



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 whilst all groups imitated biological motion kinematics, the two experimental reduced-frequency KR groups were on average ~800 ms 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.

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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 (e.g., move from target to home in a certain time) influences offline

planning (i.e., error correction between trials) processes during motor training (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). In seminal work, KR frequency was examined during the acquisition (Schmidt, Young, Swinnen, & Shapiro, 1989; Winstein & Schmidt, 1990) and imitation (Badets & Blandin, 2004) of motor timing tasks such that 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.

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Confirmation of inter-trial processing during motor learning is found by presenting KR instantaneously to learners after a motor response so that they have limited time for 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. However, motor learning was attenuated when the interpolated activity was directed towards another person. The attenuation indicated 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, evaluating, 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; Wohlschlagler, Gattis, & Bekkering, 2003). In previous work, 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). Importantly, in these studies we 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 complementary 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 imi-

tation. 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 also enables presentation of a constant velocity control stimulus without generating conflicting perception of belief (see below). The three models had the same overall movement time (1700 ms) as the movement learned during motor training, but displayed distinctly different amplitude 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 at 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 movement time in the motor learning task facilitate transfer to the imitation task, the two groups provided with reduced-frequency 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 complementary 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).

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