

**Top-down attentional processes modulate the coding of atypical biological motion
kinematics in the absence of motor signals**

Spencer J. Hayes^{1*} James W. Roberts¹ Digby Elliott^{1, 2} Simon J. Bennett¹

*Corresponding author: s.hayes@ljmu.ac.uk; Tel: +44 (0) 151 904 6237

James Roberts: j.w.Roberts@2006.ljmu.ac.uk

Simon J. Bennett: s.j.bennett@ljmu.ac.uk

Digby Elliott: d.elliott@ljmu.ac.uk

^aBrain and Behaviour Laboratory,
Tom Reilly Building, Faculty of Science,
Liverpool John Moores University,
Liverpool, L3 3AF
UK

^bDepartment of Kinesiology,
McMaster University,
Ontario,
Canada

1 The acquisition of sensorimotor parameters that control goal-directed motor behaviors
2 occurs by observing another person in the absence of efferent and afferent motor signals.
3 This is commonly referred to as *observational practice*. During such observation, biological
4 motion properties associated with the observed person are coded into a representation that
5 controls motor learning. Understanding the underlying processes, specifically associated
6 with coding biological motion, has theoretical and practical significance. In this study, we
7 examined the following questions: are the underlying velocity characteristics associated with
8 observed biological motion kinematics imitated? (Experiment 1); is attention involved in
9 imitating biological motion kinematics? (Experiment 2); can selective attention modulate how
10 biological motion kinematics are imitated/represented? (Experiment 3). To this end,
11 participants practiced by observing a model performing a movement sequence that
12 contained *typical* or *atypical* biological motion kinematics. The differences in kinematics were
13 designed to dissociate the movement constraints of the task and the anatomical constraints
14 of the observer. This way we could examine whether novel motor behaviors are acquired by
15 adopting prototypical movements or coding biological motion. The kinematic analyses
16 indicated that the timing and spatial position of peak velocity were represented during
17 learning. Using a dual-task tone counting protocol, we subsequently attenuated the coding of
18 biological motion kinematics (Experiment 2), and augmented coding using a selective
19 attention protocol (Experiment 3). Findings indicated that velocity characteristics of biological
20 motion kinematics are coded during observational practice, most likely through bottom-up
21 sensorimotor processes. By modulating motion coding using two attentional protocols, we
22 have shown that bottom-up processes are influenced by input modulation, which is
23 consistent with top-down control during observational practice.

24
25 *Keywords (five words):* observational practice, biological motion, sensorimotor processes,
26 attention, top-down processes

1 The acquisition of new motor skills through physical training is not always suitable,
2 and so the study of alternative methods has clear theoretical and practical significance.
3 Indeed, data from behavioral (Vogt, 1995) and neuropsychological (Cross, Kraemer,
4 Hamilton, Kelley, & Grafton, 2009) experiments confirm motor skills are learned through
5 observational practice. This practice procedure requires a learner to watch a model
6 performing a motor skill across a consecutive number of demonstrations. In contrast to
7 imitation learning, the observer does not perform the task concurrently with the model, but
8 only after all the observation trials have been completed. The primary difference, then, is that
9 the peripheral motor system is not engaged in a task-specific manner during practice
10 because the skill is never overtly imitated. Still, even without the contribution of task-specific
11 sensorimotor information individuals can acquire complex whole body movements (Cross, et
12 al., 2009); sequence knowledge (Bird & Heyes, 2005); motor control processes (Hayes,
13 Timmis, & Bennett, 2009); and sequence timing (Blandin, Lhuisset, & Proteau, 1999).

14 Although there is still debate regarding the specific processes by which observers
15 learn novel motor skills, it is recognized that the transformation of visual information into a
16 sensorimotor representation is fundamental, and is related to processes that overlap
17 perception-and-action (Brass & Heyes, 2005; Heyes, 2011; Iacoboni, 2005; Prinz, 1997).
18 Neurophysiological evidence shows at least part of these processes are contained in a
19 mirror-mechanism (Buccino et al., 2004; Higuchi, Holle, Roberts, Eickhoff, & Vogt, 2012; van
20 der Helden, van Schie, Rombouts, & Dickson, 2010; Vogt et al., 2007) within the action-
21 observation network (Cross, et al., 2009), which is suggested to contain neurons that
22 respond during observation and execution of the same action (Rizzolatti, Fogassi, & Gallese,
23 2001). An important property of this system is the time course of cortical activation, which is
24 synchronized to kinematic landmarks associated with the observed movement (Borroni &
25 Baldissera, 2008; Gangitano, Mottaghy, & Pascual-Leone, 2001; Press, Cook, Blakemore, &
26 Kilner, 2011). This lower-level mechanism (stimulus-driven, bottom-up process) provides the
27 basis for the direct-matching hypothesis (Iacoboni, 2005; Iacoboni et al., 1999), which
28 suggests the system automatically maps specific characteristics of observed visual stimulus

1 into a sensorimotor representation. The idea is that biological motion stimuli (i.e., produced
2 by a human) during observation activate superior temporal sulcus [STS], followed by the
3 fronto-parietal mirror-mechanism, where the goal and motor specification of the action are
4 coded (Hamilton, 2008; Iacoboni, 2005; Rizzolatti, et al., 2001).

5 Behavioral support for bottom-up processing mainly comes from studies examining
6 motor interference during automatic imitation (Brass, Bekkering, & Prinz, 2001; Press,
7 Gillmeister, & Heyes, 2006) and interpersonal execution-observation (Kilner, Hamilton, &
8 Blakemore, 2007; Kilner, Paulignan, & Blakemore, 2003; Stanley, Gowen, & Miall, 2007).
9 Motor interference (or 'motor contagion') (Blakemore & Frith, 2005) is said to be a result of
10 automatic activation of motor codes directly related to the observed stimulus, which
11 consequently interfere with the motor processes controlling ongoing incongruent movement.
12 Therefore, the basic premise is that if the mirror-mechanism is tuned by biological motion
13 (Press, 2011), there will be greater motor interference compared to observing non-biological
14 motion. Indeed, the execution of horizontal sinusoidal movements was only subject to motor
15 interference whilst observing another human (but not a robot) performing an incongruent
16 vertical movement (Kilner, et al., 2003). In follow-up experiments, Kilner and colleagues
17 (Kilner, et al., 2007; Press, et al., 2011) examined the behavioral and neural basis of motor
18 contagion using human and non-human agents (a ball, or a single point-light dot) that moved
19 with biological motion (minimum jerk; typical velocity) or non-biological motion (constant
20 velocity). Motor interference was shown to be related to the velocity characteristics
21 (minimum jerk) contained in biological motion when viewing a human agent whereas both
22 types of motion caused interference when viewing the non-human agent (Kilner, et al.,
23 2007). Subsequent recording of cortical activity using magnetoencephalography (Press, et
24 al., 2011) showed the human sensory-motor system responded in a similar manner when
25 viewing a human or non-human agent (i.e., single point-light representing the end-point of a
26 finger) in conditions that displayed either biological or non-biological (constant velocity)
27 motion. It was suggested, therefore, that the lack of difference in cortical activation between
28 human and non-human agents could be explained by separate processing of form and

1 kinematics in STS (Vangeneugden, Pollick, & Vogels, 2009). Taken together the implication
2 is that any biological tuning of the mirror-mechanism is not solely based on the perception of
3 human form, as would be present in a video or multi-segment point-light display that have
4 traditionally been used to examine perception of biological motion, but importantly on the
5 underlying movement kinematics which is present in single point-light motion.

6 To date, only a single behavioral experiment has examined bottom-up sensorimotor
7 processes during observational practice by using dual-task protocols (Mattar & Gribble,
8 2005). Findings indicated that the concurrent execution of a secondary motor task (i.e.,
9 incongruent arm movement) significantly attenuated motor learning of a novel motor
10 movement, whereas a secondary attention task (i.e., simple arithmetic calculation) had no
11 effect. The finding from a third control condition (no secondary task) confirmed individuals
12 represented the novel force parameters of the observed motor movement. It was concluded
13 that learning of the primary motor task was attenuated by motor contagion and thus
14 observational practice is underpinned by automatic sensorimotor bottom-up processes that
15 are independent of attentional control [e.g., primary motor cortex and mirror system (Brown,
16 Wilson, & Gribble, 2009)].

17 Although we do not question that bottom-up sensorimotor processes contribute to the
18 development of novel representations during observational practice (Bird & Heyes, 2005;
19 Cross, et al., 2009; Higuchi, et al., 2012), it is unlikely that these processes are always
20 automatic/implicit (Mattar & Gribble, 2005). Many studies have shown that attention is
21 fundamental in early motor learning (Jenkins, Brooks, Nixon, Frackowiak, & Passingham,
22 1994; Jueptner, Frith, Brooks, Frackowiak, & Passingham, 1997; Jueptner et al., 1997).
23 Indeed, prefrontal cortex and dorso-lateral prefrontal cortex (DLPFC), which are involved
24 with attention, information processing, and working memory operations (Itti & Koch, 2001;
25 Kane & Engle, 2002), are more active during the performance of novel compared to already
26 learned, motor skills (Jenkins, et al., 1994). DLPFC is also involved in imitation learning and
27 observational practice (Buccino, et al., 2004; Higuchi, et al., 2012; Stefan et al., 2005; Vogt,
28 et al., 2007) where it operates at a top-down level in reconfiguring existing motor priors into a

representation that matches the characteristics of visual information (i.e., biological motion) that is processed in the mirror-mechanism. Moreover, when learners are instructed to observe a model with the explicit intention to imitate the sequence properties, compared to intending to verbalize the properties, they are significantly more accurate at coding sequence timing during observational practice (Badets, Blandin, & Shea, 2006). The fact that motor learning was facilitated following a simple instruction suggests sensorimotor processes in the mirror-mechanism can be modulated in a top-down manner, although it remains to be determined whether this is reflected in the movement kinematics.

To this end, the present study was designed to determine if bottom-up sensorimotor processes known to code biological motion kinematics can be modulated by top-down attentional processes during observational practice. First, it was necessary in Experiment 1 to develop a behavioral methodology to show the biological motion characteristics (e.g., velocity) of an observed non-human agent are learned. This demonstration was vital to the examination of top-down processes in Experiments 2 and 3, because it would verify that bottom-up sensorimotor processes associated with the mirror mechanism code observed biological motion regardless of whether it is typical or atypical. For a *typical* model group, we displayed a single point that represented the movement kinematics of a human model who had practiced the sequence task until two criterion movement time goals (absolute and relative time goals) were learned accurately. Because we did not constrain how the model should execute the movements whilst learning the two time goals, the resulting kinematic profile was a prototypical (Elliott et al., 2010) aiming trajectory (i.e., *typical* biological motion model). To generate the single point stimuli for an *atypical* model, we instructed a different model to learn the two time goals using a constrained atypical aiming trajectory (i.e., *atypical* biological motion model), and thus dissociated the task and anatomical constraints. In this way, we were able to create two biological motion models (*typical*, *atypical*) that displayed exactly the same criterion time goals, but different underlying kinematic profiles (Figure 2). Our expectation was that participants would learn movement sequence timing by coding

velocity characteristics associated with biological motion observed in the *typical* and *atypical* models.

Experiment 1

Method

Participants. Data were recorded from thirty-three participants (aged between 18 to 21 years), who were randomly assigned to either a *control* group ($n = 11$) that did not observe a model, or an experimental group that observed a model displaying *typical* biological motion ($n = 11$) or *atypical* biological motion ($n = 11$). All participants had normal or corrected-to-normal vision and gave written informed consent. The experiment was designed in accordance with the Declaration of Helsinki and was approved by the ethics committee of the host University.

Apparatus, procedure and stimuli. The apparatus consisted of a PC (Dell Optiplex GX280) connected to a 21-in CRT computer monitor (Iiyama Vision Master 505). The CRT monitor operated with a resolution of 1600 x 1400 pixels and a refresh rate of 85 Hz, and a Logitech G5 laser mouse and Set-Point 2.42a mouse driver (1200 DPI; 1000 reports/s USB; 6.4 megapixels/s; 1.13–1.63 mm/ms). The visual stimuli were generated via MATLAB (The Mathworks, Inc), using Cogent 2000 toolbox (www.vislab.ucl.ac.uk/cogent.php). A second 21-in CRT computer monitor was used for the control condition (Room 2; Figure 1A).

Participants were seated on a chair positioned (Figure 1A) so that the eyes were located 555 mm from the center of a monitor. Nine grey circles that each subtended a visual angle of 2° (target size = 18.75 mm) were displayed against a black background on the monitor in a grid formation with equidistant horizontal and vertical visual angular extent of 10° (amplitude between two targets = 100 mm). Four target circles representing the spatial endpoints of the three segments within the movement sequence were illustrated to a participant using a visual template (similar to Figure 1B; the sequence configuration was fixed within the experiment). A white cursor subtending a visual angle of 0.6° (cursor size =

6.25 mm) was drawn on the monitor and represented the motion of the mouse. The two-dimensional position of the mouse was polled at 1000 Hz, and then used to update and redraw the mouse cursor on each monitor refresh.

All participants from the experimental groups were informed the motor learning study they engaged in had a pre-test, followed by an observational practice phase (the control groups observed a blank screen) and a post-test. They also received general experimental instructions indicating the to-be-learned movement sequence timing goals, which remained constant throughout all experiments, were associated with *absolute time* and *relative time*. The *absolute time* goal was 3600 ms and reflected the total time required to move a white mouse cursor from the start position through the movement sequence, before finally pressing the right mouse button once the mouse cursor was stopped within the end target circle. The *relative time* goal was 40% (1440 ms) for segment 1, 25% (900 ms) for segment 2 and 35% (1260 ms) for segment 3 (i.e., 1440 ms + 900 ms + 1260 ms = 3600 ms). This *relative time* goal was selected because it required the three upper-arm movements to be coordinated to achieve a constrained, novel timing pattern.

Each participant was instructed that the goal in the pre-test was to perform the movement sequence in order to obtain the *absolute* and *relative time* goals as accurately as possible. They performed 6 trials (1 familiarization; 5 experimental) in Room 1 using the right-arm and received no knowledge of results (KR) regarding absolute time error or relative timing error. A trial commenced with the *relative time* goal [segment 1 = 40% (1440 ms); segment 2 = 25% (900 ms); segment 3 = 35% (1260 ms)] displayed on the monitor for 2000 ms, after which it was replaced with the grid formation and the embedded to-be learned movement sequence. To start a trial, the participant pressed the left mouse button, upon which the grid formation disappeared for 2000 ms and then reappeared. The participant was then free to move the mouse so that the cursor moved through (there was no requirement to physically stop the movement in these targets) the second and third targets in order to come to a stop within the end target in accord with the *absolute time* goal and *relative time* goal. To ensure that participants performed the correct spatial dimensions of the sequence while

1 attempting to execute the required timing goals, an error message was presented on the
2 monitor if the cursor did not pass through each correct target in the sequence. NB: no error
3 trials were recorded in any phase on the experiment.

4 During the observational practice phase, participants from the experimental groups
5 (Room 1; Figure 1A) viewed an expert human model that was presented as a non-human
6 agent (i.e., white mouse cursor). The model displayed the exact *absolute time* goal and
7 *relative time* goal, but with either *typical* or *atypical* biological motion kinematics. The models
8 were created by two human volunteers who learned the movement sequence timing goals
9 by physically practicing the task using the aforementioned apparatus. This procedure
10 provided the experimental control required to ensure the *typical* and *atypical* movements
11 were attainable and also resulted in actual human biological motion rather than computer
12 simulated motion. For the *typical* model, we did not specify how the volunteer should control
13 the three upper-limb movements whilst obtaining the timing goals. The biological motion
14 kinematics (upper panel Figure 2) therefore comprised percentage time-to-peak velocity
15 (tPV) and spatial position of peak velocity (pPV) profiles achieved approximately midway
16 through the segment, which is typical of upper-limb aiming movements: segment 1 (primary
17 y-axis: tPV = 44%; pPV = 44%), segment 2 (primary x-axis: tPV = 45%; pPV = 39%) and
18 segment 3 (primary y-axis: tPV = 41%; pPV = 30%). For the *atypical* model (lower panel
19 Figure 2), we constrained the model to perform the upper-limb movements using atypical
20 tPV and pPV biological motion kinematics: segment 1 (primary y-axis: tPV = 95%; pPV =
21 78%), segment 2 (primary x-axis: tPV = 98%; pPV = 84%) and segment 3 (primary y-axis:
22 tPV = 9%; pPV = 14%). An ideal trial (i.e., the *absolute time* goal and *relative time* goal were
23 achieved) was selected from each model and the time-series data were used to create the
24 two stimulus conditions.

25 Each participant sat in front of a computer monitor and received a general
26 instructional pre-cue to “observe the model in order to learn the movement”. Each of the
27 trials during observational practice commenced with the *relative time* goal displayed on the
28 monitor for 2000 ms, followed by the presentation of a model stimulus. In total, there were 60

1 trials with a 1-minute break after every 20 trials. The participants from the *control* group sat
2 in front of the monitor and observed a blank screen for the duration of the observational
3 practice phase (~ 15 minutes; Room 2). Immediately following the observational practice
4 phase, all participants conducted a post-test in Room 1 under exactly the same conditions
5 as the pre-test.

7 Insert Figure 1 and 2

9 **Data reduction and analysis.** To quantify Total Error (*absolute time* goal) and
10 Relative Timing Error (*relative time* goal), we extracted total movement time from the five
11 experimental trials performed by each participant in the pre-test and post-test. Total Error,
12 which considers bias and stability of the difference between the *absolute time* goal and the
13 actual movement time on each trial, was calculated as: Total Error (E): $E = \sqrt{CE^2 + VE^2}$,
14 where CE is a measure of response bias, and is computed as the average of the signed
15 differences between actual total movement time and the *absolute time* goal, and variable
16 error is a measure of response variability, which is computed as the standard deviation of
17 the signed errors. The *relative time* goal was achieved when movement time was distributed
18 across the three segments in 40%, 35%, and 25% proportions of the *absolute time* goal.
19 Relative Time Error was calculated as: $(|R_1 - 0.40| + |R_2 - 0.35| + |R_3 - 0.25|)$, where $R_n =$
20 (the movement time of segment_n/total movement time). Thus, R_1 , R_2 and R_3 are the
21 proportions of total movement time utilized in segments 1 to 3.

22 To quantify whether participants learned the biological motion kinematics of the
23 observed model, we extracted the kinematics exhibited on each segment of the movement
24 sequence. The start and end of a segment was defined as the time that the center of the
25 mouse cursor moved beyond the perimeter of a particular target circle (e.g., start target) and
26 then crossed the perimeter of the next target circle within the movement sequence (i.e.,
27 center target). For each segment, the 2-dimensional displacement data sampled by the laser
28 mouse were filtered using a low-pass 4th order autoregressive filter with an 8 Hz cut-off. The

data were then differentiated using a central difference algorithm to obtain velocity. A MATLAB routine extracted the primary movement occurring within each segment (e.g., segment 1 comprised movement primarily in the y-axis; segment 2 comprised movement primarily in the x-axis). From this the routine identified peak velocity, and then extracted the time and spatial position at which it occurred. These latter two variables were chosen for analysis because they most reflected the difference between the *typical* and *atypical* biological motion models. Using the timing variable, we calculated the percentage time to peak velocity [$tPV = (\text{time to peak velocity} / \text{segment movement time}) \times 100$]. For the spatial variable, we calculated the position that peak velocity occurred within the 100 mm amplitude of each segment, and expressed that position as a percentage of the total movement amplitude [$pPV = (\text{position of peak velocity} / \text{total segment amplitude}) \times 100$].

To analyze global levels of imitation accuracy associated with timing and spatial position of peak velocity across the three segments, we developed an algorithm that computed the mean absolute difference between tPV (and pPV) exhibited by the participant in each segment and that of the *atypical* model: $IEtPV$ (and $IEpPV$) = $(|Seg_1 - ATyp_{Seg1}|) + (|Seg_2 - ATyp_{Seg2}|) + (|Seg_3 - ATyp_{Seg3}|) / \text{number of segments}$, where IE represents an imitation error score. The data values from the *atypical* model were selected as constants (i.e., $ATyp_{Seg1}$) because the primary research question was based on whether *atypical* biological motion kinematics was coded during observational practice. Lower $IEtPV$ and $IEpPV$ scores are expected after observing an *atypical* model compared to *typical* model.

To quantify changes in timing performance (Total Error; Relative Timing Error), the post-test data for all groups were examined using an analysis of covariance (ANCOVA), with pre-test scores as a covariate. ANCOVA was used because it statistically minimizes the impact of any between-group differences in performance associated with random assignment of participants to individual groups. This technique reduces the error term associated with between group post-test comparisons by taking into account within-group variability in the initial pre-test performance. Post hoc procedures involved two *a priori* planned contrasts. The first contrast analyzed the experimental (*typical*; *atypical*) groups

against the control group. The second contrast analyzed the *atypical* group against the *typical* group. For the kinematic data, we removed the *control* data from the analyses because imitation performance cannot be measured in a group that does not engage in observational practice. To examine global imitation accuracy for timing (IEtPV) and spatial position (IEpPV) of peak velocity we compared post-test data of *typical* and *atypical* groups using an ANCOVA, with pre-test as the covariate. Also, we examined the post-test data for each segment (1, 2, and 3) individually to measure specific effects of imitation for tPV and pPV using separate ANCOVAs, with pre-test as the covariate. Alpha was set at $p < 0.05$, and partial eta squared (η_p^2) expressed the size of the effect.

Results

Timing. ANCOVA returned significant main effects for Total Error [$F(2, 29) = 5.42$ $p < 0.05$, $\eta_p^2 = 0.27$] and Relative timing Error [$F(2, 29) = 19.86$ $p < 0.05$, $\eta_p^2 = 0.58$]. The first planned comparisons, which compared the two experimental groups against the *control* group, indicated significant differences for Total Error [$F(1, 29) = 9.34$ $p < 0.05$, $\eta_p^2 = 0.24$] and Relative Timing Error [$F(1, 29) = 39.63$ $p < 0.05$, $\eta_p^2 = 0.58$]. The adjusted mean differences showed the experimental groups were more accurate than the *control* group by 835 ms for Total Error and 16 units for Relative Timing Error (Table 1; Experiment 1). As can be seen in Table 1, the second comparison revealed no significant differences between the *typical* and *atypical* groups for Total Error [$F(1, 29) = 1.50$ $p > 0.05$, $\eta_p^2 = 0.05$] and Relative Timing Error [$F(1, 29) = 0.27$ $p > 0.05$, $\eta_p^2 = 0.01$].

Insert Table 1 and Figure 3 about here

Kinematics. ANCOVA conducted on IEtPV [$F(1, 19) = 4.40$ $p = 0.05$, $\eta_p^2 = 0.19$] and IEpPV [$F(1, 19) = 3.43$ $p = 0.08$, $\eta_p^2 = 0.15$] showed participants in the *atypical* group

exhibited movement trajectories (Figure 3A, timing of peak velocity; Figure 3C, spatial position of peak velocity) that were more accurate than *typical* group. The segment effects for tPV (Figure 3B) showed a group difference in segment 1 [$F(1, 19) = 29.64$ $p < 0.05$, $\eta_p^2 = 0.61$] and 2 [$F(1, 19) = 8.24$ $p < 0.05$, $\eta_p^2 = 0.30$], but not 3 [$F(1, 19) = 2.67$ $p > 0.05$, $\eta_p^2 = 0.12$]. Similar effects were observed for pPV, with a group difference in segment 1 [$F(1, 19) = 37.72$ $p < 0.01$, $\eta_p^2 = 0.65$], but not 2 [$F(1, 19) = 0.09$ $p > 0.05$, $\eta_p^2 = 0.01$] or 3 [$F(1, 19) = 0.01$ $p > 0.05$, $\eta_p^2 = 0.01$]. As illustrated in Figure 3B and D (the white bars represent the *atypical* model and *typical* model), the kinematic data in segment 1 showed the timing, and spatial position, of peak velocity occurred later (tPV = 77%), and towards the end (pPV = 71%) of the movement trajectory in segment 1 for the *atypical* group, compared to the *typical* group (tPV = 40%; pPV = 43%). This effect can also be seen in Figure 4 where the exemplar velocity trace from a representative participant in the *atypical* group (Figure 4A) indicated peak velocity occurred later in segment 1, but not 2 and 3. For the representative participant in the *typical* group (Figure 4B), peak velocity occurred towards the midpoint of the movement across the 3 segments and thus similar to the *typical* model (Figure 2 upper-panel).

Insert Figure 4 about here

Discussion

The results for Total Error and Relative Time Error confirm absolute (Blandin, et al., 1999) and relative time (Vogt, 1995) goals were learned. The significant difference between *typical* and *atypical* groups for the kinematic data (IEtPV; IEpPV; tPV; pPV) indicated biological motion kinematics were coded. Specifically tPV in segment 1 occurred at 77% and pPV occurred at 71% of the movement for the *atypical* group, which is closer to the *atypical* model (tPV = 95%; pPV = 78%). For the *typical* model condition, tPV occurred at 40% and pPV occurred at 43% of the movement which is closer to the *typical* model (tPV = 44%;

pPV = 44%). These findings are consistent with biological motion being coded through bottom-up sensorimotor processes operating in mirror-mechanism (Bird & Heyes, 2005; Brass, et al., 2001; Cross, et al., 2009; Press, et al., 2011). The *atypical* model was designed specifically to contain an *atypical* kinematic aiming profile, making it extremely unlikely learners coincidentally reproduced atypical kinematics through processes associated with goal-directed imitation (Bekkering, Wohlschlaeger, & Gattis, 2000; Wohlschlaeger, Gattis, & Bekkering, 2003) or emulation (Csibra, 2007). If goals alone dictated the learning process, it would be expected the movement should be similar to the *typical* group, with a kinematic profile that coincidentally reflected a prototypical aiming movement (Roberts, Bennett, Elliott, & Hayes, 2012). On the contrary, the temporal and spatial correspondence found between peak velocity of the imitated movement and the *atypical* model suggested velocity was coded through sensorimotor processes known to operate during action-observation, and imitation of biological motion (Iacoboni, 2009; Kilner, et al., 2007; Press, et al., 2011). Indeed, data from TMS studies showed activity in primary motor cortex, whilst viewing biological motion, was phase-locked to observed kinematic landmarks indicating the movement was dynamically coded as it unfolded over time (Borrioni & Baldissera, 2008; Gangitano, et al., 2001).

Experiment 2

Having shown movement velocity was coded during observational practice, we next examined the influence of attention on bottom-up sensorimotor processes operating during the coding of biological motion. Although such processes are suggested to function automatically during observational practice (Mattar & Gribble, 2005), there is evidence that they are influenced by attention during automatic imitation (Gowen, Bradshaw, Galpin, Lawrence, & Poliakoff, 2010; Heyes, 2011; Longo, Kosobud, & Bertenthal, 2008) and the acquisition of novel movement sequences during observational practice (Badets, et al., 2006; Higuchi, et al., 2012). To this end, a new set of participants learned the movement sequence by observing the same *typical* and *atypical* models but now simultaneously

performing a tone-counting-task. The dual-task protocol was used because it is a valid method of ensuring attentional resources are divided during sequence learning (Curran & Keele, 1993). Once again we emphasize that it is extremely difficult to confirm that kinematics of biological motion are imitated during observational practice when participants view a model performing a typical sequence movement. In this context, any resulting movement that displays typical kinematics could be a function of imitating the model, or a function of the anatomical and task constraints (Hayes, et al., 2009). For this reason, we expected participants who observed the *typical* model to execute/imitate a movement with typical kinematics. Importantly, however, if bottom-up sensorimotor processes associated with coding biological motion are modulated by top-down attentional processes, we expected attenuation in the coding of *atypical* biological motion such that kinematics would reflect typical kinematics.

Method

Participants. Thirty-three volunteers (age range 18-21 years) participated in the experiment and were randomly assigned to one of three groups. Two experimental groups both performed a dual-task while observing a *typical* or *atypical* model. A control group (*control-attention*) was included that did not observe the stimulus but performed the tone-counting-task. All participants had normal or corrected-to-normal vision. The experiment was designed in accordance with the Declaration of Helsinki and was approved by the local ethics committee of the host university.

Apparatus, procedure and stimuli. The movement sequence, apparatus and general procedures were identical to the previous experiment. Here, though, participants performed a dual-task that required them to count the number of high-pitched tones (300 Hz) that were interleaved amongst low-pitch tones (150 Hz). The tones were presented on two speakers positioned on top of the monitor that a model was observed (Figure 1A). The presentation of the auditory tones was controlled using a MATLAB routine so that eight tones in total (one tone per 450 ms) were presented during each trial. The number of high-

1 pitched tones was presented randomly with no experimental constraint as to the total
2 number of high-pitched tones per trial. Participants were instructed to keep a silent, running
3 total of the number of high-pitched tones within a trial. After a trial, participants recorded the
4 answer on a score card. Participants were instructed to consider the tasks as being equally
5 important and not to concentrate on one task at the expense of the other. We also
6 familiarized the participants on the tone-counting-task and scoring procedure prior to testing.
7 Finally, an experimenter was present throughout testing to ensure that participants observed
8 the model while performing the tone-counting-task: no participant looked away from the
9 monitor.

10 **Data reduction and analysis.** Data reduction and statistical analyses for the
11 dependent variables Timing and Kinematics were identical to Experiment 1.

13 Results

14 **Tone-counting-task.** The total number of correct trial responses recorded from each
15 participant across the 60 trials was used to calculate an accuracy score. These data were
16 analyzed using a between samples ANOVA, which indicated no significant difference
17 between the groups [$F(2, 30) = 2.70$ $p > 0.05$, $\eta_p^2 = 0.16$]. Mean number of correct responses
18 out of 60 trials for the groups was: *atypical-attention* = 48 ± 6 ; *typical-attention* = 53 ± 6 ;
19 *control-attention* = 53 ± 4 .

20 **Timing.** ANCOVA returned significant main effects for Total Error [$F(2, 29) = 17.10$ p
21 < 0.05 , $\eta_p^2 = 0.54$] and Relative timing Error [$F(2, 29) = 19.76$ $p < 0.05$, $\eta_p^2 = 0.58$]. The first
22 comparison of the two experimental groups against the *control-attention* group, revealed
23 significant differences for Total Error [$F(1, 29) = 34.05$ $p < 0.05$, $\eta_p^2 = 0.54$] and Relative
24 Timing Error [$F(1, 29) = 39.29$ $p < 0.05$, $\eta_p^2 = 0.58$]. The mean differences indicated the
25 experimental groups were more accurate than the *control-attention* group by 984 ms for
26 Total Error and 15 units for Relative Timing Error (Table 1; Experiment 2). As can be seen in
27 Table 1, the second comparison indicated no significant difference between the *typical-*

attention and the *atypical-attention* groups for Total Error [$F(1, 29) = 0.15$ $p > 0.05$, $\eta_p^2 = 0.01$] and Relative Timing Error [$F(1, 29) = 0.09$ $p > 0.05$, $\eta_p^2 = 0.003$].

Kinematics. ANCOVA conducted on IEtPV [$F(1, 19) = 0.02$ $p > 0.05$, $\eta_p^2 = 0.001$] and IEpPV [$F(1, 19) = 0.79$ $p > 0.05$, $\eta_p^2 = 0.03$] showed no significant difference between the *typical-attention* and *atypical-attention* groups in terms of timing (Figure 5A), and spatial position (Figure 5C), of peak velocity. There were also no significant differences across all segments for tPV (Figure 5B): segment 1 [$F(1, 19) = 0.53$ $p > 0.05$, $\eta_p^2 = 0.03$], 2 [$F(1, 19) = 1.68$ $p > 0.05$, $\eta_p^2 = 0.08$], or 3 [$F(1, 19) = 0.12$ $p > 0.05$, $\eta_p^2 = 0.12$]; and pPV (Figure 5D), segment 1 [$F(1, 19) = 1.25$ $p > 0.05$, $\eta_p^2 = 0.06$], 2 [$F(1, 19) = 0.11$ $p > 0.05$, $\eta_p^2 = 0.01$], or 3 [$F(1, 19) = 0.08$ $p > 0.05$, $\eta_p^2 = 0.01$]. This effect is displayed in Figure 4 where the exemplar velocity traces from the representative participants in the *atypical* (Figure 4C) and *typical* (Figure 4D) groups indicated peak velocity occurred towards the midpoint of the movement in each of the 3 segments, which was consistent with the *typical* model (Figure 2 upper-panel).

Insert Figure 5 about here

Discussion

The absolute and relative time goals were learned by observing *typical* and *atypical* models during observational practice. The fact the dual-task did not attenuate the acquisition of the timing goals indicated these representations can be developed when attentional resources are divided by a tone-counting-task. As predicted, no significant differences were found between the groups for kinematic variables, thus indicating the dual-task modulated the coding of biological motion kinematics. Specifically, both groups executed tPV (*typical-attention* = 48%; *atypical-attention* = 53%) and pPV (*typical-attention* = 48%; *atypical-attention* = 52%) in segment 1 towards the midpoint of the trajectory, which was not the case

1 in Experiment 1 (*typical* = 40%; tPV *atypical* = 77%; *typical* = 44%; pPV *atypical* = 71%),
2 where the same *atypical* model was observed but without engaging in a dual-task. For the
3 *atypical* group, there are two complimentary findings that suggest the modulatory effect was
4 related to the dual-task interfering with the sensorimotor processes involved in coding
5 biological motion. First, the high accuracy score (85% accurate) for tone counting confirmed
6 participants engaged in the dual-task. Second, and importantly, accuracy was not achieved
7 at the expense of engaging in observational practice because the timing goals were learned.

8 The finding that imitation of *atypical* biological motion kinematics was attenuated by
9 attentional loading indicated the sensorimotor system engaged in observational practice is
10 not solely an automatic mechanism, but rather one that is modulated by top-down
11 processes. Before this is discussed, we highlight the finding that the dual-task, and
12 associated sharing of attention, did not attenuate the acquisition of the two timing goals. One
13 interpretation is that the processes associated with learning higher-order timing goal
14 representations, and those related to lower-level motor properties (i.e., biological motion
15 kinematics), are based on different mechanisms (Keele, Ivry, Mayr, Hazeltine, & Heuer,
16 2003). However, a more parsimonious interpretation, given top-down and lower-level
17 processes in the mirror-system are linked by a common mechanism (Heyes, 2011), is that
18 attentional resources during observation were primarily allocated to learning the timing
19 goals, as opposed to the kinematics. This would be consistent with compliance to the
20 general task instructions (given in pre-test; and on the monitor during observational practice)
21 that directed participants to acquire the movement and timing goals, not the movement
22 kinematics. Moreover, the dual-task was used to divide attention, rather than direct the locus
23 of attention (which is examined in Experiment 3). Taken together, we suggest the
24 modulatory effect on learning movement kinematics indicated a top-down attentional
25 contribution to regulating the bottom-up sensorimotor processes engaged to code biological
26 motion. Indeed, directing attention to the nature of an observed movement has also had a
27 modulatory effect on the behavioral response during automatic imitation (Chong,
28 Cunnington, Williams, & Mattingley, 2009; Longo, et al., 2008). When an observer is

1 informed (via explicit instructions) a movement stimulus is biologically possible, the
2 processes operating in the sensorimotor system produce an enhanced motor response time,
3 compared to when the movement is identified as biologically impossible (Longo, et al.,
4 2008). This was not present when instructions were removed. Such attentional control is
5 referred to as ‘input’ modulation because instructions influence processing of the observed
6 stimulus (Heyes, 2011). Attentional ‘input’ modulation has been replicated in other automatic
7 imitation protocols (Chong, et al., 2009; Leighton, Bird, Orsini, & Heyes, 2010; Liepelt &
8 Brass, 2010); selective attention in action-observation (Bach, Peatfield, & Tipper, 2007) and
9 intention during observational practice of sequence timing (Badets, et al., 2006). To our
10 knowledge, however, the present data are the first to indicate top-down attentional
11 processes modulate (perhaps via an input route) the coding of biological motion kinematics
12 during observational practice.

14 **Experiment 3**

15 The results from Experiment 2 provided evidence for a contributing role of top-down
16 attentional processes during observational practice, but a stronger test of an ‘input’
17 hypothesis would be to reverse the direction of the attentional modulation and thereby
18 facilitate the coding of *atypical* biological motion kinematics. To this end, we used a selective
19 attention protocol (Bach, et al., 2007; Chong, et al., 2009; Jeannerod, 1999), which has been
20 shown to regulate ‘input’ modulatory processes. For example, motor response times during
21 action-observation are faster when selective attention is modulated by positioning an
22 imperative pre-cue (a colored dot) near to a compatible location of an action stimulus (i.e., a
23 foot in a full body action) (Bach, et al., 2007). Based on the findings from Experiment 2,
24 where we showed attenuation in the acquisition of kinematics when attention was shared
25 with a secondary tone counting task, we further examined the role of attention by
26 manipulating selective attention where learners were instructed to focus on the movement
27 trajectory displayed by the model. If bottom-up sensorimotor processes, associated with
28 coding biological motion, are modulated by selective attention, we expected participants to

1 be more accurate at coding *atypical* biological motion when attention was focused to the
2 trajectory than participants who received ‘general’ instructions in Experiment 1. Also, in
3 Experiment 2 we found the acquisition of the time goals remained accurate and
4 unmodulated despite the kinematics being attenuated, which we interpreted to indicate the
5 processes underpinning the timing goals and kinematics competed for attentional resources
6 during learning. If this is correct, we expect any increase in accuracy for the kinematics in
7 Experiment 3 to result in a decrease in accuracy for the timing goals.

8 9 **Method**

10 **Participants.** A new set of 11 volunteers (age range 18-21 years) were recruited and
11 assigned to a group that observed an *atypical* model and received a specific task
12 instructional cue: *atypical-trajectory*. These data were compared against those from two of
13 the groups in Experiment 1: *atypical-general* and *control* group. All participants had normal
14 or corrected-to-normal vision. The experiment was designed in accordance with the
15 Declaration of Helsinki and was approved by the local ethics committee of the host
16 university.

17 **Apparatus, procedure and stimuli.** The movement sequence apparatus and
18 general procedures were identical to Experiment 1. The *atypical-general* group was provided
19 with a general instructional pre-cue to observe the *atypical* model with a view to learning the
20 movement time goals. The *atypical-trajectory* group received a specific task instructional pre-
21 cue stating that “while observing the model to learn the time goals, you should focus your
22 attention onto the characteristics of the model’s movement trajectory with the intention to
23 imitate the exact trajectory”. Before practice commenced, all participants confirmed they
24 understood the specific task instructions.

25 **Data reduction and analysis.** Data reduction and analysis for Timing and
26 Kinematics were the same as Experiment 2. First, we compared the two experimental
27 groups with the *control* group. Then we compared the *atypical-general* group and the
28 *atypical-trajectory* group.

Results

Timing. ANCOVA returned significant main effects for Total Error [$F(2, 29) = 5.19$ $p < 0.05$, $\eta_p^2 = 0.26$] and Relative timing Error [$F(2, 29) = 8.98$ $p < 0.05$, $\eta_p^2 = 0.38$]. The first comparison revealed significant differences for Total Error [$F(1, 29) = 10.19$ $p < 0.05$, $\eta_p^2 = 0.21$] and Relative Timing Error [$F(1, 29) = 9.57$ $p < 0.05$, $\eta_p^2 = 0.23$]. The mean differences indicated the experimental groups were more accurate than the *control* group by 688 ms for Total Error and 11 units for Relative Timing Error (Table 1; Experiment 3). The second comparison indicated there was no significant difference between the *atypical-general* and *atypical-trajectory* groups for Total Error [$F(1, 29) = 0.20$ $p > 0.05$, $\eta_p^2 = 0.01$]. Importantly, there was a significant difference for Relative Timing Error [$F(1, 29) = 8.82$ $p < 0.05$, $\eta_p^2 = 0.23$], with the *atypical-general* group being significantly more accurate than the *atypical-trajectory* group by 12 units of relative timing error.

Kinematics. ANCOVA for IEtPV indicated a significant difference of 16 units between the *atypical-trajectory* and *atypical-general* groups [$F(1, 19) = 12.19$ $p < 0.05$, $\eta_p^2 = 0.39$], and a group difference of 5 units for IEpPV [$F(1, 19) = 3.22$ $p = 0.09$, $\eta_p^2 = 0.15$]. These effects showed the *atypical-trajectory* group was more accurate than the *atypical-general* group at imitating timing (Figure 6A), and spatial position (Figure 6C), of peak velocity. The segment results for tPV showed no group differences in segment 1 [$F(1, 19) = 1.81$ $p > 0.05$, $\eta_p^2 = 0.09$] and 3 [$F(1, 19) = 2.80$ $p > 0.05$, $\eta_p^2 = 0.13$], but a significant difference in segment 2 [$F(1, 19) = 6.43$ $p < 0.05$, $\eta_p^2 = 0.25$]. Similarly, no group differences were observed for pPV in segment 1, [$F(1, 19) = 0.10$ $p > 0.05$, $\eta_p^2 = 0.01$] and 3 [$F(1, 19) = 2.24$ $p > 0.05$, $\eta_p^2 = 0.11$], but a significant difference was observed in segment 2 [$F(1, 19) = 7.25$ $p < 0.05$, $\eta_p^2 = 0.29$]. The effects for segment 1 are important because they showed the experimental groups exhibited kinematics similar to the model. Specifically, timing (tPV), and spatial position (pPV) of peak velocity, occurred later (Figure 6B), and towards the end (Figure 6D), of the movement trajectory (the white bars represent the *atypical* model and

1 *typical* model). More importantly, and as per the *atypical* model, the significant effects
2 observed in segment 2 showed the *atypical-trajectory* group exhibited timing and spatial
3 position of peak velocity that occurred later (tPV = 65 %), and towards the end (pPV = 57%),
4 of the movement trajectory, than the *atypical-general* group (tPV = 44%; pPV = 38%). This
5 effect can also be seen in Figure 4 where the exemplar velocity trace from a representative
6 participant in the *atypical* group (Figure 4E) indicated peak velocity occurred later in segment
7 1 and 2, but not significantly in 3. For the representative participant in the typical group
8 (Figure 4F), peak velocity occurred towards the midpoint of the movement across the 3
9 segments and thus similar to the *typical* model (Figure 2 upper-panel).

10
11 Insert Figure 6 about here
12

13 Discussion

14 Independent of task instructions, and compared to the control group, the
15 experimental groups learned the absolute and relative time goals. As predicted, directing
16 attention to the movement trajectory modulated imitation with the *atypical-trajectory* group
17 coding biological motion more accurately than those that received general instructions. This
18 effect was specifically related to significant changes in segment 2 where timing (tPV) and
19 spatial position (pPV) of peak velocity was imitated more accurately. Notably, although the
20 findings from segment 3 were not significant (tPV and pPV; see Figure 6B and D), there was
21 an advantage for those receiving instructions, with the peak tending to occur earlier in the
22 movement trajectory and thus consistent with the model. As predicted, we also showed that
23 directing attention to the trajectory led to significant cost in relative timing accuracy which
24 further confirmed the processes associated the acquisition of timing and kinematics compete
25 for attentional resources. Although the *atypical-trajectory* group was more accurate than the
26 control group, relative timing error was significantly higher than that exhibited by the *atypical-*
27 *general* group. The implication is that selective attention did not override the acquisition of

relative timing, but instead modulated how it was represented within a hierarchy of learning processes (Longo, et al., 2008; Wohlschlager, et al., 2003).

General Discussion

The primary aim of this study was to determine if, during observational practice, top-down attentional processes modulate bottom-up sensorimotor processes known to be involved in coding biological motion (i.e., a single point-light produced by a human). To this end, the following research questions were examined: are the underlying velocity characteristics associated with observed biological motion kinematics imitated? (Experiment 1); is attention involved in imitating biological motion kinematics? (Experiment 2); can selective attention modulate how biological motion kinematics are imitated/represented? (Experiment 3).

With respect to the first research question, we found that tPV and pPV in segment 1 occurred later in the movement having observed an *atypical* model. This was not achieved at the expense of absolute and relative timing goals, both of which were learned irrespective of the model observed. The finding of temporal (Gangitano, et al., 2001) and spatial correspondence between observed and learned movement kinematics is consistent with biological motion being coded through sensorimotor processes operating in human mirror-mechanism (Casile et al., 2010; Dayan et al., 2007; Kilner, et al., 2007; Kilner, et al., 2003; Press, et al., 2011), as opposed to processes related only to goal-directed imitation (Wohlschlager, et al., 2003) and/or emulation (Csibra, 2007; Csibra & Gergely, 2007). Such bottom-up processing of velocity information has been linked to a neural substrate containing posterior superior temporal sulcus, which detects biological motion (Allison, Puce, & McCarthy, 2000), and has projections to the fronto-parietal mirror-mechanism (Di Dio et al., 2013; Press, et al., 2011) that codes the goal and kinematic properties of an observed action (Hamilton, 2008; Iacoboni, 2009).

In suggesting that our findings regarding movement kinematics provide strong evidence that biological motion was imitated, it is important to consider the nature and

properties of biological motion investigated in the present experiment. Notably, the observed models were displayed as a single-point light that represented the human-generated motion of a hand-held computer mouse. The same apparatus and stimulus display were experienced by participants in the experimental groups, thus ensuring task compatibility between the observed and imitated movement (i.e., body posture, limbs involved, friction during movement of the mouse). Therefore, at a basic level, the observed *typical* and *atypical* kinematics were both biological because they were goal-directed and the product of human movement (i.e., contained velocity, acceleration, and jerk) when interacting with a familiar device. The method of using a non-human agent to present stimuli is common when exploring biological motion (Kilner, et al., 2007; Press, et al., 2011; Stanley, et al., 2007), and provides participants with real-time biological stimuli in the absence of other factors such as form and expectation that may influence a participant's perception and interpretation. Such stimuli have been shown to result in similar cortical activation as human agents viewed in video displays (Press et al., 2011), thus indicating that form is not necessary to perceive biological motion. Moreover, even when human form is present in the stimulus (e.g., video displays), evidence for biological motion processing has often been found when participants are instructed to focus on a single point such as the finger tip. That said, it should be acknowledged that for imitation of more complex multi-segment human motion it would likely be required to present the stimulus as either video or point-light display (Hayes, Hodges, Huys, & Williams, 2007) that maintains important inter-joint and intra-joint relations (Cutting & Kozlowski, 1977; Johansson, 1973; Kozlowski & Cutting, 1977).

Although this is not the first demonstration that coding of biological motion involves sensorimotor processes, there is a specific difference between the current observational practice study and work using observation-execution or automatic imitation protocols (Brass, et al., 2001; Kilner, et al., 2007; Kilner, et al., 2003; Press, et al., 2006; Stanley, et al., 2007). Namely, observation-execution and automatic imitation both involve activation of the peripheral motor system between consecutive observations, which could thereby provide sensorimotor experience that facilitates perception (Calvo-Merino, Glaser, Grezes,

1 Passingham, & Haggard, 2005) and coding of biological motion over-time (Heyes, Bird,
2 Johnson, & Haggard, 2005; Press, et al., 2006). During observational practice, however, the
3 limb is always at rest, thus making it extremely unlikely the peripheral motor system provided
4 a functional contribution to the sensorimotor processes that coded biological motion.
5 Nevertheless, even without task specific afferent and efferent contributions between
6 observations (a participant did not overtly generate motor signals) our data provided strong
7 evidence that biological motion was imitated. This finding is novel and indicated that even in
8 the context of pure action-observation, central (Dayan, et al., 2007) bottom-up sensorimotor
9 processes are engaged to facilitate the acquisition of novel motor sequence timing by coding
10 biological motion.

11 With respect to attentional processes and biological motion kinematics, the findings
12 from Experiment 2 and 3 indicated bottom-up sensorimotor processes do not act
13 independently of top-down control (Brown, et al., 2009; Mattar & Gribble, 2005). To
14 summarize the key findings, we have schematically represented how attention, via input
15 modulation, could control the coding of *atypical* biological motion kinematics and timing
16 goals (Figure 7). When attention is not divided or directed, and learners are instructed to
17 acquire the timing goals by observing a model, they do so by coding kinematics and timing
18 goals (Exp. 1 -x-). When attention is divided by a dual-task tone counting protocol,
19 kinematics are attenuated because attentional resources are linked to relative, and absolute,
20 timing following the general instruction to learn the movement (Exp. 2 -■-). When attention is
21 directed to the movement trajectory, the coding of kinematics is augmented, but at the
22 expense of relative timing (Exp. 3 -○-). The fact that we systematically augmented, and
23 attenuated the coding of movement kinematics, in conjunction with relative timing, provided
24 strong evidence that top-down and bottom-up processes engaged during observational
25 practice are embedded within a common network. These findings support evidence on
26 automatic imitation (Bach, et al., 2007; Chong, et al., 2009; Liepelt & Brass, 2010; Longo, et
27 al., 2008) and motor mimicry (Wang, Newport, & Hamilton, 2011; Wang, Ramsey, &
28 Hamilton, 2011), which suggest bottom-up sensorimotor processes within the mirror-system

1 are mediated by attentional (Heyes, 2011) and social (Wang & Hamilton, 2012) factors.
2 Finally, our finding that selective attention directly influenced how kinematics and timing
3 goals are learned supports the notion of 'input modulation' (Heyes, 2011; Heyes & Bird,
4 2007), where in specific situations the sensorimotor processes that form the learned motor
5 response can be under top-down attentional control.

6
7 Insert Figure 7 about here
8

9 To conclude, we confirmed that motor learning occurred by engaging in practice that
10 required a learner to observe, not physically imitate, a novel action. This showed that a novel
11 movement representation was developed by coding *atypical* biological motion kinematics,
12 even in the absence of overt efferent signals. Because coding was attenuated when
13 attentional resources were divided, and augmented when selective attention was directed to
14 the properties of biological motion, we confirmed the sensorimotor processes operating
15 during observational practice are influenced by input modulation.

References

- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in Cognitive Sciences*, 4(7), 267-278.
- Bach, P., Peatfield, N., & Tipper, S. (2007). Focusing on body sites: the role of spatial attention in action perception. *Experimental Brain Research*, 178(4), 509-517. doi: 10.1007/s00221-006-0756-4
- Badets, A., Blandin, Y., & Shea, C. H. (2006). Intention in motor learning through observation. *Quarterly Journal of Experimental Psychology*, 59(2), 377-386. doi: 10.1080/02724980443000773
- Bekkering, H., Wohlschlaeger, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *The Quarterly Journal of Experimental Psychology Section A*, 53(1), 153-164.
- Bird, G., & Heyes, C. (2005). Effector-Dependent Learning by Observation of a Finger Movement Sequence. *Journal of Experimental Psychology: Human Perception and Performance*, 31(2), 262-275.
- Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, 43(2), 260-267.
- Blandin, Y., Lhuisset, L., & Proteau, L. (1999). Cognitive Processes Underlying Observational Learning of Motor Skills. *The Quarterly Journal of Experimental Psychology Section A*, 52(4), 957-979. doi: 10.1080/713755856
- Borroni, P., & Baldissera, F. (2008). Activation of motor pathways during observation and execution of hand movements. *Social Neuroscience*, 3(3-4), 276-288. doi: 10.1080/17470910701515269
- Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, 106(1-2), 3-22.
- Brass, M., & Heyes, C. (2005). Imitation: is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, 9(10), 489-495. doi: 10.1016/j.tics.2005.08.007

- 1 Brown, L. E., Wilson, E. T., & Gribble, P. L. (2009). Repetitive transcranial magnetic
2 stimulation to the primary motor cortex interferes with motor learning by observing.
3 *Journal of Cognitive Neuroscience*, 21(5), 1013-1022.
- 4 Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., & Rizzolatti, G. (2004).
5 Neural circuits underlying imitation learning of hand actions: An event-related fMRI
6 study. *Neuron*, 42(2), 323-334. doi: Doi 10.1016/S0896-6273(04)00181-3
- 7 Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005). Action
8 observation and acquired motor skills: an fMRI study with expert dancers. *Cerebral*
9 *Cortex*, 15(8), 1243-1249.
- 10 Casile, A., Dayan, E., Caggiano, V., Hendler, T., Flash, T., & Giese, M. A. (2010). Neuronal
11 Encoding of Human Kinematic Invariants during Action Observation. *Cerebral Cortex*,
12 20(7), 1647-1655. doi: 10.1093/cercor/bhp229
- 13 Chong, T. T., Cunnington, R., Williams, M. A., & Mattingley, J. B. (2009). The role of
14 selective attention in matching observed and executed actions. *Neuropsychologia*,
15 47(3), 786-795. doi: 10.1016/j.neuropsychologia.2008.12.008
- 16 Cross, E. S., Kraemer, D. J. M., Hamilton, A. F. d. C., Kelley, W. M., & Grafton, S. T. (2009).
17 Sensitivity of the action observation network to physical and observational learning.
18 *Cerebral Cortex*, 19(2), 315-326.
- 19 Csibra, G. (2007). Action mirroring and action understanding: An alternative account. In P.
20 Haggard, Y. Rossetti & M. Kawato (Eds.), *Sensorimotor foundations of higher*
21 *cognition: Attention and performance XX* (Vol. 22, pp. 427-451). Oxford, England:
22 Oxford University Press.
- 23 Csibra, G., & Gergely, G. (2007). 'Obsessed with goals': Functions and mechanisms of
24 teleological interpretation of actions in humans. *Acta Psychologica*, 124(1), 60-78.
25 doi: DOI 10.1016/j.actpsy.2006.09.007
- 26 Curran, T., & Keele, S. W. (1993). Attentional and nonattentional forms of sequence
27 learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*,
28 19(1), 189-202. doi: 10.1037/0278-7393.19.1.189

- 1 Cutting, J. E., & Kozlowski, L. T. (1977). Recognizing friends by their walk: Gait perception
2 without familiarity cues. *Bulletin of the Psychonomic Society*, 9(5), 353-356. doi:
3 10.3758/BF03337021
- 4 Dayan, E., Casile, A., Levit-Binnun, N., Giese, M. A., Hendler, T., & Flash, T. (2007). Neural
5 representations of kinematic laws of motion: Evidence for action-perception coupling.
6 *Proceedings of the National Academy of Sciences*, 104(51), 20582-20587. doi:
7 10.1073/pnas.0710033104
- 8 Di Dio, C., Di Cesare, G., Higuchi, S., Roberts, N., Vogt, S., & Rizzolatti, G. (2013). The
9 neural correlates of velocity processing during the observation of a biological effector
10 in the parietal and premotor cortex. *Neuroimage*, 64(0), 425-436. doi:
11 dx.doi.org/10.1016/j.neuroimage.2012.09.026
- 12 Elliott, D., Hansen, S., Grierson, L. E. M., Lyons, J., Bennett, S. J., & Hayes, S. J. (2010).
13 Goal-directed aiming: Two components but multiple processes. *Psychological*
14 *Bulletin*, 136(6), 1023-1044. doi: 10.1037/a0020958
- 15 Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2001). Phase-specific modulation of
16 cortical motor output during movement observation. *Neuroreport*, 12(7), 1489-1492.
- 17 Gowen, E., Bradshaw, C., Galpin, A., Lawrence, A., & Poliakoff, E. (2010). Exploring
18 visuomotor priming following biological and non-biological stimuli. *Brain and*
19 *Cognition*, 74(3), 288-297. doi: 10.1016/j.bandc.2010.08.010
- 20 Hamilton, A. F. d. C. (2008). Emulation and mimicry for social interaction: A theoretical
21 approach to imitation in autism. *The Quarterly Journal of Experimental Psychology*,
22 61(1), 101-115.
- 23 Hayes, S. J., Hodges, N. J., Huys, R., & Williams, A. M. (2007). End-point focus
24 manipulations to determine what information is used during observational learning.
25 *Acta Psychologica*, 126(2), 120-137.
- 26 Hayes, S. J., Timmis, M. A., & Bennett, S. J. (2009). Eye movements are not a prerequisite
27 for learning movement sequence timing through observation. *Acta Psychologica*,
28 131(3), 202-208.

- 1 Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, 137(3), 463-483. doi:
2 10.1037/a0022288
- 3 Heyes, C., & Bird, G. (2007). Mirroring, association, and the correspondence problem. In P.
4 Haggard, Y. Rossetti & M. Kawato (Eds.), *Sensorimotor foundations of higher*
5 *cognition: Attention and performance XX* (pp. 461-479). Oxford, England: Oxford
6 University Press.
- 7 Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic
8 imitation. *Cognitive Brain Research*, 22(2), 233-240. doi:
9 10.1016/j.cogbrainres.2004.09.009
- 10 Higuchi, S., Holle, H., Roberts, N., Eickhoff, S. B., & Vogt, S. (2012). Imitation and
11 observational learning of hand actions: prefrontal involvement and connectivity.
12 *Neuroimage*, 59(2), 1668-1683. doi: 10.1016/j.neuroimage.2011.09.021
- 13 Iacoboni, M. (2005). Neural mechanisms of imitation. *Current Opinion in Neurobiology*,
14 15(6), 632-637. doi: DOI 10.1016/j.conb.2005.10.010
- 15 Iacoboni, M. (2009). Neurobiology of imitation. *Current Opinion in Neurobiology*, 19(6), 661-
16 665. doi: DOI 10.1016/j.conb.2009.09.008
- 17 Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G.
18 (1999). Cortical mechanisms of human imitation. *Science*, 286(5449), 2526-2528.
19 doi: DOI 10.1126/science.286.5449.2526
- 20 Itti, L., & Koch, C. (2001). Computational modeling of visual attention. *Nature Reviews*
21 *Neuroscience*, 2(3), 194-203.
- 22 Jeannerod, M. (1999). The 25th Bartlett Lecture. *Quarterly Journal of Experimental*
23 *Psychology: Section A*, 52(1), 1-29. doi: 10.1080/027249899391205
- 24 Jenkins, I., Brooks, D., Nixon, P., Frackowiak, R., & Passingham, R. (1994). Motor sequence
25 learning: a study with positron emission tomography. *The Journal of Neuroscience*,
26 14(6), 3775-3790.
- 27 Johansson, G. (1973). Visual perception of biological motion and a model for its analysis.
28 *Perception & Psychophysics*, 14(2), 201-211. doi: 10.3758/BF03212378

- 1 Jueptner, M., Frith, C. D., Brooks, D. J., Frackowiak, R. S. J., & Passingham, R. E. (1997).
2 Anatomy of Motor Learning. II. Subcortical Structures and Learning by Trial and
3 Error. *Journal of Neurophysiology*, 77(3), 1325-1337.
- 4 Jueptner, M., Stephan, K. M., Frith, C. D., Brooks, D. J., Frackowiak, R. S. J., &
5 Passingham, R. E. (1997). Anatomy of Motor Learning. I. Frontal Cortex and
6 Attention to Action. *Journal of Neurophysiology*, 77(3), 1313-1324.
- 7 Kane, M., & Engle, R. (2002). The role of prefrontal cortex in working-memory capacity,
8 executive attention, and general fluid intelligence: An individual-differences
9 perspective. *Psychonomic Bulletin & Review*, 9(4), 637-671. doi:
10 10.3758/bf03196323
- 11 Keele, S. W., Ivry, R., Mayr, U., Hazeltine, E., & Heuer, H. (2003). The cognitive and neural
12 architecture of sequence representation. *Psychological Review*, 110(2), 316-339.
- 13 Kilner, J. M., Hamilton, A. F. d. C., & Blakemore, S. J. (2007). Interference effect of observed
14 human movement on action is due to velocity profile of biological motion. *Social*
15 *Neuroscience*, 2(3), 158-166.
- 16 Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed
17 biological movement on action. *Current Biology*, 13(6), 522-525.
- 18 Kozlowski, L. T., & Cutting, J. E. (1977). Recognizing the sex of a walker from a dynamic
19 point-light display. *Perception & Psychophysics*, 21(6), 575-580. doi:
20 10.3758/BF03198740
- 21 Leighton, J., Bird, G., Orsini, C., & Heyes, C. (2010). Social attitudes modulate automatic
22 imitation. *Journal of Experimental Social Psychology*, 46(6), 905-910.
- 23 Liepelt, R., & Brass, M. (2010). Top-down modulation of motor priming by belief about
24 animacy. *Experimental Psychology* 57(3), 221-227.
- 25 Longo, M. R., Kosobud, A., & Bertenthal, B. I. (2008). Automatic imitation of biomechanically
26 possible and impossible actions: effects of priming movements versus goals. *Journal*
27 *of Experimental Psychology: Human Perception and Performance*, 34(2), 489-501.
28 doi: 10.1037/0096-1523.34.2.489

- 1 Mattar, A. A. G., & Gribble, P. L. (2005). Motor learning by observing. *Neuron*, 46(1), 153-
2 160.
- 3 Press, C. (2011). Action observation and robotic agents: Learning and anthropomorphism.
4 *Neuroscience & Biobehavioral Reviews*, 35(6), 1410-1418.
- 5 Press, C., Cook, J., Blakemore, S. J., & Kilner, J. M. (2011). Dynamic modulation of human
6 motor activity when observing actions. *The Journal of Neuroscience*, 31(8), 2792-
7 2800.
- 8 Press, C., Gillmeister, H., & Heyes, C. (2006). Bottom-up, not top-down, modulation of
9 imitation by human and robotic models. *The European Journal of Neuroscience*,
10 24(8), 2415-2419. doi: 10.1111/j.1460-9568.2006.05115.x
- 11 Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive*
12 *Psychology*, 9(2), 129-154.
- 13 Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying
14 the understanding and imitation of action. *Nature Reviews Neuroscience*, 2(9), 661-
15 670.
- 16 Roberts, J. W., Bennett, S. J., Elliott, D., & Hayes, S. J. (2012). Top-down and bottom-up
17 processes during observation: Implications for motor learning. *European Journal of*
18 *Sport Science*, 1-7.
- 19 Stanley, J., Gowen, E., & Miall, R. C. (2007). Effects of agency on movement interference
20 during observation of a moving dot stimulus. *Journal of Experimental Psychology:*
21 *Human Perception and Performance*, 33(4), 915-926.
- 22 Stefan, K., Cohen, L. G., Duque, J., Mazzocchio, R., Celnik, P., Sawaki, L., . . . Classen, J.
23 (2005). Formation of a motor memory by action observation. *The Journal of*
24 *Neuroscience*, 25(41), 9339-9346.
- 25 van der Helden, J., van Schie, H. T., Rombouts, C., & Dickson, C. T. (2010). Observational
26 Learning of New Movement Sequences Is Reflected in Fronto-Parietal Coherence.
27 *PLoS ONE*, 5(12), 661-670.

- 1 Vangeneugden, J., Pollick, F., & Vogels, R. (2009). Functional Differentiation of Macaque
2 Visual Temporal Cortical Neurons Using a Parametric Action Space. *Cerebral*
3 *Cortex*, 19(3), 593-611. doi: 10.1093/cercor/bhn109
- 4 Vogt, S. (1995). On relations between perceiving, imagining and performing in the learning
5 of cyclical movement sequences. *British Journal of Psychology*, 86(2), 191-216.
- 6 Vogt, S., Buccino, G., Wohlschlaeger, A. M., Canessa, N., Shah, N. J., Zilles, K., . . . Fink, G.
7 R. (2007). Prefrontal involvement in imitation learning of hand actions: effects of
8 practice and expertise. *Neuroimage*, 37(4), 1371-1383.
- 9 Wang, Y., & Hamilton, A. F. d. C. (2012). Social Top-down Response Modulation (STORM):
10 A model of the control of mimicry in social interaction. *Frontiers in Human*
11 *Neuroscience*, 6, 1. doi: 10.3389/fnhum.2012.00153
- 12 Wang, Y., Newport, R., & Hamilton, A. F. d. C. (2011). Eye contact enhances mimicry of
13 intransitive hand movements. *Biology Letters*, 7(1), 7-10. doi: 10.1098/rsbl.2010.0279
14
- 15 Wang, Y., Ramsey, R., & Hamilton, A. F. d. C. (2011). The control of mimicry by eye contact
16 is mediated by medial prefrontal cortex. *The Journal of Neuroscience*, 31(33), 12001-
17 12010.
- 18 Wohlschlaeger, A., Gattis, M., & Bekkering, H. (2003). Action generation and action
19 perception in imitation: an instance of the ideomotor principle. *Philosophical*
20 *Transactions of the Royal Society B: Biological Sciences*, 358(1431), 501-515. doi:
21 10.1098/rstb.2002.1257
22

Figure Captions

Figure 1. An illustration of the experimental set-up (A). An illustration of a CRT monitor displaying the 3 x 3 grid formation and embedded movement sequence. The white circle represents the model; the white dashed lines indicate the 3 segment movement sequence and (in parentheses) the relative timing goals (B).

Figure 2. Displays the velocity profiles (x axis = light grey trace; y axis = dark grey trace) for the *typical* (upper panel) and *atypical* (lower panel) biological motion models.

Figure 3. Displays adjusted group mean data (error bars represent standard error) from Experiment 1 for (A) IEtPV (B) tPV across segments (C) IEpPV (D) pPV across segments. The atypical (attached to the dark grey bar) and typical (attached to the light grey bar) model segment data are represented by the white bars within panels B and D. * $p < 0.05$

Figure 4. The velocity traces (x axis = light grey trace; y axis = dark grey trace) displayed in panels A (Experiment 1), C (Experiment 2) and E (Experiment 3) are exemplar data from a representative participant in the *atypical* condition. Panels B (Experiment 1), D (Experiment 2) and F (Experiment 3) display exemplar data from a representative participant in the *typical* condition.

Figure 5. Displays adjusted group mean data (error bars represent standard error) from Experiment 2 for (A) IEtPV (B) tPV across segments (C) IEpPV (D) pPV across segments. The atypical (attached to the dark grey bar) and typical (attached to the light grey bar) model segment data are represented by the white bars within panels B and D.

Figure 6. Displays adjusted group mean data (error bars represent standard error) from Experiment 3 for (A) IEtPV (B) tPV across segments (C) IEpPV (D) pPV across segments. The atypical (attached to the dark grey bar) and typical (attached to the light grey bar) model segment data are represented by the white bars within panels B and D. * $p < 0.05$

Figure 7. Displays a schematic representation of how input modulation influences the coding of biological motion kinematics and timing goals during observational practice. The left-hand y axis is attention, right-hand y axis is accuracy, and x axis is kinematics and timing goals. N.B. the data presented have been simulated for representational purposes and so the magnitude of these differences is neither absolute nor examined. The figure is intended to illustrate how the acquisition of *atypical* kinematics and timing goals might compete under different attentional modulations.

Table 1

Group Means (standard error of the mean) for Total Error (ms) and Relative Time Error (%) in Experiment 1, 2 and 3

Experiment 1					Experiment 2					Experiment 3				
Group	Total Error		Relative Time Error		Group	Total Error		Relative Time Error		Group	Total Error		Relative Time Error	
	Mean	(SEM)	Mean	(SEM)		Mean	(SEM)	Mean	(SEM)		Mean	(SEM)	Mean	(SEM)
Atypical	948.83	223.21	15.50	2.08	Atypical-attention	918.14	138.42	20.06	1.80	Atypical-general	982.60	205.00	15.85	2.78
Typical	562.01	223.01.	17.01	2.04	Typical-attention	841.49	138.43	19.32	1.77	Atypical-trajectory	851.46	205.00	27.38	2.74
Control	1590.71	223.16	32.40	2.08	Control-attention	1869.09	138.41	35.15	1.92	Control	1606.65	205.62	32.40	2.81

Figure 1

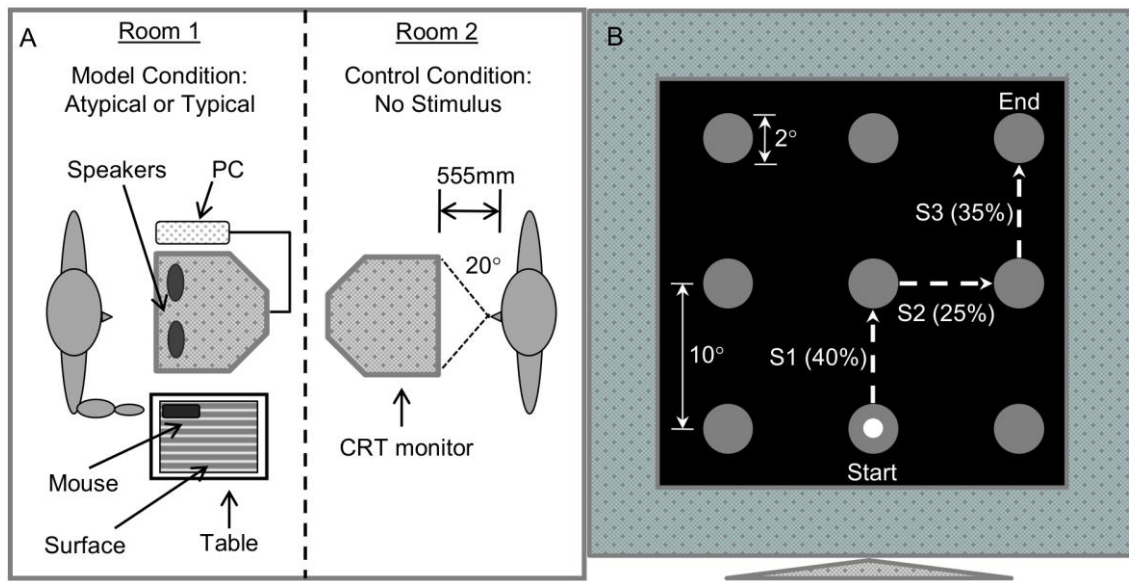


Figure 2

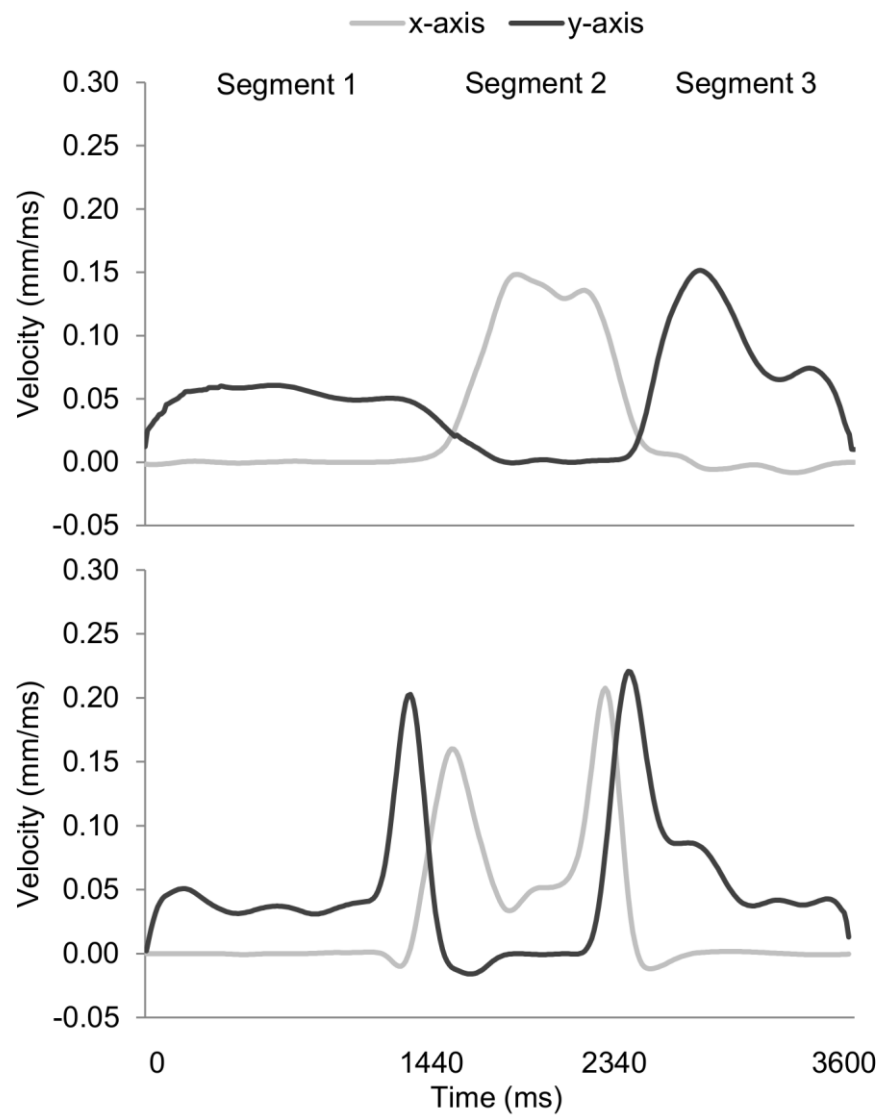


Figure 3

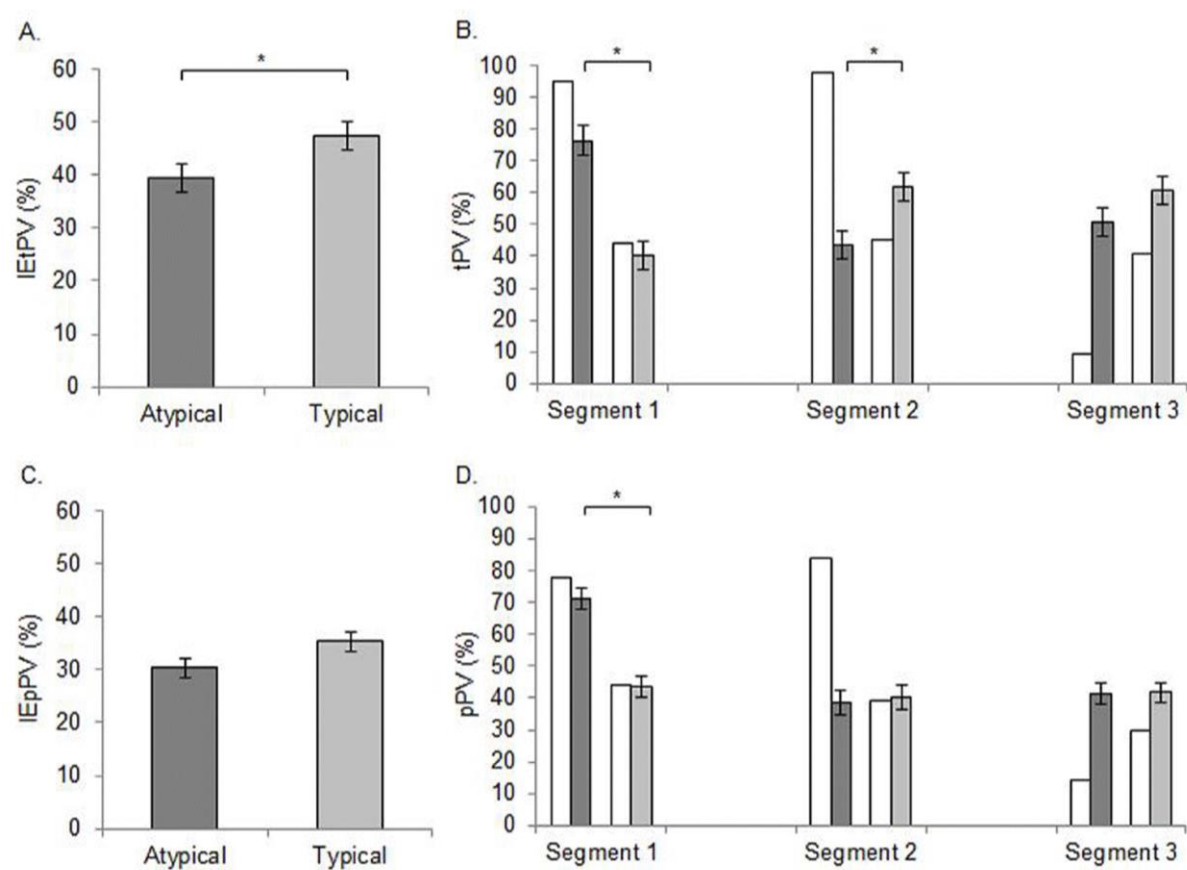


Figure 4

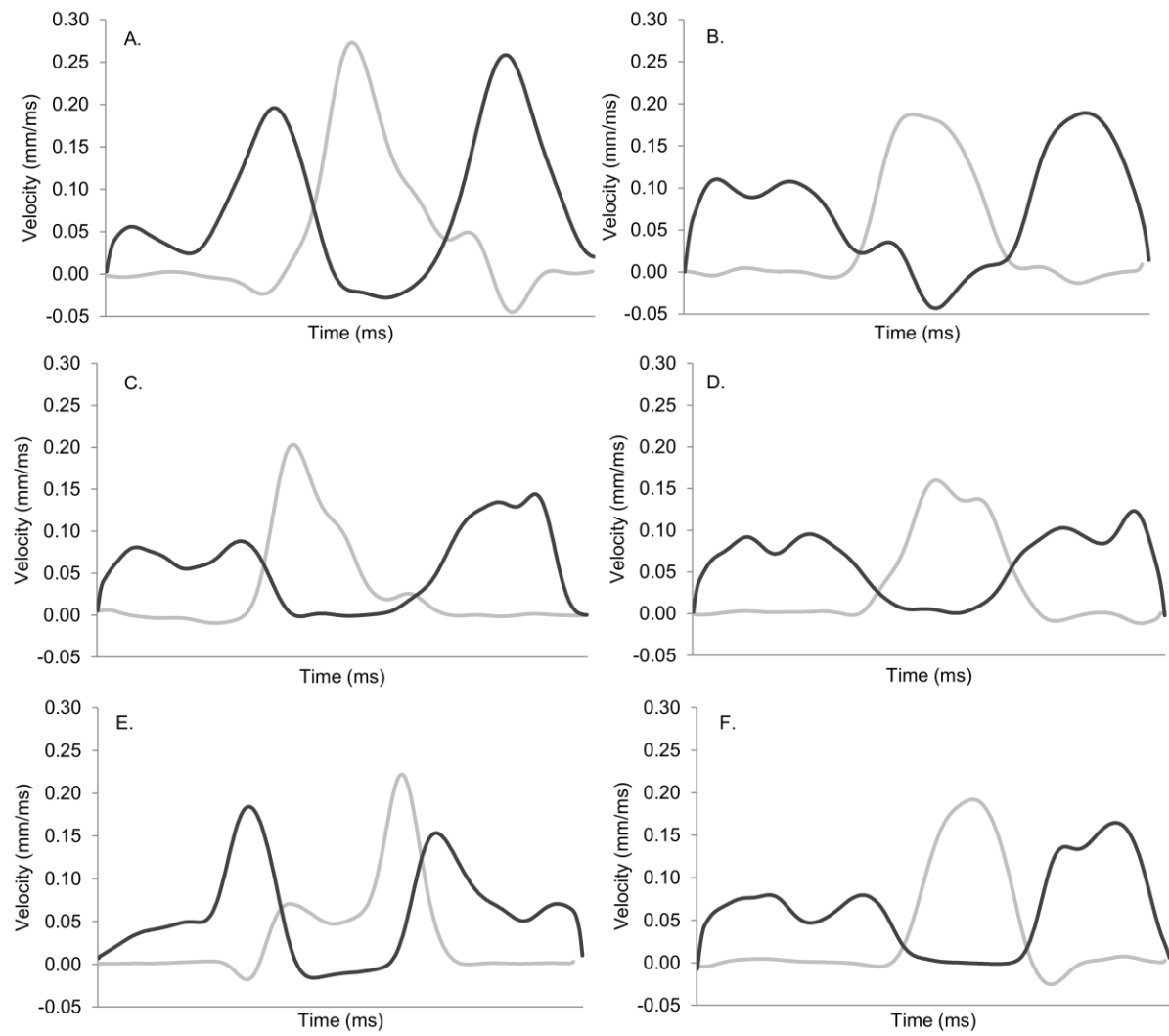


Figure 5

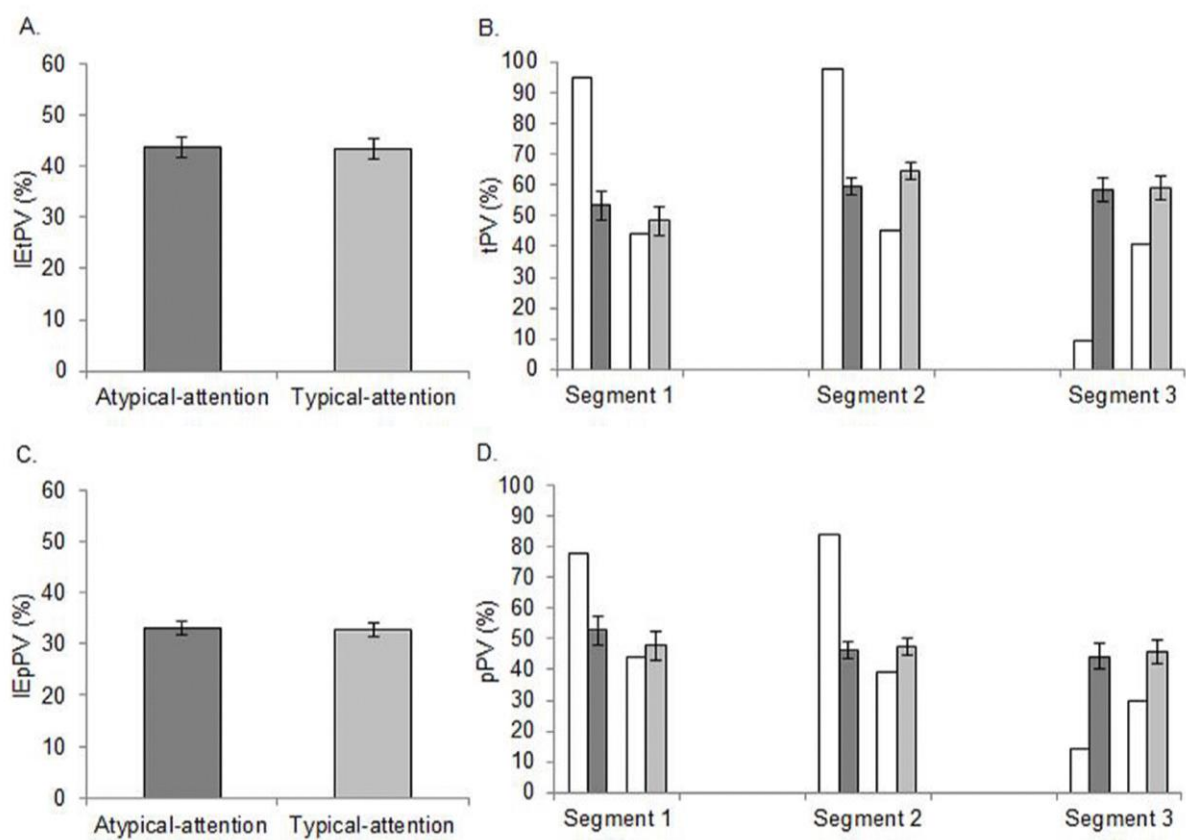


Figure 6

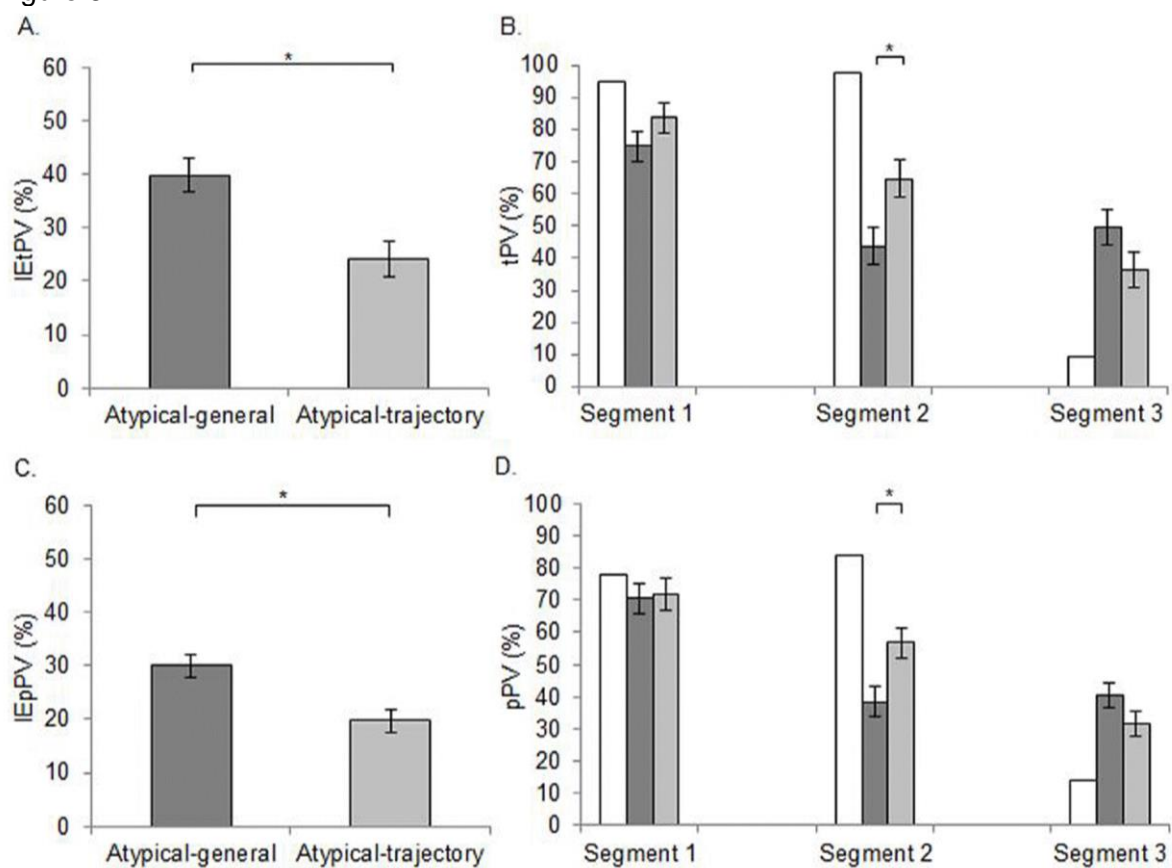


Figure 7

