Motion trajectory information and agency influence motor learning during observational practice

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Abstract

Fundamental to performing actions is the acquisition of motor behaviours. We examined if motor learning, through observational practice, occurs by viewing an agent displaying naturalistic or constant velocity, and whether motion trajectory, as opposed to end-state, information is required. We also investigated if observational practice is sensitive to belief regarding the origin of an agent. Participants had to learn a novel movement sequence timing task, which required upper-limb movements to a series of targets within a pre-specified absolute and relative time goal. Experiment 1 showed learning after viewing naturalistic and constant velocity, but not end-state information. For Experiment 2, in addition to learning the movement sequence, participants observed a series of movement stimuli that were either the trained or new sequences and asked to rate their confidence on whether the observed sequence was the same or different to observational practice. The results indicated agency belief modulates how naturalistic and constant velocity is coded. This indicated the processes associated with belief are part of an interpretative predictive coding system where the association between belief and observed motion is determined. When motion is constant velocity, or believed to be computer-generated, coding occurs through top-down processes. When motion is naturalistic velocity, and believed to be human-generated, it is most likely coded by gaining access to bottom-up sensorimotor processes in the action-observation network.

Keywords: observational practice; naturalistic velocity; constant velocity; end-state goals; belief; top-down modulation.

PsycINFO classification: 2300, 2323, 2330, 2343

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1.   Introduction

Fundamental to performing goal-directed actions is precise spatio-temporal parameterisation, movement sequencing and sequence knowledge. The representation and acquisition of these processes occurs during observational practice (Bird & Heyes, 2005; Vogt, 1995). This visuomotor learning takes place during a training period of pure stimulus observation. As such, no overt physical practice is performed during training, resulting in a learner not receiving response-produced feedback (reafference). This process is said to occur within the action-observation network [AON] (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009), where neurons respond in a similar manner during observation and execution (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Linked to this network is the superior temporal sulcus which provides input to the fronto-parietal cortices (Grossman et al., 2000) where the spatial-temporal characteristics (i.e., kinematics) and action-goal (Hamilton, 2008; Iacoboni, 2005) of the observed stimulus are processed.

The processing of kinematics is partly based on the perception of biological motion, as indicated by a motor interference effect during interpersonal execution-observation (Kilner, Paulignan, & Blakemore, 2003). Here, then, participants exhibited increased variability in an intended movement whilst observing an incongruent movement performed by a human (naturalistic velocity; biological motion), not a robot (constant velocity; nonbiological motion), model. In this context, it is important to note that naturalistic velocity is different to constant velocity because it contains task specific changes in acceleration based on human anatomy and the external constraints (gravity; direction; target size) associated with a particular task. These factors combined underpin a velocity profile that is bell-shaped (Flash & Hogan, 1985), which is reflective of typical goal-directed aiming movements. Thus, motor interference is suggested to occur from the automatic activation of motor codes that directly respond to the naturalistic velocity characteristics of the observed biological motion (Blakemore & Frith, 2005). This automatic activation is commonly referred to as bottom-up processing, which involves the preferential treatment of information directly available via the stimulation of sensory receptors (Teufel, Fletcher, & Davis, 2010), and is linked to the fronto-

parietal mirror region where stimuli consistent with these biological laws of motion are processed (Casile et al., 2010; Dayan et al., 2007). Indeed, it is the coding of this biological motion that is also suggested to drive automatic imitation (Brass, Bekkering, & Prinz, 2001), voluntary imitation (Wild, Poliakoff, Jerrison, & Gowen, 2010) and observational practice (Hayes, Roberts, Elliott, & Bennett, 2014; Hayes, Timmis, & Bennett, 2009).

Although there has been reported differences in contagion when viewing biological and nonbiological motion, the AON also is activated by (Cross et al., 2011; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Ramsey & Hamilton, 2010) and adapts to (Press, Gillmeister, & Heyes, 2007) nonbiological motion. In the case of motor contagion, interference occurs when a non-human agent (a ball) displays both naturalistic and constant velocity motion (Kilner, Hamilton, & Blakemore, 2007). Unlike naturalistic velocity, which is suggested to directly generate contagion via the automatic activation of motor codes, constant velocity displayed via a non-human agent is suggested to be processed by individuals forming an interpretation, or predicting, the agency, and action goal, based on prior knowledge (Kilner, et al., 2007; Stanley, Gowen, & Miall, 2007, 2010). This effect can be explained by modulation through top-down processes. 'Top-down' processing depends on an observer's knowledge and expectation of a situation (Teufel et al., 2010), and may be underpinned by contextual factors such as motion trajectory (Tremoulet & Feldman, 2000), belief (Stanley, et al., 2007) and social context (Hogeveen & Obhi, 2013). Another top-down process that influences motion coding is goal interpretation and assignment (Bekkering, Gattis, Wohlschläger, 2000) whereby an end-state goal organises the motor response during imitation. For example, an end-state goal (grasping the right ear) might be achieved using a motor response (right-arm) that differs from the observed movement (left-arm). Furthermore, there is some suggestion that the aforementioned motor interference effects are influenced by the perceived end-state goal (Stanley, et al., 2007), as well as information contained within the movement trajectory (Kilner et al. 2007).

The consensus therefore is that the AON involves regions that perform specialised processing, with the contribution being dependent on the nature of the observed stimulus

and interpretation of agency (Liepelt & Brass, 2010; Press, Gillmeister, & Heyes, 2006; Stanley, et al., 2007; Stenzel et al., 2012). To date these factors have been studied during interpersonal execution-observation, voluntary imitation and automatic imitation tasks where visual information is processed in combination with efferent and afferent sensory information from the peripheral motor system. This sensorimotor experience underpins enhanced action perception in experts (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005), and facilitates response times during action-observation (Catmur, Walsh, & Heyes, 2007). It is therefore important to understand if the coding of biological and nonbiological stimulus motion information occurs during observational practice in the absence of reafference.

2.   Experiment 1

To examine biological (naturalistic velocity) and nonbiological (constant velocity) motion trajectory information during observational practice we had participants acquire a 5 segment movement sequence timing task. The goal was to learn how to perform the absolute, and relative, timing parameters associated with the sequence. Absolute time is the total time required to successfully perform the 5 segments. Relative timing is the proportion of time required to successfully perform each segment within the sequence. Because the goal was to learn the timing parameters, we displayed the spatial position of the 5 segment end-points on the computer monitor. By keeping the spatial locations constant, participants in the experimental conditions observed a non-human agent (a white cursor) perform the 5 segment movement sequence with a motion trajectory that displayed naturalistic or constant velocity.

Given the AON is activated by naturalistic and constant velocity it is not possible to make specific predictions regarding the learning effects after observing these two motion trajectories. However, any additional benefit of observing naturalistic velocity motion over constant velocity would depend on the relative contribution of bottom-up and top-down coding processes during observational practice. We do predict however those participants exposed to motion trajectory information will learn the sequence timing more accurately than

the control participants who did not perform observational practice. Finally, to further examine the effects of motion trajectory information, we used a third control model (end-state model) that displayed the relative, and absolute, timing parameters, but here motion trajectory information was removed so that the model appeared as a sequence of 5 flashes presented at the spatial segment end-points. If motion trajectory information is processed during observational practice the groups that observed naturalistic and constant velocity will learn timing parameters more accurately than those who observed the end-state control model.

2.1   Method

2.1.1   Participants

Data were recorded from forty-eight volunteers (aged 18 to 21 years; three participants were removed from the analyses due to missing data from technical errors). All participants had normal or corrected-to-normal vision, and gave informed consent. The experiment was approved by the local ethics committee.

2.1.2   Experimental procedures

The apparatus was the same as that used in our lab for a previous experiment (Hayes, Elliott, & Bennett, 2013). The current experiment had a pre-test, observational practice phase and post-test (Figure 1A). Before the pre-test, all volunteers received information regarding the spatial layout of the movement sequence pattern and the two timing goals (Figure 1B). Here, participants were informed that they were required to successfully navigate a mouse so that a cursor moved between each of the pre-defined target end-points. In the event of a spatial error involving the cursor not reaching a target, an error message was displayed on the monitor and the participant was required to repeat the trial. Also, by keeping the spatial segment end-points controlled the volunteers were instructed the primary goal was to learn the absolute time goal and the relative time goal. The absolute time goal required participants to control the mouse so that the cursor left the

start position, passed through five segments and terminated (pressing the right mouse button) within the final target (Figure 1B) in a time of 4625 ms. The relative timing goal required participants to perform the absolute time goal by ensuring the segment proportions met the criterion structure: 13% (segment 1; 601 ms), 32% (segment 2; 1480 ms), 14% (segment 3; 648 ms,), 17% (segment 4; 786 ms) and 24% (segment 5; 1110 ms).

Insert Figure 1 about here

We created three models: biological motion, nonbiological motion, and end-state. A biological motion model was created by an experimenter who practised the sequence until the criterion time goals were performed accurately. The time-series data from a representative trial were used to generate the model. These data were then presented on the monitor, and as such displayed both vertical (y-axis) (black trace; Figure 2A) and horizontal (x-axis) (black trace; Figure 2B) motion. This was important in order to ensure high fidelity replication of biological motion, which does not typically comprise movement in a single axis.

Insert Figure 2 about here

A nonbiological motion model displaying constant velocity within each segment was generated using the amplitude and time constraints. The displacement time-series data for the model had the same time goals but included motion only in the primary direction (e.g., y-axis of segment 1) (grey trace; Figure 2A), and thus without any deviations in the perpendicular axis (e.g., x-axis of segment 1) (grey trace; Figure 2B). Therefore, the nonbiological model comprised both biologically implausible velocity and spatial trajectory. An end-state model was created that had the same time parameters, but only displayed the single-point light as it entered and left each target (a series of flashes). The flashes were

displayed for 35 ms to provide visual information about the cursor position, and thus absolute and relative timing, but not velocity (Snowden & Braddick, 1991).

Prior to observational practice, participants were randomly allocated to a biological motion group (n = 10), nonbiological motion group (n = 12), end-state group (n = 11) and a control group (n = 12). Experimental participants were instructed the goal was to learn the two time goals by performing observational practice. No instructions were provided as to the agency of the models. The control group received no instructions and sat in front of a monitor that was switched off.

Following observational practice, participants performed a post-test identical to the pre-test. The experimental groups performed the movement sequence according to the time goals, but with the instruction to imitate what they had observed from the model. The control group was instructed to perform the task according to the time goals.

2.1.3 Analysis

Total movement time and segment movement times were extracted from the five trials performed during pre-test and post-test. To quantify learning of the absolute time goal, Total Error was calculated: $\sqrt{CE^2 + VE^2}$, where CE (constant error) is a measure of response bias and VE (variable error) is a measure of response variability (the data for Total Error in Experiment 1 and 2 are not presented because the analyses did not reveal any significant effects (this is not that unusual in movement sequence learning tasks; see Blandin & Proteau, 2000). Learning of the relative time goal was quantified by comparing actual and required relative timing of each segment to derive a composite Relative Timing Error score (%) (Wulf & Schmidt, 1989): $|R_{seg1} - .13_{seg1}| + |R_{seg2} - .32_{seg2}| + |R_{seg3} - .14_{seg3}| + |R_{seg4} - .17_{seg4}| + |R_{seg5} - .24_{seg5}|$: where R_{seg} = (the absolute segment movement time (ms) for a specific segment (e.g., $_{seg1}$) within a trial / total movement time (ms) of that trial). This proportion is subtracted from the criterion proportion for that segment. For example, if a participant performed a trial that had an overall movement of 5000 ms, and the time taken to perform segment 1 was 800 ms, the calculation for this segment within the overall algorithm is:

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$|(800/5000)_{seg1} - .13_{seg1}| = .03$. This is then carried out for each segment and a total composite error score is calculated. A score of 0 would indicate a participant had performed the relative time goal perfectly.

Post-test data for Relative Timing Error were analysed using analysis of covariance (ANCOVA) with pre-test as a covariate. This approach statistically minimises the impact of initial between-group differences in performance and, with respect to pre-test to post-test motor learning, it allows the post-test performance of the experimental groups to be compared to the control group that might realise some change in performance due to repeated testing. When significant effects were present, we determined which movement segments were most affected by the manipulation by adopting the same statistical approach for each individual segment. All significant effects were decomposed using Newman-Keuls post hoc procedures ($p < .05$). Effect sizes (η_p^2) are reported for all significant effects, as well as important non-significant effects.

2.2   Results and Discussion

For Relative Timing Error, there was a significant effect of group, $F(3, 40) = 7.82$, $p < .001$, $\eta_p^2 = .37$. Post hoc analysis revealed the biological motion (M = 30, $SE_M = 4$) and nonbiological motion (M = 32, $SE_M = 3$) groups were significantly more accurate at performing the relative timing pattern than the end-state (M = 44, $SE_M = 3$) and control (M = 49, $SE_M = 3$) groups (ps < .05). There was no significant difference between the biological motion and nonbiological groups, nor between the end-state and control groups (ps > .05) (Figure 3A).

Figure 3 about here

To determine where in the movement sequence Relative Timing Error effects were most pronounced, we conducted follow-up ANCOVA on relative timing of each movement

segment. There was a significant effect of group for segment 1, $F(3, 40) = 7.99$, $p < .001$, η_p^2 = .38, segment 2, $F(3, 40) = 6.47$, $p < .01$, $\eta_p^2 = .33$ and segment 5, $F(3, 40) = 5.17$, $p < .01$, $\eta_p^2 = .28$ (Figure 3B). Post hoc analyses revealed a similar pattern of results for Relative Timing Error with the biological motion and nonbiological motion groups being significantly more accurate than the end-state and control groups (ps < .05). There were no further significant differences between groups (ps > .05). .

The results showed that observing biological or nonbiological motion trajectory information facilitates motor learning in the absence of reafference. Indeed, both groups exhibited relative timing closer to the model than the end-state control group where trajectory information was experimentally removed. The learning effect occurred in the initial (1, 2) and late (5) segments, which indicates the coding of segment-specific motion information. This effect is consistent with the imitation of unfamiliar sequences (Agam, Bullock, & Sekuler, 2005) which report primacy (e.g., initial) and recency (e.g., late) effects (Agam, Galperin, Gold, & Sekuler, 2007). This effect also is common during perception of motion (Blake, Cepeda, & Hiris, 1997), and is underpinned by a neural system that controls the acquisition of a sequence, by coding the components (segments) within the sequence based on a memory storage mechanism and practice. Although we have suggested (Hayes, Elliott, Andrew, Roberts, & Bennett, 2012; Hayes, et al., 2014; Hayes, et al., 2009) motor sequence timing is learned by processing information contained in trajectory of the model, the removal of continuous motion in the end-state control model experimentally confirmed that relative timing was learned by processing stimulus motion. This is consistent with work from perceptual-psychophysics where the optimal detection of velocity (Snowden & Braddick, 1991) or time duration (Brown, 1995) is associated with integrating motion information over space and time. Moreover, processing motion trajectory information also provides contextual information regarding the movement goal (Gergely, Nádasdy, Csibra, & Biro, 1995; Scholl & Tremoulet, 2000; Tremoulet & Feldman, 2000).

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Although the coding of biological motion involves bottom-up processing of visual information (via superior temporal sulcus linked to AON; Grossman et al. 2000) leading to automatic sensorimotor activity (Brass et al., 2001), in certain contexts this is influenced by the intentionality attributed to an agent. Previously, it was suggested that observers predict an action displayed by a non-human agent by modifying their 'intentional stance' (Dennett, 1989) so that it is believed to possess intention and desires (Stanley, et al., 2007). That is, the bottom-up sensorimotor processes associated with stimulus motion become modulated by the top-down interpretation of stimulus agency (Stanley, et al., 2010). It is this process that is thought to regulate motor behaviour during automatic imitation (Liepelt & Brass, 2010), action co-representation (Stenzel, et al., 2012) and interpersonal execution-observation (Stanley, et al., 2007). In relation to our findings, the implication is that although bottom-up sensorimotor processes most likely code naturalistic velocity (Bird, Osman, Saggerson, & Heyes, 2005; Brass, et al., 2001; Kilner, et al., 2007), top-down processes may have mediated the coding of constant velocity by contextualising the non-human agent model as being a human movement (Kilner, et al., 2007). In Experiment 2 we manipulated belief regarding the agency of observed stimulus motion to examine the mediating role of top-down processes on bottom-up processes.

3.   **Experiment 2**

To engender intentionality via belief, participants were instructed prior to observation that the non-human agent model was either human or computer-generated (Stanley, et al., 2007). This resulted in a 2 x 2 factorial combination of model (biological or nonbiological) and agency instruction (human or computer). In addition to measuring relative timing error, we examined the processes undertaken during observational practice by using a recognition test that quantifies awareness of sequence knowledge (Shanks & Johnstone, 1999; Shanks, Wilkinson, & Channon, 2003). This was inspired by use of a similar recognition test to examine sequence awareness following observational practice (Bird & Heyes, 2005; Bird, et

al., 2005). High sequence awareness, and thus good recognition, is suggested to indicate explicit sequence knowledge developed through top-down processes, whereas low awareness indicates implicit sequence knowledge developed through bottom-up sensorimotor processes. Importantly, in addition to significant differences in sequence knowledge, and compared to the control group, the observation and execution groups (see Bird et al., 2005) demonstrated similar levels of sequence acquisition, which is essential when examining the underpinning processes.

As per Experiment 1, we expected the experimental groups to show similar levels of relative timing acquisition, which would result in them being significantly more accurate than a control group. We also expected implicit sequence knowledge to develop, indicating a greater contribution of bottom-up processes, when an agent displaying naturalistic velocity is believed to be human-generated (Bird & Heyes, 2005; Liepelt & Brass, 2010). On the other hand, explicit sequence knowledge, indicating additional top-down processes (Bird & Heyes, 2005), was expected to develop when an agent displaying constant velocity is believed to be computer-generated (Stanley, et al., 2007). Of greater importance to understanding top-down effects during observational practice are the conditions where a mismatch occurs between agency instruction (e.g., human) and motion type (e.g., constant velocity). Here, it was predicted that if top-down processes primarily modulate bottom-up processes, implicit sequence knowledge would develop when an agent displaying constant velocity is believed to be human-generated, and explicit sequence knowledge would develop when the agent displaying naturalistic velocity is believed to computer-generated.

3.2   Method

3.2.1   Participants

A different cohort of sixty volunteers (aged 18 to 21 years) participated. All participants had normal or corrected-to-normal vision and gave written informed consent.

3.2.2   Experimental Procedures

The apparatus, task and model stimuli were identical to Experiment 1. Prior to instructions the participants were randomly assigned to one of four groups (N = 12 per group) that differed in respect of stimulus (biological motion, nonbiological motion) and agency instruction (human; computer). A further 12 participants formed a control group. To ensure the agency instructions were not confounded by prior knowledge of the movement sequence we eliminated the pre-test phase (Figure 4). Only instructions regarding the agency (Stanley, et al., 2007) of the model stimulus differed between the experimental groups. All participants confirmed they understood the instructions.

Insert Figure 4 about here

Immediately following the motor post-test, the experimental groups performed a recognition test adapted from Bird and colleagues (Bird & Heyes, 2005; Bird, et al., 2005) that was originally used to examine implicit and explicit sequence knowledge during a stimulus-response reaction-time task. Our test was used to examine the representation of motion information during stimulus-observation. Participants observed a series of 5 segment sequence models that displayed the same or different motion to that observed during observational practice. After each observation, participants gave a forced-choice Likert-scale rating regarding whether the model was the "same or different" than the model previously observed in observational practice. Ratings were given on a scale from 1 to 6: 1 = certain I have not seen the sequence before; 2 = fairly certain I have not seen the sequence before; 3 = guess I have not seen the sequence before; 4 = guess I have seen the sequence before; 5 = fairly certain I have seen the sequence before; 6 = certain I have seen the sequence before. Participants received 12 recognition trials that were presented in a random order: 4 trained, 4 new and 4 filler. The trained trials corresponded with the model stimuli viewed during observational practice (e.g., biological motion), whereas the new trials featured the

alternative motion characteristics (e.g., nonbiological motion), and thus identical time goals. These sequences were chosen because our primary aim in this experiment was associated with stimulus-motion processing, as opposed to the relative timing goal. Thus, any differences between the groups in the recognition test were expected to be specific to the representation of stimulus-motion trajectories. This procedure ensured the recognition test measured the processes involved in coding motion trajectory information rather than the timing goals. If recognised, the biological motion groups should rate the biological motion model as the trained sequence and the nonbiological motion model as the new sequence, and the reverse would be true for the nonbiological motion groups. The filler trials were added to limit participants from making simple judgments between trained and new trials, and as such, control for response biases based on comparisons of sequences between recognition trials. With the addition of filler trials participants are more likely to make comparisons between the stimulus presented in the recognition test and the previously learned stimulus. Compared to the trained sequence, the filler trials featured the same origin of motion (biological or nonbiological) and similar relative times, although these were ordered differently [17% (segment 1), 25% (segment 2), 14% (segment 3), 33% (segment 4), 11% (segment 5)]. Therefore, though the origin of motion information corresponded with the trained sequence, both the underlying movement kinematics and relative timing structure were different.

After the recognition test, participants were issued a Likert-scale (adapted from Longo, Kosobud, and Bertenthal (2008)) to assess agency belief. They were asked two questions associated with whether they believed "the stimuli you previously observed were generated by a human?" and "the stimuli you previously observed were generated by a computer?" (NB. order of questions was counterbalanced within each group). They rated their agreement using a 7-point Likert scale (upper anchor 3 = strongly agreed, lower anchor –3 = strongly disagreed, 0 = neither agreed nor disagreed).

3.2.3   Analysis

Relative Timing Error was analysed using a one-way between-group analysis of variance (ANOVA). Similar to Experiment 1, when Relative Timing Error effects were present, we conducted ANOVAs on individual segments to further assess the acquisition of relative timing.

Because the recognition test was not applicable to the control group, recognition performance was evaluated via a factorial design. To this end, we calculated the median of each individual's scores within a condition as a measure of central tendency. To compare recognition performance when relative timing of the stimuli was equal, the median data were submitted to a 2 Motion (biological motion, nonbiological motion) x 2 Agency Instruction (human, computer) x 2 Sequence (trained, new) mixed-design ANOVA. Significant effects featuring more than two means were decomposed via Tukey HSD post hoc procedures.

The Shapiro-Wilk test of normality for the agency belief Likert-scale data indicated a non-normal distribution for all the groups ($ps < .05$). Furthermore, the biological motion + human agency group exhibited significant skewness ($z = -2.35$). Thus, a series of non-parametric Wilcoxon signed-rank tests were conducted to compare the level of agreement/disagreement for each individual group (a Bonferroni correction was applied to alpha to control for multiple testing – the adjusted p was .013). These comparisons determined if the responses to each of the two questions were complementary such that agreement with one statement would be contrasted by disagreement in another. In the event participants did not follow agency instructions, we would anticipate little or no difference between the two ratings.

3.3   Results and Discussion

For Relative Timing Error, there was a significant effect of group, $F(4, 55) = 22.13$, $p < .001$, $\eta_p^2 = .62$ (Figure 5A). Post hoc analysis indicated the experimental groups [biological motion + human agency (M = 28.1, SE$_M$ = 2.23), biological motion + computer agency (M =

28.4, SE_M = 2.54), nonbiological motion + human agency (M = 29.3, SE_M = 2.16),

nonbiological motion + computer agency (M = 25.5, SE_M = 2.88)] were significantly more

accurate than the control group (M = 51.3, SE_M = 0.96). As per Experiment 1, the individual

segment analysis indicated (Figure 5B) the experimental groups outperformed the control

group in Segment 1, $F(4, 55) = 49.99$, $p < .001$, $\eta_p^2 = .78$; Segment 2, $F(4, 55) = 7.38$, $p <$

.001, $\eta_p^2 = .35$, and Segment 5, $F(4, 55) = 16.48$, $p < .001$, $\eta_p^2 = .71$).

Insert Figure 5 about here

For recognition performance when the stimuli had equal relative timing, there was a

significant main effect of sequence, $F(1, 44) = 583.15$, $p < .001$, $\eta_p^2 = .93$, indicating

increased certainty of having seen the trained compared to the new sequences. There was a

significant interaction between sequence and motion, $F(1, 44) = 6.50$, $p < .05$, $\eta_p^2 = .13$, and

a significant interaction between sequence and agency, $F(1, 44) = 14.15$, $p < .001$, $\eta_p^2 = .24$.

These effects were superseded by a three-way interaction between motion, agency and

sequence $F(1, 44) = 4.26$, $p < .05$, $\eta_p^2 = .09$ (Figure 6). Post hoc analysis showed that

significantly lower median ratings of trained sequences were given by the biological motion +

human agency group compared to the biological motion + computer agency group and

nonbiological motion + computer agency group (p < .05). Also, significantly higher median

ratings of new sequences were given by the biological motion + human agency group

compared to all other groups (p < .05). Combined, the median ratings given for the trained

and new sequences by the biological motion + human agency group indicate greater

uncertainty.[1]

Insert Figure 6 about here

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Likert-scale data on belief rating indicated participants in the biological motion + human agency group more strongly agreed (Mdn = 3.0, IQR = 1.0) than disagreed (Mdn = -2.5, IQR = 1.3) that the stimuli were human-generated, T = 0, z = -2.99, p < .001 (Figure 7). A similar but opposite finding was evident for the nonbiological motion + computer agency group, who more strongly agreed (Mdn = 3.0, IQR = 1.0) than disagreed (Mdn = -2.5, IQR = 1.3) that the stimuli were computer-generated, T = 0, z = -3.09, p < .005. The biological motion + computer agency group provided a mid-level score that showed a trend towards more agreement (Mdn = 3.0, IQR = 4.0), than disagreement (Mdn = -3.0, IQR = 4.3), in terms of the stimuli being computer-generated, T = 15, z = -1.95, p = .051. Finally, for the nonbiological motion + human agency group, there was no significant difference between ratings of agreement (Mdn = -1.5, IQR = 6.0) and disagreement (Mdn = 2.5, IQR = 6.0), T = 32, z = -.58, p > .05, suggesting neither agreed, nor disagreed, the stimuli were human-generated.

Insert Figure 7 about here

As predicted, and compared to the control group, the experimental groups learned relative timing by acquiring early (1, 2) and late (5) segments, which confirmed segment-specific motion trajectory information was coded (Agam, et al., 2007). This finding is important because although we expected no difference between the experimental groups, the results show the agency instructions did not interfere with the acquisition of timing (Shanks & Johnstone, 1999). As predicted (Bird et al. 2005), the recognition data indicated different levels of implicit and explicit sequence knowledge. Participants who had observed biological motion stimuli with a human agency instruction were less certain in the recognition of trained and new sequences compared to those who had observed biological or nonbiological motion stimuli with a computer-generated agency instruction. Lower certainty, and thus awareness, of trained and new sequences, is suggestive of the development of implicit sequence knowledge by the biological motion + human agency group (Bird & Heyes,

2005; Bird, et al., 2005), which is thought to result from a greater contribution of bottom-up sensorimotor processes (Stanley, et al., 2007). Conversely, higher certainty, and thus better awareness, exhibited by the nonbiological motion + computer agency group is consistent with the development of explicit sequence knowledge and a greater contribution of top-down processes (Bird, et al., 2005). The potential for agency instruction to impact upon sequence knowledge was confirmed by the belief rating data, which showed the agency instructions were believed by these two groups. Moreover, the biological motion + computer agency group developed explicit sequence knowledge which is consistent with the processing of biological motion being subject to top-down influences such as belief. Though there was only a close to significant level of agreement for the stimulus being computer-generated, there was no such agreement that the stimulus were human-generated. Interestingly, and contrary to our expectation, the recognition data for the nonbiological motion + human agency group indicated greater explicit than implicit sequence knowledge. In addition, the belief rating data for this group indicated neither agreement nor disagreement regarding agency. Thus, it would seem that a greater contribution of bottom-up stimulus processes does not occur when there is a specific mismatch between agency and motion.

4.   General Discussion

Experiment 1 confirmed that motor learning occurs following observation of a non-human agent displaying either naturalistic or constant velocity motion. Although learning was not found in the end-state condition, it is important to stress that information on absolute and relative timing was available in this model (Snowden & Braddick, 1991). Therefore, by manipulating the way temporal information was displayed, we confirmed motion trajectory information, and the processes that code it, underpin observational practice. These results extend upon previous findings by qualifying the conditions where humans learn motor skills by observing movement trajectories. For instance, relative timing has been shown to be learned by observing human (Badets, Blandin, & Shea, 2006) and non-human (Hayes, et al., 2012) agents displaying naturalistic velocity. Here, we showed that relative timing can be

learned by observing constant velocity. This finding also extends and complements work showing nonbiological motion is coded during interpersonal execution-observation (Kilner et al., 2007; Press et al., 2012; Stanley et al., 2007), and automatic imitation tasks (Press et al., 2007), where participants have the opportunity to adapt motor behaviour by processing reafferent sensorimotor information generated by overtly imitating the stimulus across successive trials.

During interpersonal execution-observation tasks it has been shown that interacting with a non-human agent (a ball) displaying naturalistic or constant velocity causes motor contagion (Kilner, et al., 2007). It has therefore been suggested the brain processes motion properties of both stimuli in a manner subject to top-down influences. This processing is reported to occur in an AON, including the anterior intraparietal cortex, which codes goal-directed movements of the human hand (Hamilton & Grafton, 2006) and non-human agents (a triangle) with constant velocity trajectories (Ramsey & Hamilton, 2010). These cerebral localizations were identified using repetition suppression of event-related fMRI. Specifically, a previously displayed action goal (e.g., identity of task object) resulted in lower cerebral blood flow in the parietal cortex following a repeated presentation of the same action goal. Alternatively, the repeated presentation of movement kinematics (e.g., precision or whole-hand grasp) resulted in suppression of the inferior frontal gyrus (Hamilton & Grafton, 2007). Based on these data, the hierarchical model of visual-motor control and action-understanding (Hamilton, 2008; Hamilton & Grafton, 2007) was developed, suggesting the action goal is coded via the parietal pathway and the movement kinematics are coded via the frontal pathway. With respect to the similar learning effects of naturalistic and constant velocity stimulus motion in Experiment 1, it is reasonable to suggest that these stimuli were coded via processes operating in the frontal pathway.

To further understand the top-down influences acting during observational practice, we conducted a second experiment that included a novel factorial combination of observed stimulus motion (biological motion, nonbiological motion) and agency instruction (human, computer). In addition to replicating the effects for learning relative timing, recognition test

data indicate that observing naturalistic or constant velocity led to different types of sequence knowledge depending on agency instruction, and thereby belief. The participants that received a human agency instruction and observed biological motion responded with more uncertainty to recognising trained and new sequences. This finding indicates that these participants developed a more implicit representation of sequence knowledge than those who received a computer agency instruction and/or observed nonbiological motion.

Interestingly, while this interpretation is consistent with most other work, we found somewhat larger differences between recognition of trained and new sequences (Bird et al., 2005; Shanks & Johnstone, 1999). This is most likely explained by differences in the recognition protocol adopted here and elsewhere. Typically, the recognition of trained and new sequences is coincident with physically performing the sequence, whereas the current study examined recognition independent of any concurrent sensorimotor reafference. Furthermore, the sequences adopted previously feature a higher number of movement segments (e.g., 12 items; Bird et al., 2005), which may have increased task complexity. By limiting sensorimotor processing during physical performance, and using a less complex task, participants here could have allocated more attention to the recognition task, thus resulting in better overall recognition performance.

The modulatory impact of agency on representing stimulus motion is consistent with a modulation in the contribution of bottom-up sensorimotor processes by a top-down mechanism (e.g., Bird & Heyes, 2005). With the stimuli observed in the current study, we suggest plausibility of matching observed stimulus motion with the agency instructions was most likely determined through a predictive coding mechanism (Kilner, 2011). Here, it is suggested that a prediction is made regarding the expected visual afference, which could conceivably be determined by agency beliefs, and then compared with the actual visual afference (the model). Subsequent prediction error is returned to higher levels within the AON until a suitable inference of the motion stimulus is distinguished. In the current study, we propose that participants activated a representation of the anticipated sensory consequences (afference) associated with the pre-instructed agency belief (computer or

human). Thus, and consistent with our rating data, we suggest that during observational practice the biological motion + human agency group activated the anticipated sensory consequences associated with human motor control (i.e., minimum jerk; naturalistic velocity), which was congruent with actual sensory consequences, resulting in the stimulus being believed as human (Stanley et al., 2010). The development of implicit sequence knowledge would then be consistent with the 'gating hypothesis' (Liepelt & Brass, 2010), which suggests belief, via top-down processes, affords biological motion privileged access to bottom-up sensorimotor processes in the mirror-mechanism.

The finding of explicit sequence knowledge developed by the other experimental groups can also be associated with a top-down 'gating' mechanism. The rating data for the biological motion + computer agency group showed the non-human agent was believed to be computer-generated. Here, the development of explicit sequence knowledge suggested that naturalistic velocity was not provided privileged access to bottom-up sensorimotor processes (Bird & Heyes, 2005). Also, our finding that different sequence knowledge was acquired when observing naturalistic velocity following the human and computer agency instructions is consistent with belief being a top-down modulatory mechanism associated with agency attribution (Liepelt & Brass, 2010; Stanley, et al., 2007), rather than merely processes associated with selective attention. For instance, providing participants with explicit instructions to direct attention to a specific location on an observed movement regulates bottom-up sensorimotor processes in the mirror-mechanism (Bach, Peatfield, & Tipper, 2007). Indeed, the coding of biological motion kinematics during observational practice is facilitated by explicitly instructing participants to learn motion trajectory information (Hayes, Roberts, Elliott, & Bennett, 2014). Therefore, an increase in bottom-up sensorimotor processes through the modulation of selective attention would lead to implicit sequence knowledge (i.e., mid-scale recognition certainty); as opposed to explicit sequence knowledge (i.e., extreme recognition certainty) (see Figure 6). However, it is unlikely that selective attention underpinned the belief effect because naturalistic velocity observed

following a computer-generated instruction developed explicit sequence knowledge, thus indicating top-down processing.

The recognition and belief rating data provided evidence that processing constant velocity stimuli was modulated by top-down processes (Stanley, et al., 2007). For the nonbiological motion + computer agency group there would have been a similarity between the anticipated (computer-generated) and actual sensory consequences (constant velocity), leading to top-down processes (e.g., goal-directed coding; Ramsey & Hamilton, 2010) potentially associated with analysing sequences and spatial components (Stanley, et al., 2010). A similar mechanism could have been engaged by the nonbiological motion + human agency group, but in this case as a result of the mismatch between anticipated (human-generated) and actual sensory consequences (constant velocity). Indeed, at least some individuals in this group were not convinced by the agency instruction, thus showing that belief is a top-down interpretive process (Liepelt & Brass, 2010; Stanley, et al., 2007), where predictive coding (Kilner, 2011) regulates the contribution of bottom-up sensorimotor or other top-down processes.

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Figure Legends

Figure 1. A representation of the protocol in Experiment 1 (panel A). Each trial in the pre- and post-test commenced with information regarding the time goals being displayed on a monitor for 2000 ms. To start a trial, the participants located the cursor within the home target and pressed the left mouse button. The participants then moved the mouse to complete the movement sequence and the trial ended on reaching the final target. During observation, participants observed a biological motion model, nonbiological motion model, end-state model or a blank screen. Panel B depicts the 5-segment movement sequence, the white circle represents the mouse cursor (non-human agent), the arrows depict the movement direction, and the segment numbers (e.g., S1) indicate the order of segments within the sequence.

Figure 2. Displays the velocity profile in the Y axis (panel A) and X axis (panel B) for the biological motion and nonbiological motion models. The vertical dotted lines represent the end point of each segment in the movement sequence. Numbers above the x-axis in panel B indicate the segment order (segments 1 to 5).

Figure 3. Adjusted group means for relative timing error (panel A) and segment relative timing error (panel B). Error bars represent standard error of the mean.
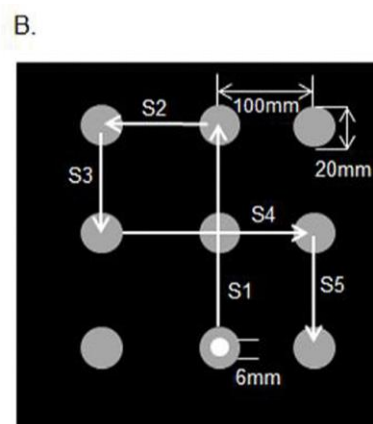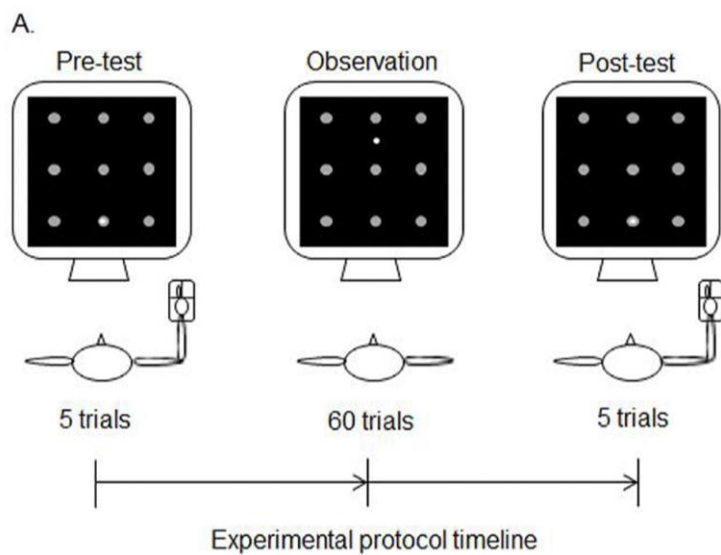
Figure 4. A representation of the protocol for Experiment 2. Prior to observation, the participants were provided with an 'agency instruction' that indicated the stimulus motion was human-generated or computer-generated. Observational practice (observation) was then performed with participants observing biological or nonbiological motion. Following observation, a motor post-test was performed where participants imitated the observed motion sequence using the mouse. Thereafter, participants completed a recognition test which required them to rate how confident they were that the learned stimulus was congruent (trained) or incongruent (new) to the stimulus observed in the observation phase.

Motion trajectory information and agency during observational practice

Finally, participants completed an agency rating task that required them to state whether they agreed or disagreed that the learned stimulus was human-generated or computer-generated.

Figure 5. Group means for relative timing error (panel A) and segment relative timing error (panel B). Error bars represent standard error of the mean.

Figure 6. Group mean recognition performance for trained and new sequence observations. Error bars represent standard error of the mean.

Figure 7. Box-and-whisker plots for belief rating as a function of agency instruction and motion. In each of the four panels, the upper and lower plots reflect the belief ratings given in response to the computer-generated questions and human-generated questions, respectively. The *light grey* bars represent the lower portion of the IQR (25th percentile to the median) and *dark grey* bars represent the upper portion of the IQR (median to the 75th percentile). Note that in some instances, the median and upper/lower quartiles were the same, thus appearing only as a single quartile.
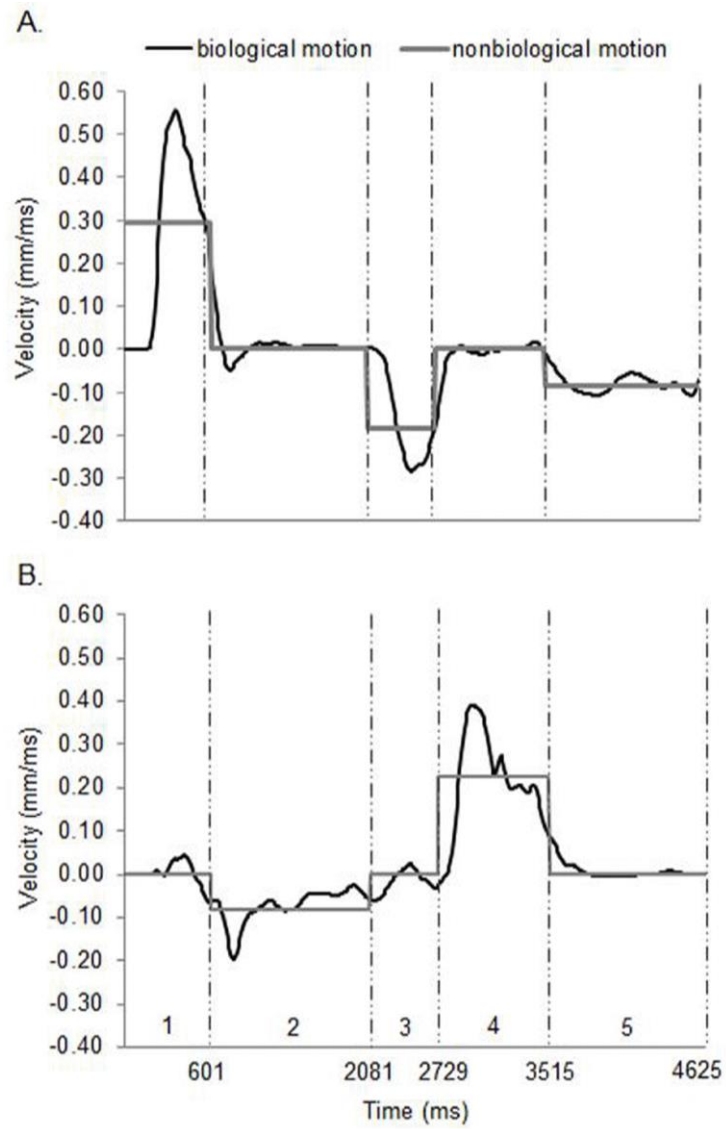
Footnote

1. To examine recognition performance when both relative timing and movement kinematics differed from trained trials, a subsidiary analysis of trained and filler trials was conducted using a 2 Motion (biological motion, nonbiological motion) x 2 Agency Instruction (human, computer) x 2 Sequence (trained, filler) mixed-design ANOVA. The following analysis therefore addressed whether participants were able to identify a filler sequence that had a different relative timing structure and movement kinematics compared to the criterion learned sequence. The results revealed a significant main effect of motion, $F(1, 44) = 4.78$, $p < .05$, $\eta_p^2 = .57$, indicating a generally higher rating for nonbiological (M = 3.74) than biological motion (M = 3.27). There was also a main effect of sequence, $F(1, 44) = 399.95$, $p < .05$, $\eta_p^2 = .90$, indicating a significant higher rating for trained (M = 5.47) compared to filler trials (M = 1.54). Of greater interest was the finding of a significant interaction between agency and sequence, $F(1, 44) = 4.28$, $p < .05$, $\eta_p^2 = .09$. Post hoc analysis confirmed significantly lower ratings of trained sequences by the human (M = 5.06) than the computer agency group (M = 5.88), whilst there were no differences for filler trials (human agency M = 1.54, computer agency M = 1.54).

A.

Pre-test | Observation | Post-test

5 trials | 60 trials | 5 trials

Experimental protocol timeline

B.

A.

B.

A.

B.

Agency instruction — Observation — Motor post-test — Recognition test — Agency rating

(Instruction)

"Human" or "Computer"

60 trials — 5 trials — 12 trials

Experimental protocol timeline