: making the unobservable observable. *Journal of Motor Behavior, 14*(2), 153-167.

Cross, E. S., Kraemer, D. J. M., Hamilton, A. F. d. C., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral Cortex*, *19*(2), 315-326.

de Lange, F. P., Spronk, M., Willems, R. M., Toni, I., & Bekkering, H. (2008). Complementary Systems for Understanding Action Intentions. *Current Biology, 18*(6), 454-457.

Debener, S., Ullsperger, M., Siegel, M., Fiehler, K., von Cramon, D. Y., & Engel, A. K. (2005). Trial-by-Trial Coupling of Concurrent Electroencephalogram and Functional Magnetic Resonance Imaging Identifies the Dynamics of Performance Monitoring. *The Journal of Neuroscience, 25*(50), 11730-11737. doi: 10.1523/jneurosci.3286-05.2005

Elliott, D., Helsen, W. F., & Chua, R. (2001). A century later: Woodworth's (1899) two-component model of goal-directed aiming. *Psychological Bulletin, 127*(3), 342-357.

Hamilton, A. F. d. C. (2008). Emulation and mimicry for social interaction: A theoretical approach to imitation in autism. *The Quarterly Journal of Experimental Psychology, 61*(1), 101-115.

Hamilton, A. F. d. C. (2014). Cognitive underpinnings of social interaction. *The Quarterly Journal of Experimental Psychology*, 1-16. doi: 10.1080/17470218.2014.973424

Hamilton, A. F. d. C., & Grafton, S. T. (2007). The motor hierarchy: from kinematics to goals and intentions. In P. Haggard, Y. Rosetti & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition: Attention and performance XXII.* (pp. 381-408). Oxford, UK: Oxford University Press.

Hayes, S. J., Dutoy, C. A., Elliott, D., Gowen, E., & Bennett, S. J. (2016). Atypical biological motion kinematics are represented by complementary lower-level and top-down processes during imitation learning. *Acta Psychologica, 163*, 10-16. doi: http://dx.doi.org/10.1016/j.actpsy.2015.10.005

Hayes, S. J., Elliott, D., & Bennett, S. J. (2010). General motor representations are developed during action-observation. *Experimental Brain Research, 204*, 1-8.

Hayes, S. J., Roberts, J. W., Elliott, D., & Bennett, S. J. (2014). Top-Down Attentional Processes Modulate the Coding of Atypical Biological Motion Kinematics in the Absence of Motor Signals. *Journal of Experimental Psychology: Human Perception and Performance, 40*(4), 1641-1653.

Hecht, H., Vogt, S., & Prinz, W. (2001). Motor learning enhances perceptual judgment: a case for action-perception transfer. *Psychological Research*, *65*(1), 3-14. doi: 10.1007/s004260000043

Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences, 5*(6), 253-261.

Heyes, C. (2011). Automatic imitation. *Psychological Bulletin, 137*(3), 463-483. doi: 10.1037/a0022288

Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Cognitive Brain Research, 22*(2), 233-240. doi: 10.1016/j.cogbrainres.2004.09.009

Iacoboni, M. (2005). Neural mechanisms of imitation. *Current Opinion in Neurobiology, 15*(6), 632-637. doi: DOI 10.1016/j.conb.2005.10.010

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cognitive Processing, 8*(3), 159-166. doi: 10.1007/s10339-007-0170-2

Kilner, J. M., Hamilton, A. F. d. C., & Blakemore, S. J. (2007). Interference effect of observed human movement on action is due to velocity profile of biological motion. *Social Neuroscience, 2*(3), 158-166.

Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of Mirror Neurons in Human Inferior Frontal Gyrus. *The Journal of Neuroscience, 29*(32), 10153-10159. doi: 10.1523/jneurosci.2668-09.2009

Levine, T. R., & Hullett, C. R. (2002). Eta Squared, Partial Eta Squared, and Misreporting of Effect Size in Communication Research. *Human Communication Research, 28*(4), 612-625. doi: 10.1111/j.1468-2958.2002.tb00828.x

Miltner, W. H., Braun, C. H., & Coles, M. G. (1997). Event-related brain potentials following incorrect feedback in a time-estimation task: Evidence for a “generic” neural system for error detection. *Journal of Cognitive Neuroscience, 9*(6), 788-798.

Press, C., Cook, J. L., Blakemore, S.-J., & Kilner, J. M. (2011). Dynamic modulation of human motor activity when observing actions. *The Journal of Neuroscience, 31*(8), 2792-2800.

Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology, 9*(2), 129-154.

Rowe, J. B., Toni, I., Josephs, O., Frackowiak, R. S. J., & Passingham, R. E. (2000). The Prefrontal Cortex: Response Selection or Maintenance Within Working Memory? *Science, 288*(5471), 1656-1660. doi: 10.1126/science.288.5471.1656

Rumiati, R. I., Carmo, J. C., & Corradi-Dell'Acqua, C. (2009). Neuropsychological perspectives on the mechanisms of imitation. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1528), 2337-2347.

Rumiati, R. I., Papeo, L., & Corradi-Dell’Acqua, C. (2010). Higher-level motor processes. *Annals of the New York Academy of Sciences, 1191*(1), 219-241. doi: 10.1111/j.1749-6632.2010.05442.x

Rumiati, R. I., Weiss, P. H., Tessari, A., Assmus, A., Zilles, K., Herzog, H., & Fink, G. R. (2005). Common and differential neural mechanisms supporting imitation of meaningful and meaningless actions. *Journal of Cognitive Neuroscience, 17*(9), 1420-1431.

Salmoni, A. W., Schmidt, R. A., & Walter, C. B. (1984). Knowledge of results and motor learning: a review and critical reappraisal. *Psychological Bulletin, 95*(3), 355-386.

Schmidt, R. A., Young, D. E., Swinnen, S., & Shapiro, D. C. (1989). Summary knowledge of results for skill acquisition: support for the guidance hypothesis. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15*(2), 352-359.

Swinnen, S. P. (1990). Interpolated activities during the knowledge-of-results delay and post-knowledge-of-results interval: Effects on performance and learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 16*(4), 692-702.

Swinnen, S. P., Schmidt, R. A., Nicholson, D. E., & Shapiro, D. C. (1990). Information feedback for skill acquisition: instantaneous knowledge of results degrades learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 16*(4), 706-716.

Wang, Y., & Hamilton, A. F. d. C. (2014). Anterior medial prefrontal cortex implements social priming of mimicry. *Social Cognitive and Affective Neuroscience*, 1-8. doi: 10.1093/scan/nsu076

Winstein, C. J., & Schmidt, R. A. (1990). Reduced frequency of knowledge of results enhances motor skill learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 16*(4), 677-691.

Wohlschlager, A., Gattis, M., & Bekkering, H. (2003). Action generation and action perception in imitation: an instance of the ideomotor principle. *Philosophical Transactions of the Royal Society B: Biological Sciences., 358*(1431), 501-515. doi: 10.1098/rstb.2002.1257

Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society B-Biological Sciences, 358*(1431), 593-602. doi: DOI 10.1098/rstb.2002.1238

Figure Captions

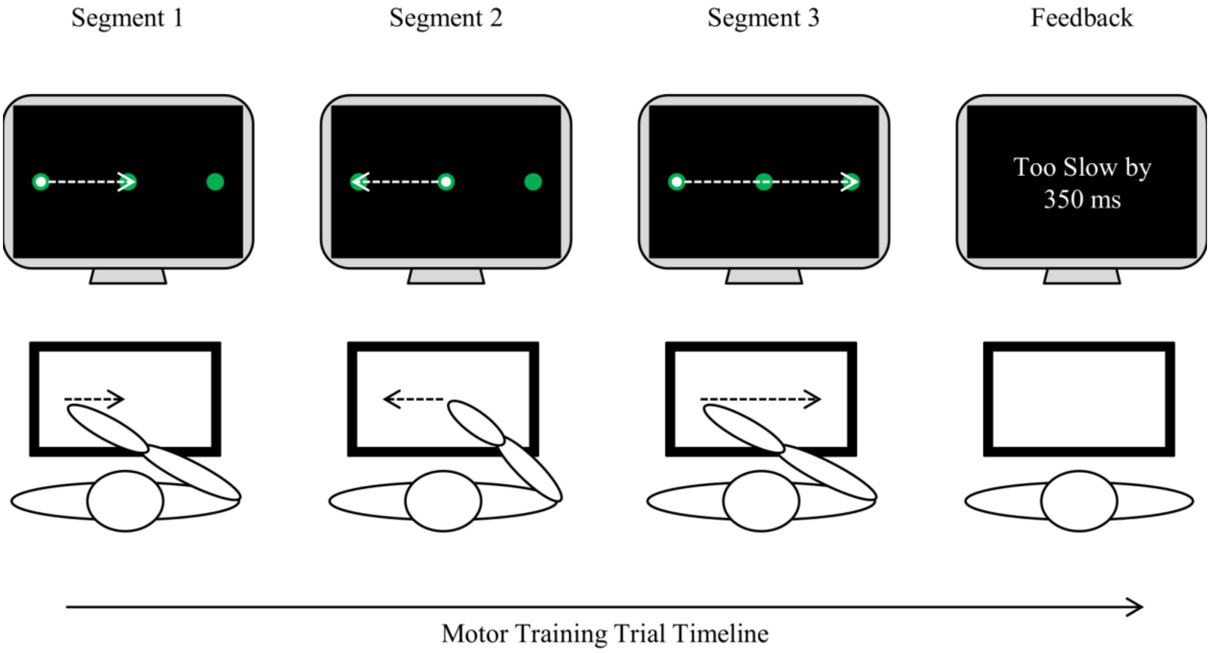
Fig. A.1 A schematic representation of the laboratory/experimental set-up for the motor training task. The white circle represents the motion of a participant's movement. The three-segment movement sequence is depicted by the arrows in segment 1 (start target to centre target), segment 2 (centre target to start target), and segment 3 (start target to end target). Information on the CRT monitor represents the knowledge-of-results provided to the participant.

Fig. B (B.1) A schematic representation of the laboratory/experimental set-up for the imitation task. The white circle represents a model. The single-segment movement sequence is depicted by the arrows (i.e. from the start position to the final position). **(B.2)** Velocity profiles for the atypical (black trace), typical (dark grey trace) and constant velocity (light grey trace) movement trajectories presented as a function of time.

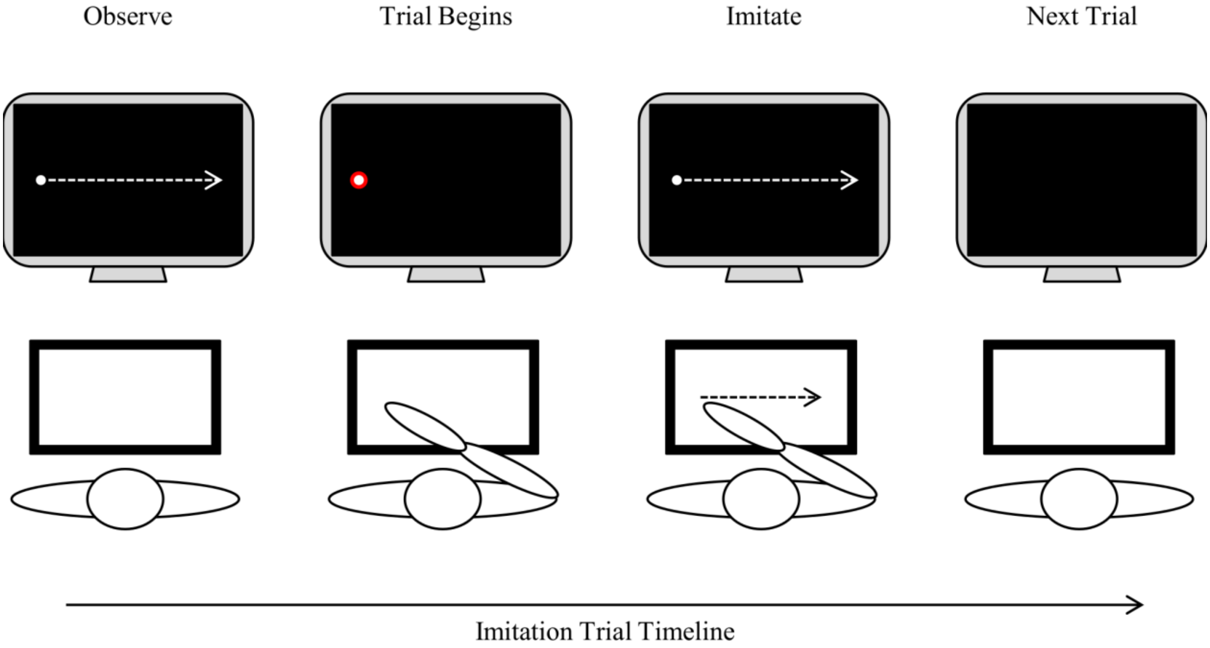
Fig. C Mean absolute constant error **(C.1)** and variable error **(C.2)** (error bars represent standard error of the mean) presented as a function of Group and Phase.

Fig. D Mean movement time **(D.1)**, peak velocity **(D.2)**, and percentage-time-to-peak-velocity **(D.3)** presented as a function of Group and Model (red dashed line represents model movement).

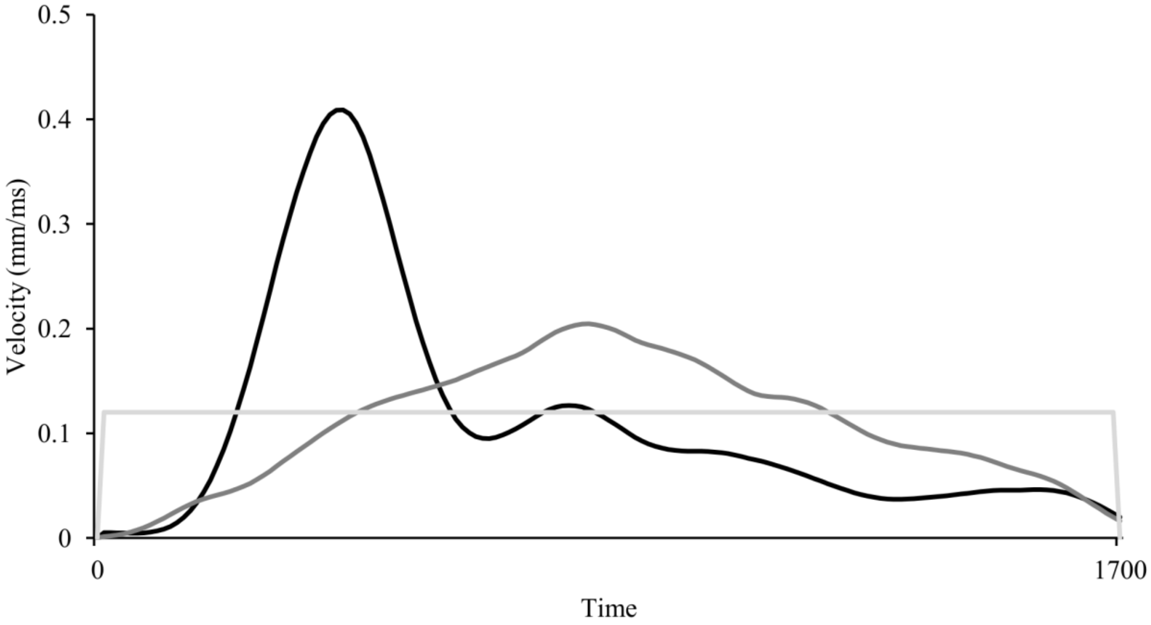
A.1


Segment 1
Segment 2
Segment 3
Feedback
Too Slow by 350 ms
Motor Training Trial Timeline

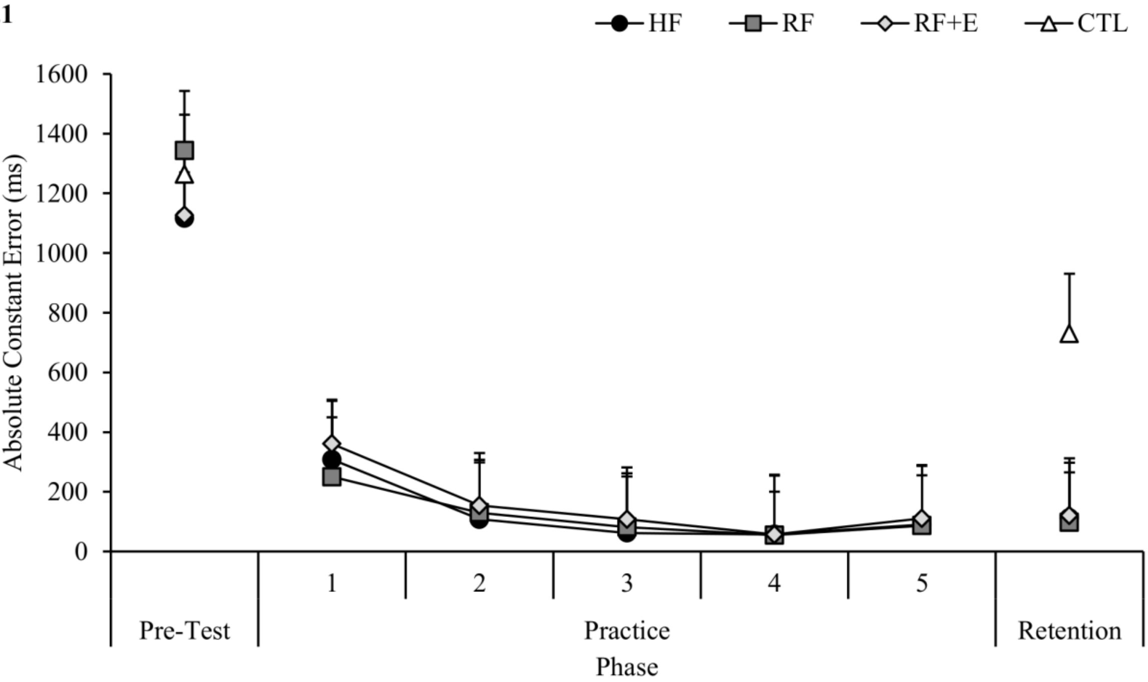
B.1


Observe
Trial Begins
Imitate
Next Trial
Imitation Trial Timeline

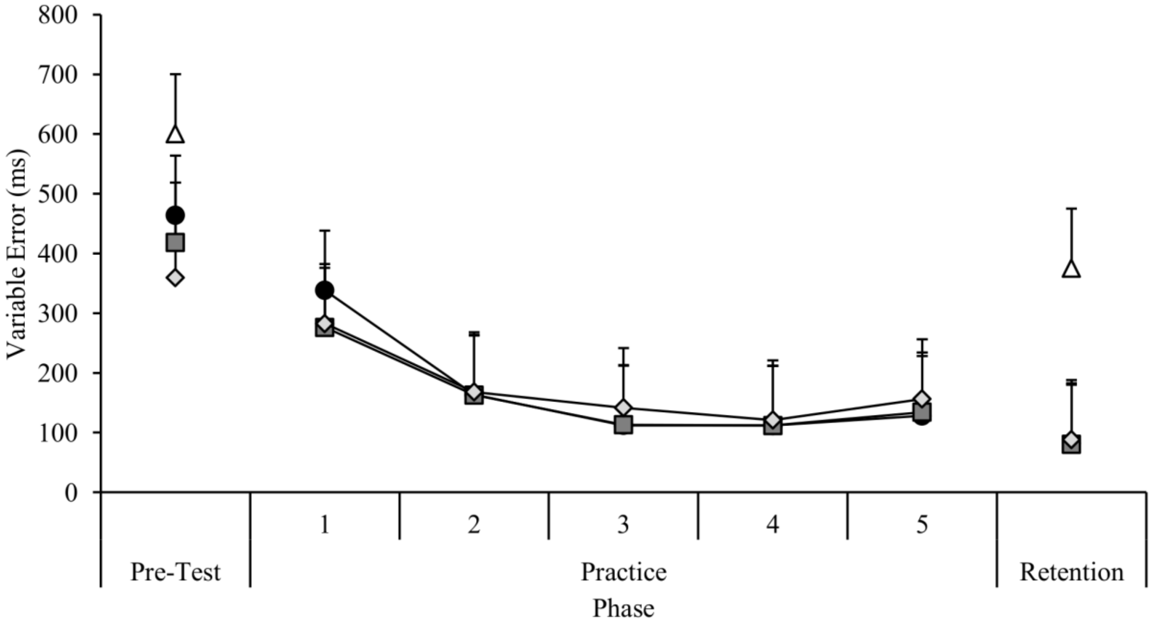
B.2


0.5
0.4
0.3
0.2
0.1
0
Velocity (mm/ms)
0
1700
Time

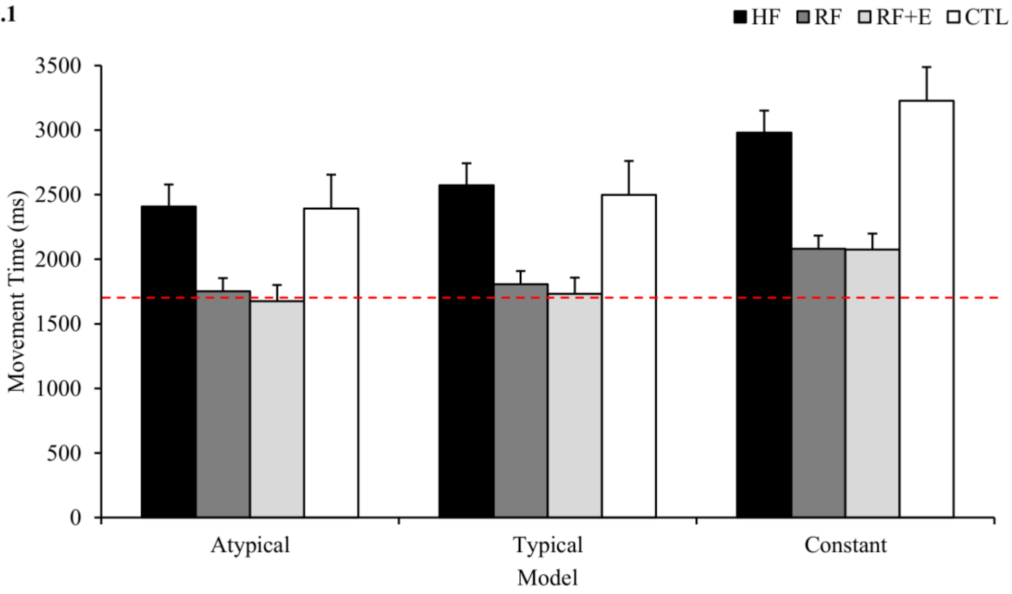
C.1


HF
RF
RF+E
CTL
Absolute Constant Error (ms)
1600
1400
1200
1000
800
600
400
200
0
1
2
3
4
5
Pre-Test
Practice
Retention
Phase

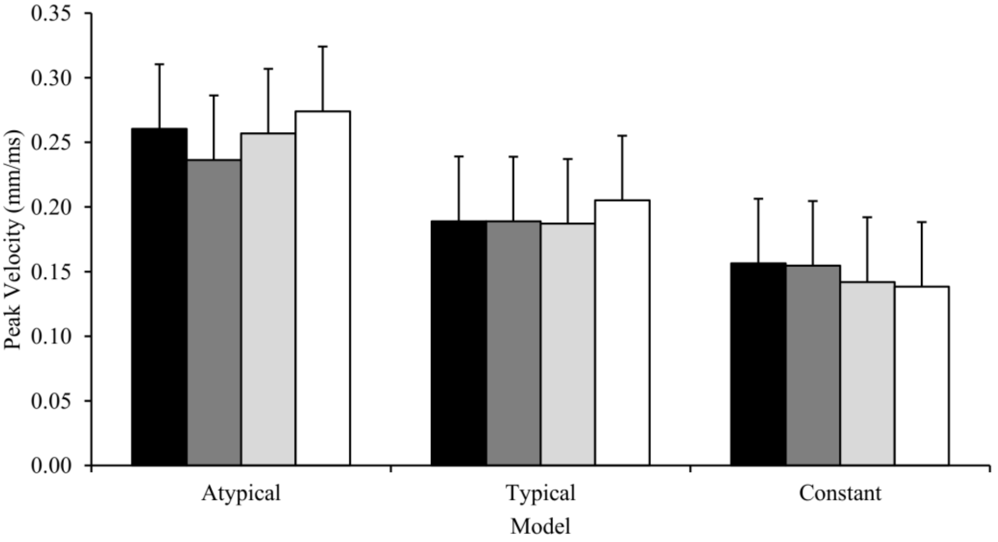
C.2


Variable Error (ms)
800
700
600
500
400
300
200
100
0
1
2
3
4
5
Pre-Test
Practice
Retention
Phase

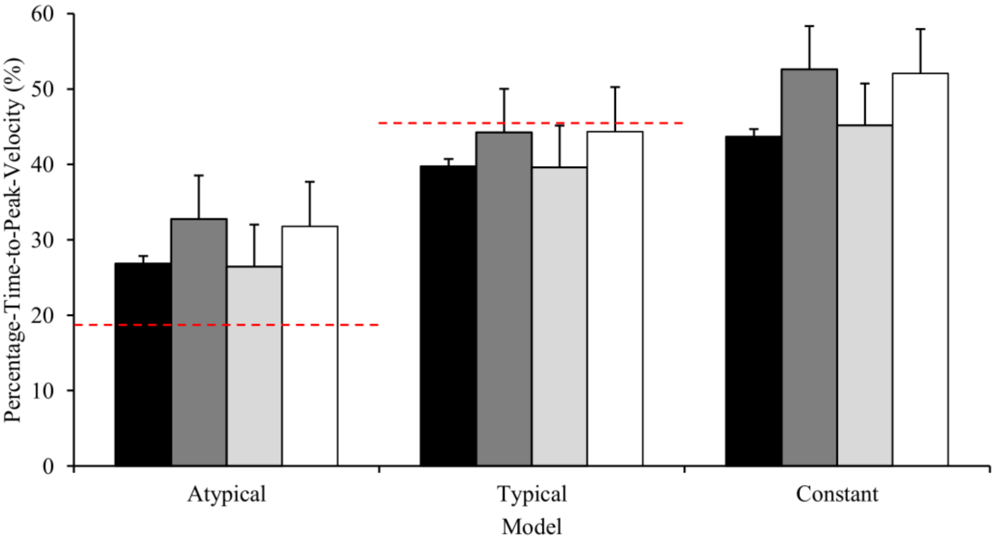
D.1


■HF ■RF ☐RF+E ☐CTL
Movement Time (ms)
3500
3000
2500
2000
1500
1000
500
0
Atypical
Typical
Constant
Model

D.2


Peak Velocity (mm/ms)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Atypical
Typical
Constant
Model

D.3


Percentage-Time-to-Peak-Velocity (%)
60
50
40
30
20
10
0
Atypical
Typical
Constant
Model