

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

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## 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.

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

17 The contribution of higher-order (cognitive; attention; error detection) and lower-level (visuo-  
18 motor) processes, and the similar findings compared to motor training protocols, indicate imitation is  
19 underpinned by general purpose perceptual, motor, and attentional systems that interact based on the  
20 environmental/task requirements (Bird, Brindley, Leighton, & Heyes, 2007; Brass & Heyes, 2005;  
21 Hamilton, 2008; Heyes, Bird, Johnson, & Haggard, 2005; Wohlschlagel, Gattis, & Bekkering, 2003).  
22 We examined the interaction between higher-order (attention) and lower-level (sensorimotor)  
23 processes during imitation using a novel protocol that required learners to acquire an atypical  
24 biological motion pattern that was not already represented in an existing sensorimotor repertoire  
25 (Hayes, Dutoy, Elliott, Gowen, & Bennett, 2016; Hayes, Roberts, Elliott, & Bennett, 2014). Because  
26 the novel movement pattern was atypical, imitation of biological motion was suggested to be  
27 underpinned predominantly via lower-level sensorimotor systems (Brass & Heyes, 2005; Hamilton,  
28 2008), rather than higher-order semantic processes (Rumiati et al., 2005). We also enhanced imitation

1 accuracy of atypical biological motion via selective attention (Hayes, et al., 2014), but importantly  
2 imitation fidelity was not attenuated by the presence of spatially distracting end-state goals (Hayes, et  
3 al., 2016). In these studies, however, we importantly reversed the performance effects of imitating  
4 atypical biological motion by attenuating the representation of associated temporal movement time  
5 goals. These specific modulatory effects suggest imitation of atypical biological motion is  
6 underpinned by higher-order cognitive and lower-level sensorimotor processes that operate as distinct,  
7 but complimentary systems.

8         It is precisely these systems, and the involvement of similar neural circuits (Buccino et al.,  
9 2004; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Prinz, 1997), that enable participants to  
10 exhibit positive transfer from imitation to subsequent motor performance (Hecht, Vogt, & Prinz,  
11 2001). In the current study, we took a novel approach to examining the distinct, but similar, higher-  
12 order and lower-level processes underpinning motor training and imitation. A two-phase study  
13 determined whether a higher-order temporal representation (Keele, Ivry, Mayr, Hazeltine, & Heuer,  
14 2003) developed through prior motor training using reduced-frequency KR protocols transfers to  
15 subsequent imitation. Participants first engaged in motor training that required a three-segment motor  
16 timing movement to be acquired under different feedback conditions. Participants were randomly  
17 allocated to four groups, two of which acted as typical controls that received no-KR, or KR regarding  
18 movement time error following every (high-frequency) trial. To examine the development of self-  
19 generated error-detection and correction processes (Winstein & Schmidt, 1990), and thus a better  
20 representation of the temporal goal, we had two experimental groups that received reduced-frequency  
21 KR regarding movement time error on every other trial. One of these groups acted as an experimental-  
22 control group and received explicit instructions from an experimenter to estimate their own response  
23 produced movement time error on no-KR trials, and use this information to plan the next motor  
24 response. This condition is vital because it provides the experimental control needed to suggest any  
25 learning benefit following reduced-frequency KR in the group that did not receive explicit instructions  
26 to estimate is associated with self-generated error processing on no-KR trials (Swinnen, 1990).

27         Following motor training, participants transferred to an imitation phase where they imitated a  
28 non-human agent model moving through a single-segment with different biological (i.e., typical or

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

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

28

## 2.1 Methods

### 2.2 Volunteers

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](http://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

1 that it was first positioned in the left-hand start target. The movement sequence required the cursor to  
2 be moved horizontally to hit the centre target (segment 1), followed by a reversal movement back to  
3 the start target (segment 2), and finally another reversal to move the cursor back through the centre  
4 target and finally to stop in the right-hand end target (segment 3). Once participants confirmed they  
5 understood the sequence order, they were informed the goal of the task was to learn to perform the  
6 movement sequence with a criterion timing goal of 1700 ms. All participants were informed, and  
7 confirmed they understood the unit of milliseconds in relation to the more typical unit of seconds.

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

16 During the practice-phase participants performed 30 trials with the goal to meet the exact  
17 timing goal. To manipulate the processes developed during motor training, knowledge-of-results  
18 associated with each practice attempt was presented on the monitor (e.g., “Too Fast or Too Slow by  
19 350 ms”) following each trial (HF) or every other trial (RF). To confirm the RF group engaged in self-  
20 generated error detection and correction processing, an additional KR control group (RF+E) was  
21 instructed to estimate the response outcome on no KR trials. To do this, they provided a verbal  
22 statement to an experimenter as to whether the response movement time was shorter or longer than  
23 the timing goal, and consequently how to correct the error. There was no requirement to specify the  
24 exact duration of the absolute difference in milliseconds. Participants in the experimental groups were  
25 informed, and subsequently confirmed they understood how knowledge-of-results should be  
26 processed after practice trial  $n$  in order to adapt trial  $n+1$ . The control group performed an unrelated  
27 reading task for the time duration of the practice-phase. Following the practice-phase, a 10-minute  
28 retention test was performed in which participants from all groups completed four trials without the



1 guiding presence of KR. The objective in retention was to perform a movement so that the exact 1700  
2 ms timing goal was met, but this was completed by recalling what was learned during practice, rather  
3 than being guided by KR.

4  
5 Insert Fig. A about here

### 6 7 2.3.2 Imitation Task

8 After completing the motor training task, participants performed the imitation task where they  
9 observed, and imitated, a movement displayed by a non-human agent model (a white cursor) on a 21-  
10 inch CRT monitor (Fig. B.1). The model had a horizontal trajectory that originated from a home  
11 position located on the left-hand side of the screen and ended at the right-hand 'end' position. The  
12 amplitude of the movement was 200 mm, and the total movement time was 1700 ms. To examine the  
13 imitation of movement kinematics, three non-human agent models were created that displayed typical,  
14 atypical or constant velocity profiles. The typical model was created by a human volunteer who  
15 practised the task by performing typical goal-directed aiming movements using a hand-held stylus on  
16 a graphics tablet until a white cursor, which represented the stylus, moved from the left-hand home-  
17 target to the right-hand end-target in 1700 ms. The displacement time-series data recorded from a  
18 successful practice trial was selected to create the typical velocity model. The model displayed a  
19 typical (Elliott, et al., 2001) bell-shaped velocity profile in which the peak occurred at 44% of  
20 movement time (dark grey trace; Fig. B.2). The atypical model was created by the same volunteer, but  
21 an atypical movement profile was practised until the 200 mm amplitude was performed in 1700 ms. A  
22 successful trial was selected to create the atypical velocity model, and had a velocity profile where the  
23 peak occurred at 18% of the movement time (black trace; Fig. B.2). The method of using a human  
24 volunteer to generate the atypical model was critical because it ensured the kinematics of the  
25 movement were biological in origin, and further that the movement was achievable by human  
26 participants. The model displaying constant velocity was created according to the amplitude (200  
27 mm) and time (1700 ms) constraints associated with the task. The model displayed the exact  
28 movement time but with a constant velocity profile that also had no deviations in the perpendicular

1 axis (light grey trace; Fig. B.2). The imitation task comprised 10 blocks of 6 trials (60 trials). A block  
2 contained the typical, atypical and constant velocity models each presented twice. Trial order within a  
3 block, as well as block order, was pseudo-randomised across participants. The randomised structure  
4 reduced predictability of an upcoming model(s) and thus promoted imitation on a trial-by-trial basis.

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

15  
16 Insert Fig. B about here

## 17 18 *2.4 Data Reduction and Analysis*

### 19 2.4.1 Motor Training Task

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

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

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

#### 8 2.4.2 Imitation Task

9 To quantify imitation performance, we extracted participant's movement kinematics exhibited  
10 on each imitation trial. The start of the movement was defined as the time the centre of the cursor  
11 moved beyond the perimeter of the 'home' position, and end was calculated when the participant  
12 clicked on the lower-button on the stylus. For each trial, the 2-dimensional displacement data sampled  
13 (85 Hz) from the graphics tablet were filtered using a low pass 4<sup>th</sup> order autoregressive filter with a 8  
14 Hz cut-off. The filtered data were differentiated using a central difference algorithm to obtain  
15 velocity. A MATLAB routine extracted the primary movement occurring in the x-axis and then  
16 returned the following dependent variables: movement time, peak velocity, and percentage-time-to-  
17 peak-velocity. Individual-participant means of these data were submitted to separate 4 Group (HF,  
18 RF, RF+E, CTL) x 3 Model (atypical; typical; constant velocity) mixed ANOVA. Significant main  
19 and/or interactions effects involving more than two means were analysed using Tukey HSD post-hoc  
20 procedure. Alpha was set at  $p < 0.05$ , and eta squared ( $\eta^2$ ) expressed the size of the effect.

### 22 **3.1 Results**

#### 24 3.2 Motor Training Task

25 For absolute constant error, there was no main effect of Group [ $F(2, 27) = .92, p > 0.05, \eta^2 =$   
26  $0.06$ ] or Group x Block interaction [ $F(8, 108) = .68, p > 0.05, \eta^2 = 0.03$ ] in the 3 x 5 ANOVA. A  
27 significant main effect of Block [ $F(4, 108) = 11.78, p < 0.01, \eta^2 = 0.29$ ] showed participants in the  
28 experimental groups modified movement timing accuracy across the 5 blocks of practice (see Fig.

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

6 For variability of error, there was no main effect of Group [ $F(2, 27) = 1.10, p > 0.05, \eta^2 =$   
7  $0.08$ ] or Group x Block interaction [ $F(8, 108) = .60, p > 0.05, \eta^2 = 0.03$ ] in the 3 x 5 ANOVA. A main  
8 effect of Block [ $F(4, 108) = 17.40, p < 0.01, \eta^2 = 0.38$ ] showed participants improved consistency  
9 across the 5 blocks of practice (Fig. C.2). ). Post-hoc tests showed consistency improved from block 1  
10 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  
11 4 by 230 ms ( $p < 0.01$ ) and from block 1 to block 5 by 245 ms ( $p < 0.01$ ). No significant changes  
12 occurred across blocks 2 to 5 ( $ps > 0.05$ ).

13 When KR was removed in the retention test, the 4 group ANCOVA revealed that the  
14 experimental groups were significantly more accurate [ $F(3, 35) = 5.36, p < 0.01, \eta^2 = 0.32$ ] and  
15 consistent [ $F(3, 35) = 5.71, p < 0.01, \eta^2 = 0.31$ ] than the control group. Post-hoc testing showed that  
16 in comparison to the control group, accuracy was greater in the HF group by 598 ms, the RF group by  
17 601 ms, and the RF+E group by 629 ms. For the variability, post-hoc testing showed that in  
18 comparison to the control group, consistency was greater in the HF group by 312 ms, the RF group by  
19 269 ms, and the RF+E group by 300 ms.

20

21 Insert Fig. C about here

22

### 23 3.3 Imitation Task

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

1 The RF+E group showed similar performance with movement time being 826 ms and 878 ms more  
2 accurate than the HF and CTL groups. Independent of group, a main effect for Model [ $F(2, 72) =$   
3  $83.23, p < 0.01, \eta^2 = 0.63$ ] indicated shorter and more accurate movement times were imitated after  
4 observing the atypical (2057 ms) and typical (2153 ms) velocity models, compared to the constant  
5 (2591 ms) velocity model ( $ps < 0.01$ ). These effects were associated with a main effect of Model [ $F$   
6  $(2, 72) = 128.92, p < 0.01, \eta^2 = 0.76$ ] where the magnitude of peak velocity was significantly greater  
7 imitating atypical (0.26 mm/ms) compared to typical (0.19 mm/ms) and constant (0.15 mm/ms)  
8 velocity models (all  $ps < 0.01$ ; Fig. D.2). A similar main effect of Model [ $F(2, 72) = 60.27, p < 0.01,$   
9  $\eta^2 = 0.63$ ] was evident for percentage-time-to-peak-velocity, which revealed peak velocity occurred  
10 earlier in the movement trajectory when imitating atypical (29 %), compared to typical (42 %) and  
11 constant (48 %) velocity models (all  $ps < 0.01$ ; Fig. D.3).

12  
13 Insert Fig. D about here

#### 14 15 **4.1 Discussion**

16  
17 Similar higher-order and lower-level processes underpin performance and learning during  
18 motor training and imitation learning (Bird & Heyes, 2005; Buccino, et al., 2004; Cross, et al., 2009;  
19 Hayes, Elliott, & Bennett, 2010; Hecht, et al., 2001). These processes are part of general purpose  
20 perceptual, motor and attentional systems (Bird, et al., 2007; Brass & Heyes, 2005), and thereby  
21 facilitate positive transfer from imitation to subsequent motor performance (Hecht, et al., 2001). In the  
22 current study, we further examined whether higher-order processes developed using reduced-  
23 frequency feedback procedures in motor training transfer to imitation. The results from motor training  
24 indicated the experimental groups were more accurate and consistent at performing the timing goal  
25 than the control group. The finding of similar performance effects for the reduced-frequency and  
26 high-frequency KR groups is consistent with previous studies (Schmidt, et al., 1989; Swinnen, 1990;  
27 Winstein & Schmidt, 1990). Indeed, no difference between the groups in an immediate retention test  
28 would be expected because the beneficial effects of reduced frequency KR are not typically observed

1 until performance is measured in a 24-hour delayed retention test (Schmidt, et al., 1989; Swinnen,  
2 1990; Winstein & Schmidt, 1990). This does not mean that higher-order cognitive processes  
3 associated with representing movement time were not developed by the reduced-frequency KR  
4 protocols. Indeed, the main effect of group for movement time in the subsequent imitation phase  
5 showed the reduced frequency KR groups exhibited a performance advantage compared to the two  
6 other groups. Specifically, the reduced frequency KR groups outperformed the high-frequency KR  
7 and control groups by an average of ~800 ms, which resulted in movement times that were on average  
8 ~154 ms away from the model time goal of 1700 ms. The finding of such an advantage for both  
9 reduced-frequency KR groups, combined with evidence of similar performance in motor training,  
10 indicates the group that did not receive explicit instructions to perform error-detection and correction  
11 procedures on no KR trials must have done so via self-generation. The lack of difference between the  
12 high frequency KR and control groups indicates these higher-order cognitive processes were not  
13 effectively acquired, and subsequently transferred in imitation, when participants were able to rely on  
14 KR to correct their motor response between trials in motor training (Salmoni, et al., 1984; Swinnen,  
15 1990).

16 As predicted, the frequency of KR received during motor training did not modulate or  
17 attenuate the imitation of biological motion kinematics with all groups exhibiting a higher magnitude  
18 of peak velocity, which occurred earlier in the movement trajectory, after imitating the atypical  
19 compared to typical and constant velocity models. These effects are consistent with our previous work  
20 that also showed accurate imitation of atypical biological motion was not attenuated by the presence  
21 of spatially distracting end-state goals (Hayes, et al., 2016). Given that atypical biological motion  
22 kinematics were not already part of an existing motor repertoire (Hayes, et al., 2016; Hayes, et al.,  
23 2014), the representation of these kinematics most likely involved lower-level sensorimotor processes  
24 (Brass, Bekkering, Wohlschlaeger, & Prinz, 2000; Heyes, 2001; Iacoboni, 2005; Kilner, Hamilton, &  
25 Blakemore, 2007; Prinz, 1997) as opposed to being imitated via a semantic coding route where the  
26 observed kinematics are recalled from memory (Rumiati, Carmo, & Corradi-Dell'Acqua, 2009).  
27 Whilst this supports the idea that visual features of an action are mapped directly to motor features  
28 (Heyes, 2001), it is important to bear in mind that the representation of biological movement

1 kinematics was not achieved at the expense of performance outcome (i.e., both reduced-frequency  
2 groups exhibiting more accurate movement time). The implication is that although the interplay  
3 between lower-level and higher-order systems during imitation are distinct, the processes are  
4 complementary and regulated based on the action context and experience.

5         Complementarity in these processes is consistent with the suggestion that multiple routes  
6 underpin imitation (Bekkering, Wohlschlaeger, & Gattis, 2000; Buxbaum & Kalénine, 2010;  
7 Hamilton, 2008, 2014; Heyes, 2011; Rumiati, et al., 2009; Rumiati, Papeo, & Corradi-Dell'Acqua,  
8 2010). An observed stimulus is represented in a hierarchical fashion based on rationality and social  
9 cues, goals, kinematics, and muscle activity (Hamilton, 2014). For example, the kinematic features  
10 (i.e., atypical biological motion in the present study) are suggested to be coded via visual areas  
11 (middle temporal gyrus; superior temporal sulcus) and inferior frontal gyrus (Hamilton & Grafton,  
12 2007; Kilner, Neal, Weiskopf, Friston, & Frith, 2009) in the perception-action system, whereas the  
13 goal of an action (e.g., grasping an ear) is processed via a parietal (inferior parietal lobule; anterior  
14 intraparietal sulcus) network. We suggest that an area in the frontal cortex, which provides input and  
15 control to the perception-action system during imitation (Buccino, et al., 2004; Burke, et al., 2010; de  
16 Lange, Spronk, Willems, Toni, & Bekkering, 2008; Wang & Hamilton, 2014), could have  
17 underpinned the performance advantage observed here for the reduced-frequency KR groups.  
18 Specifically, dorsal lateral pre-frontal cortex, which is active between learning trials during imitation  
19 (Buccino, et al., 2004), and associated with response selection (Rowe, Toni, Josephs, Frackowiak, &  
20 Passingham, 2000) and action-prediction error processing during imitation learning (Burke, et al.,  
21 2010), could have provided the means to transfer the temporal goal learned during motor training.

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

28

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## Figure Captions

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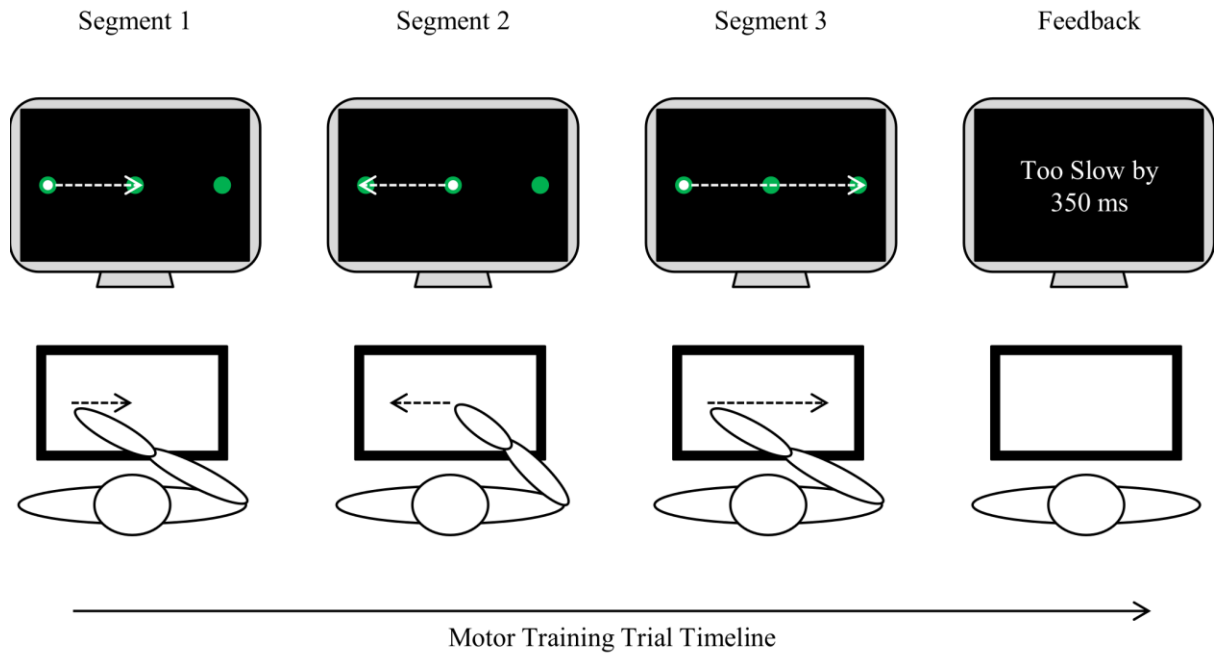
**Fig. A.1** A schematic representation of the laboratory/experimental set-up for the motor training task. The white circle represents the motion of a participant's movement. The three-segment movement sequence is depicted by the arrows in segment 1 (start target to centre target), segment 2 (centre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

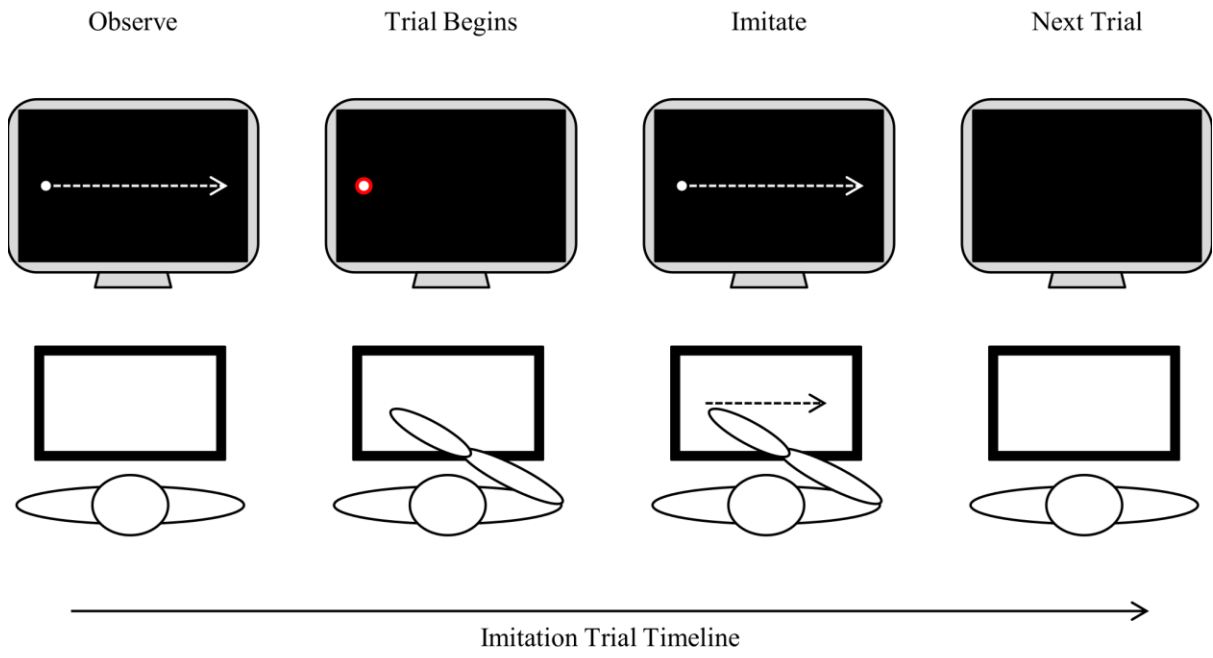
**Fig. C** Mean absolute constant error **(C.1)** and variable error **(C.2)** (error bars represent standard error of the mean) presented as a function of Group and Phase.

**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).

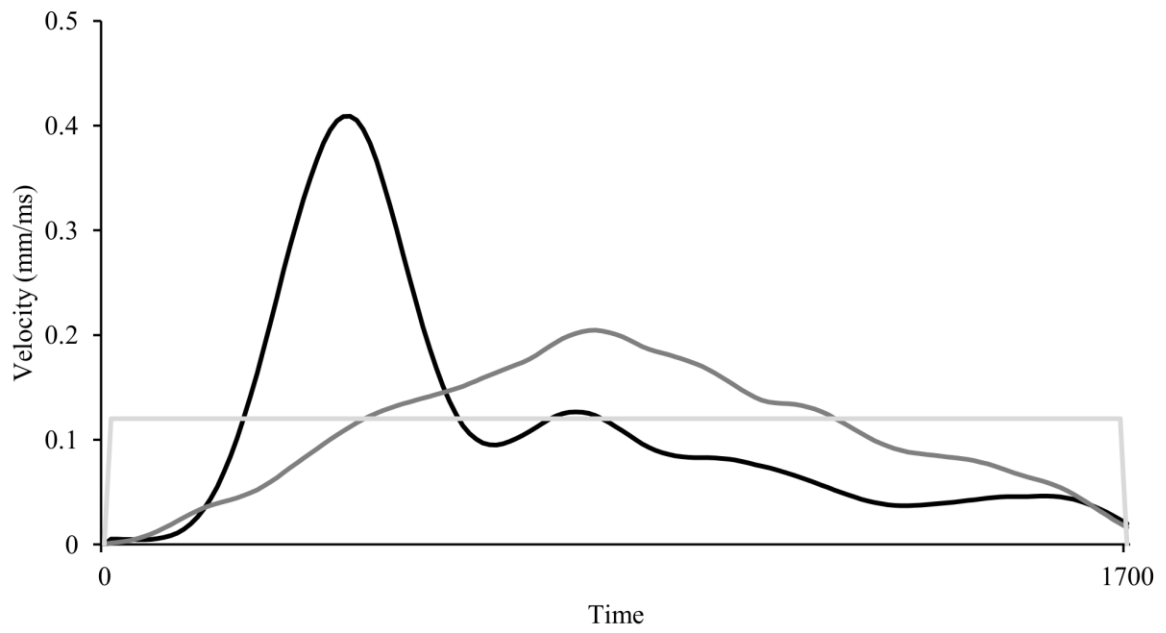
A.1



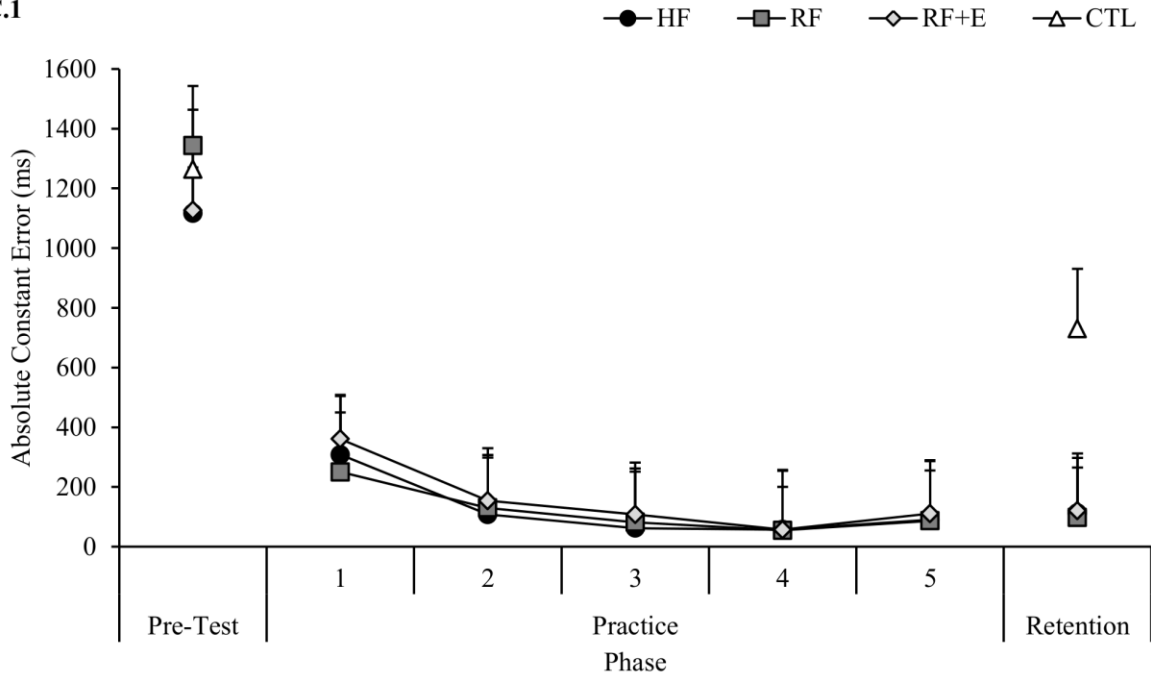
**B.1**



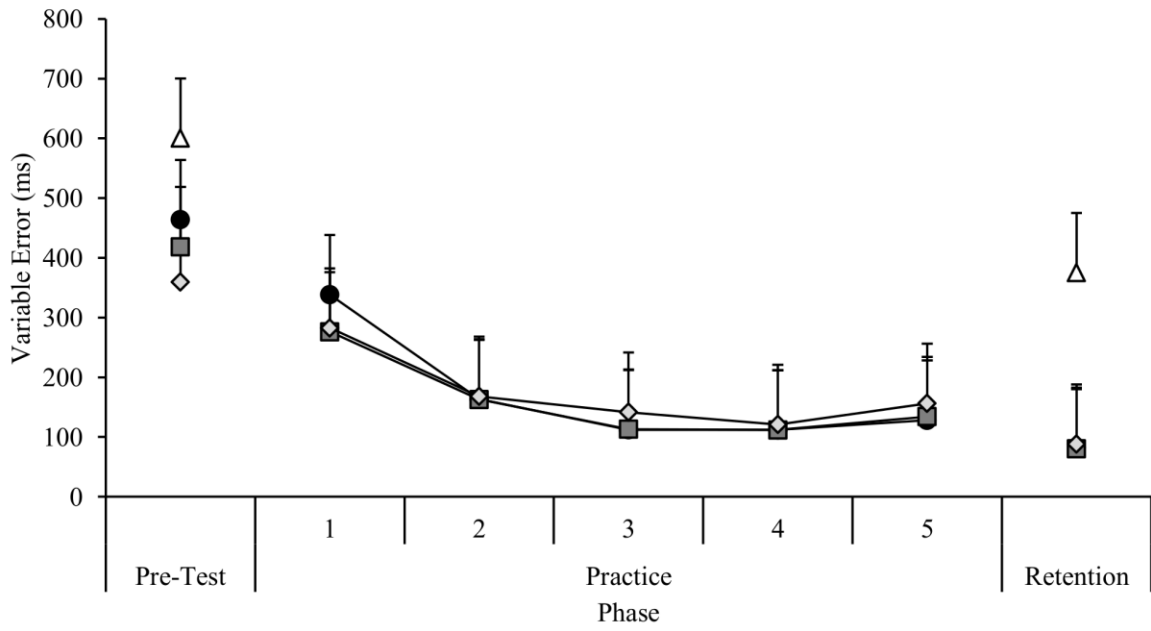
**B.2**



C.1

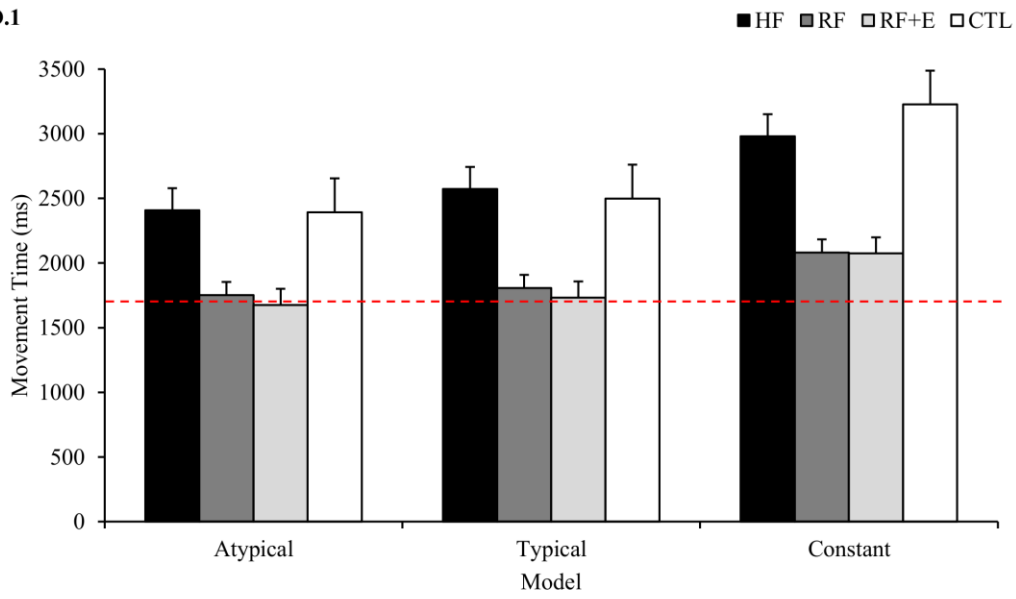


C.2

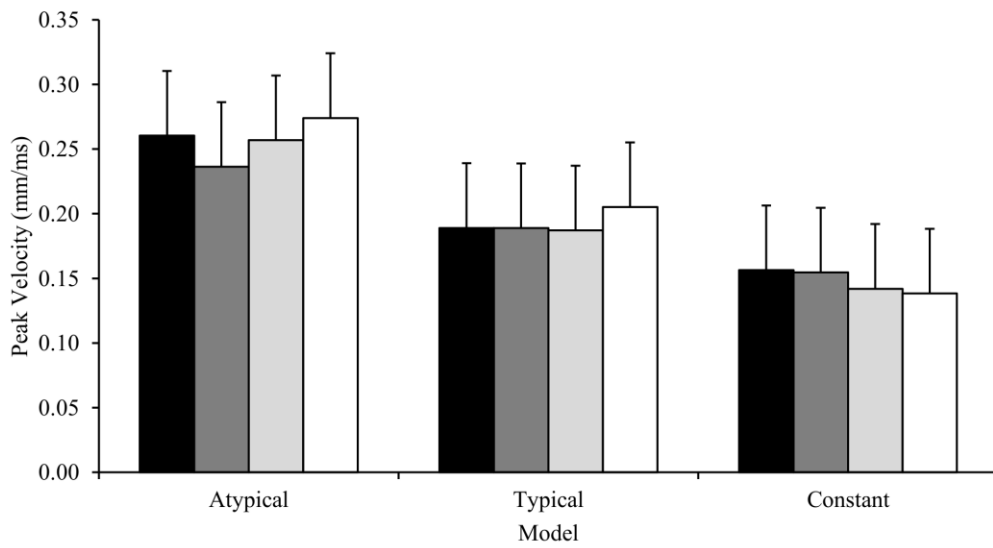




**D.1**



**D.2**



**D.3**

