

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

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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

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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 (DLFPC), 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

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

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

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

3

4

Experiment 1

5 Method

6 **Participants.** Data were recorded from thirty-three participants (aged between 18 to
7 21 years), who were randomly assigned to either a *control* group (n = 11) that did not
8 observe a model, or an experimental group that observed a model displaying *typical*
9 biological motion (n = 11) or *atypical* biological motion (n = 11). All participants had normal or
10 corrected-to-normal vision and gave written informed consent. The experiment was designed
11 in accordance with the Declaration of Helsinki and was approved by the ethics committee of
12 the host University.

13 **Apparatus, procedure and stimuli.** The apparatus consisted of a PC (Dell Optiplex
14 GX280) connected to a 21-in CRT computer monitor (Iiyama Vision Master 505). The CRT
15 monitor operated with a resolution of 1600 x 1400 pixels and a refresh rate of 85 Hz, and a
16 Logitech G5 laser mouse and Set-Point 2.42a mouse driver (1200 DPI; 1000 reports/s USB;
17 6.4 megapixels/s; 1.13–1.63 mm/ms). The visual stimuli were generated via MATLAB (The
18 Mathworks, Inc), using Cogent 2000 toolbox (www.vislab.ucl.ac.uk/cogent.php). A second
19 21-in CRT computer monitor was used for the control condition (Room 2; Figure 1A).

20 Participants were seated on a chair positioned (Figure 1A) so that the eyes were
21 located 555 mm from the center of a monitor. Nine grey circles that each subtended a visual
22 angle of 2° (target size = 18.75 mm) were displayed against a black background on the
23 monitor in a grid formation with equidistant horizontal and vertical visual angular extent of
24 10° (amplitude between two targets = 100 mm). Four target circles representing the spatial
25 endpoints of the three segments within the movement sequence were illustrated to a
26 participant using a visual template (similar to Figure 1B; the sequence configuration was
27 fixed within the experiment). A white cursor subtending a visual angle of 0.6° (cursor size =

1 6.25 mm) was drawn on the monitor and represented the motion of the mouse. The two-
2 dimensional position of the mouse was polled at 1000 Hz, and then used to update and
3 redraw the mouse cursor on each monitor refresh.

4 All participants from the experimental groups were informed the motor learning study
5 they engaged in had a pre-test, followed by an observational practice phase (the control
6 groups observed a blank screen) and a post-test. They also received general experimental
7 instructions indicating the to-be-learned movement sequence timing goals, which remained
8 constant throughout all experiments, were associated with *absolute time* and *relative time*.
9 The *absolute time* goal was 3600 ms and reflected the total time required to move a white
10 mouse cursor from the start position through the movement sequence, before finally
11 pressing the right mouse button once the mouse cursor was stopped within the end target
12 circle. The *relative time* goal was 40% (1440 ms) for segment 1, 25% (900 ms) for segment
13 2 and 35% (1260 ms) for segment 3 (i.e., 1440 ms + 900 ms + 1260 ms = 3600 ms). This
14 *relative time* goal was selected because it required the three upper-arm movements to be
15 coordinated to achieve a constrained, novel timing pattern.

16 Each participant was instructed that the goal in the pre-test was to perform the
17 movement sequence in order to obtain the *absolute* and *relative time* goals as accurately as
18 possible. They performed 6 trials (1 familiarization; 5 experimental) in Room 1 using the
19 right-arm and received no knowledge of results (KR) regarding absolute time error or relative
20 timing error. A trial commenced with the *relative time* goal [segment 1 = 40% (1440 ms);
21 segment 2 = 25% (900 ms); segment 3 = 35% (1260 ms)] displayed on the monitor for 2000
22 ms, after which it was replaced with the grid formation and the embedded to-be learned
23 movement sequence. To start a trial, the participant pressed the left mouse button, upon
24 which the grid formation disappeared for 2000 ms and then reappeared. The participant was
25 then free to move the mouse so that the cursor moved through (there was no requirement to
26 physically stop the movement in these targets) the second and third targets in order to come
27 to a stop within the end target in accord with the *absolute time* goal and *relative time* goal.
28 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.

6
7 Insert Figure 1 and 2
8

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

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

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

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

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

10

11 **Results**

12 **Timing.** ANCOVA returned significant main effects for Total Error [$F(2, 29) = 5.42 p <$
13 $0.05, \eta_p^2 = 0.27$] and Relative timing Error [$F(2, 29) = 19.86 p < 0.05, \eta_p^2 = 0.58$]. The first
14 planned comparisons, which compared the two experimental groups against the *control*
15 group, indicated significant differences for Total Error [$F(1, 29) = 9.34 p < 0.05, \eta_p^2 = 0.24$]
16 and Relative Timing Error [$F(1, 29) = 39.63 p < 0.05, \eta_p^2 = 0.58$]. The adjusted mean
17 differences showed the experimental groups were more accurate than the *control* group by
18 835 ms for Total Error and 16 units for Relative Timing Error (Table 1; Experiment 1). As can
19 be seen in Table 1, the second comparison revealed no significant differences between the
20 *typical* and *atypical* groups for Total Error [$F(1, 29) = 1.50 p > 0.05, \eta_p^2 = 0.05$] and Relative
21 Timing Error [$F(1, 29) = 0.27 p > 0.05, \eta_p^2 = 0.01$].

22

23 Insert Table 1 and Figure 3 about here

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

1 exhibited movement trajectories (Figure 3A, timing of peak velocity; Figure 3C, spatial
2 position of peak velocity) that were more accurate than *typical* group. The segment effects
3 for tPV (Figure 3B) showed a group difference in segment 1 [$F(1, 19) = 29.64$ $p < 0.05$, $\eta_p^2 =$
4 0.61] and 2 [$F(1, 19) = 8.24$ $p < 0.05$, $\eta_p^2 = 0.30$], but not 3 [$F(1, 19) = 2.67$ $p > 0.05$, $\eta_p^2 =$
5 0.12]. Similar effects were observed for pPV, with a group difference in segment 1 [$F(1, 19)$
6 $= 37.72$ $p < 0.01$, $\eta_p^2 = 0.65$], but not 2 [$F(1, 19) = 0.09$ $p > 0.05$, $\eta_p^2 = 0.01$] or 3 [$F(1, 19) =$
7 0.01 $p > 0.05$, $\eta_p^2 = 0.01$]. As illustrated in Figure 3B and D (the white bars represent the
8 *atypical* model and *typical* model), the kinematic data in segment 1 showed the timing, and
9 spatial position, of peak velocity occurred later (tPV = 77%), and towards the end (pPV =
10 71%) of the movement trajectory in segment 1 for the *atypical* group, compared to the *typical*
11 group (tPV = 40%; pPV = 43%). This effect can also be seen in Figure 4 where the exemplar
12 velocity trace from a representative participant in the *atypical* group (Figure 4A) indicated
13 peak velocity occurred later in segment 1, but not 2 and 3. For the representative participant
14 in the *typical* group (Figure 4B), peak velocity occurred towards the midpoint of the
15 movement across the 3 segments and thus similar to the *typical* model (Figure 2 upper-
16 panel).

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18 Insert Figure 4 about here
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20 Discussion

21 The results for Total Error and Relative Time Error confirm absolute (Blandin, et al.,
22 1999) and relative time (Vogt, 1995) goals were learned. The significant difference between
23 *typical* and *atypical* groups for the kinematic data (IEtPV; IEpPV; tPV; pPV) indicated
24 biological motion kinematics were coded. Specifically tPV in segment 1 occurred at 77% and
25 pPV occurred at 71% of the movement for the *atypical* group, which is closer to the *atypical*
26 model (tPV = 95%; pPV = 78%). For the *typical* model condition, tPV occurred at 40% and
27 pPV occurred at 43%% of the movement which is closer to the *typical* model (tPV = 44%;

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

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Experiment 2

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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

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

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14 **Method**

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

22 **Apparatus, procedure and stimuli.** The movement sequence, apparatus and
23 general procedures were identical to the previous experiment. Here, though, participants
24 performed a dual-task that required them to count the number of high-pitched tones (300 Hz)
25 that were interleaved amongst low-pitch tones (150 Hz). The tones were presented on two
26 speakers positioned on top of the monitor that a model was observed (Figure 1A). The
27 presentation of the auditory tones was controlled using a MATLAB routine so that eight
28 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.

12

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-*

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

3 **Kinematics.** ANCOVA conducted on IEtPV [$F(1, 19) = 0.02$ $p > 0.05$, $\eta_p^2 = 0.001$]
4 and IEpPV [$F(1, 19) = 0.79$ $p > 0.05$, $\eta_p^2 = 0.03$] showed no significant difference between
5 the *typical-attention* and *atypical-attention* groups in terms of timing (Figure 5A), and spatial
6 position (Figure 5C), of peak velocity. There were also no significant differences across all
7 segments for tPV (Figure 5B): segment 1 [$F(1, 19) = 0.53$ $p > 0.05$, $\eta_p^2 = 0.03$], 2 [$F(1, 19) =$
8 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),
9 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
10 [$F(1, 19) = 0.08$ $p > 0.05$, $\eta_p^2 = 0.01$]. This effect is displayed in Figure 4 where the exemplar
11 velocity traces from the representative participants in the *atypical* (Figure 4C) and *typical*
12 (Figure 4D) groups indicated peak velocity occurred towards the midpoint of the movement
13 in each of the 3 segments, which was consistent with the *typical* model (Figure 2 upper-
14 panel).

15
16 Insert Figure 5 about here
17

18 Discussion

19 The absolute and relative time goals were learned by observing *typical* and *atypical*
20 models during observational practice. The fact the dual-task did not attenuate the acquisition
21 of the timing goals indicated these representations can be developed when attentional
22 resources are divided by a tone-counting-task. As predicted, no significant differences were
23 found between the groups for kinematic variables, thus indicating the dual-task modulated
24 the coding of biological motion kinematics. Specifically, both groups executed tPV (*typical-*
25 *attention* = 48%; *atypical-attention* = 53%) and pPV (*typical-attention* = 48%; *atypical-*
26 *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.

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Experiment 3

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

1 Results

2 **Timing.** ANCOVA returned significant main effects for Total Error [$F(2, 29) = 5.19$ $p <$
3 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
4 comparison revealed significant differences for Total Error [$F(1, 29) = 10.19$ $p < 0.05$, $\eta_p^2 =$
5 0.21] and Relative Timing Error [$F(1, 29) = 9.57$ $p < 0.05$, $\eta_p^2 = 0.23$]. The mean differences
6 indicated the experimental groups were more accurate than the *control* group by 688 ms for
7 Total Error and 11 units for Relative Timing Error (Table 1; Experiment 3). The second
8 comparison indicated there was no significant difference between the *atypical-general* and
9 *atypical-trajectory* groups for Total Error [$F(1, 29) = 0.20$ $p > 0.05$, $\eta_p^2 = 0.01$]. Importantly,
10 there was a significant difference for Relative Timing Error [$F(1, 29) = 8.82$ $p < 0.05$, $\eta_p^2 =$
11 0.23], with the *atypical-general* group being significantly more accurate than the *atypical-*
12 *trajectory* group by 12 units of relative timing error.

13 **Kinematics.** ANCOVA for IEtPV indicated a significant difference of 16 units
14 between the *atypical-trajectory* and *atypical-general* groups [$F(1, 19) = 12.19$ $p < 0.05$, $\eta_p^2 =$
15 0.39], and a group difference of 5 units for IEpPV [$F(1, 19) = 3.22$ $p = 0.09$, $\eta_p^2 = 0.15$].
16 These effects showed the *atypical-trajectory* group was more accurate than the *atypical-*
17 *general* group at imitating timing (Figure 6A), and spatial position (Figure 6C), of peak
18 velocity. The segment results for tPV showed no group differences in segment 1 [$F(1, 19) =$
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
20 difference in segment 2 [$F(1, 19) = 6.43$ $p < 0.05$, $\eta_p^2 = 0.25$]. Similarly, no group differences
21 were observed for pPV in segment 1, [$F(1, 19) = 0.10$ $p > 0.05$, $\eta_p^2 = 0.01$] and 3 [$F(1, 19) =$
22 2.24 $p > 0.05$, $\eta_p^2 = 0.11$], but a significant difference was observed in segment 2 [$F(1, 19) =$
23 7.25 $p < 0.05$, $\eta_p^2 = 0.29$]. The effects for segment 1 are important because they showed the
24 experimental groups exhibited kinematics similar to the model. Specifically, timing (tPV), and
25 spatial position (pPV) of peak velocity, occurred later (Figure 6B), and towards the end
26 (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).

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Insert Figure 6 about here

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13 **Discussion**

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

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

3

4

General Discussion

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

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

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

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

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

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Insert Figure 7 about here

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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.

16

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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

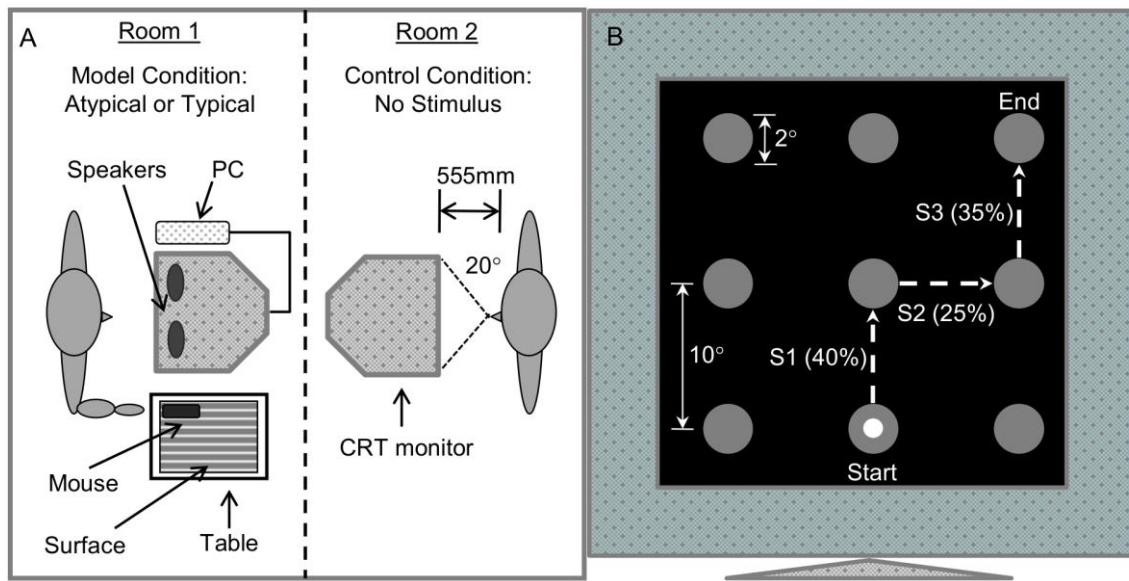


Figure 2

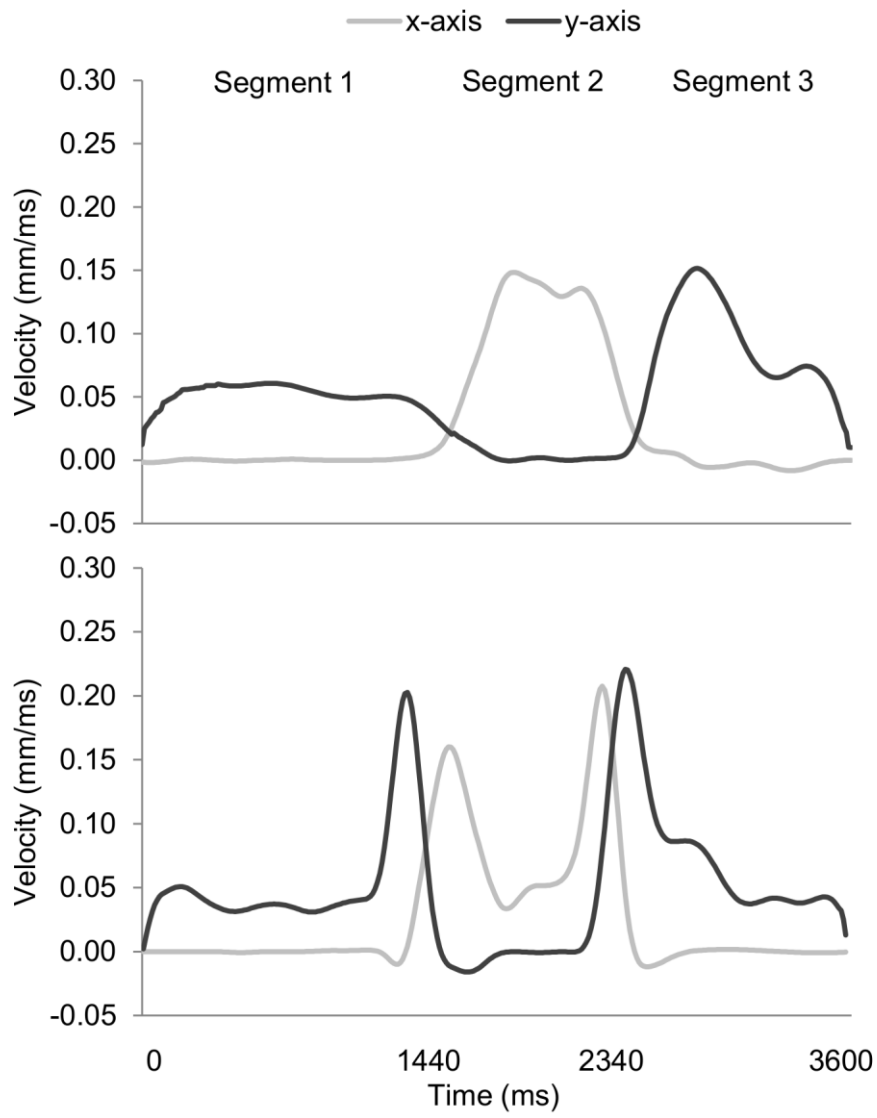


Figure 3

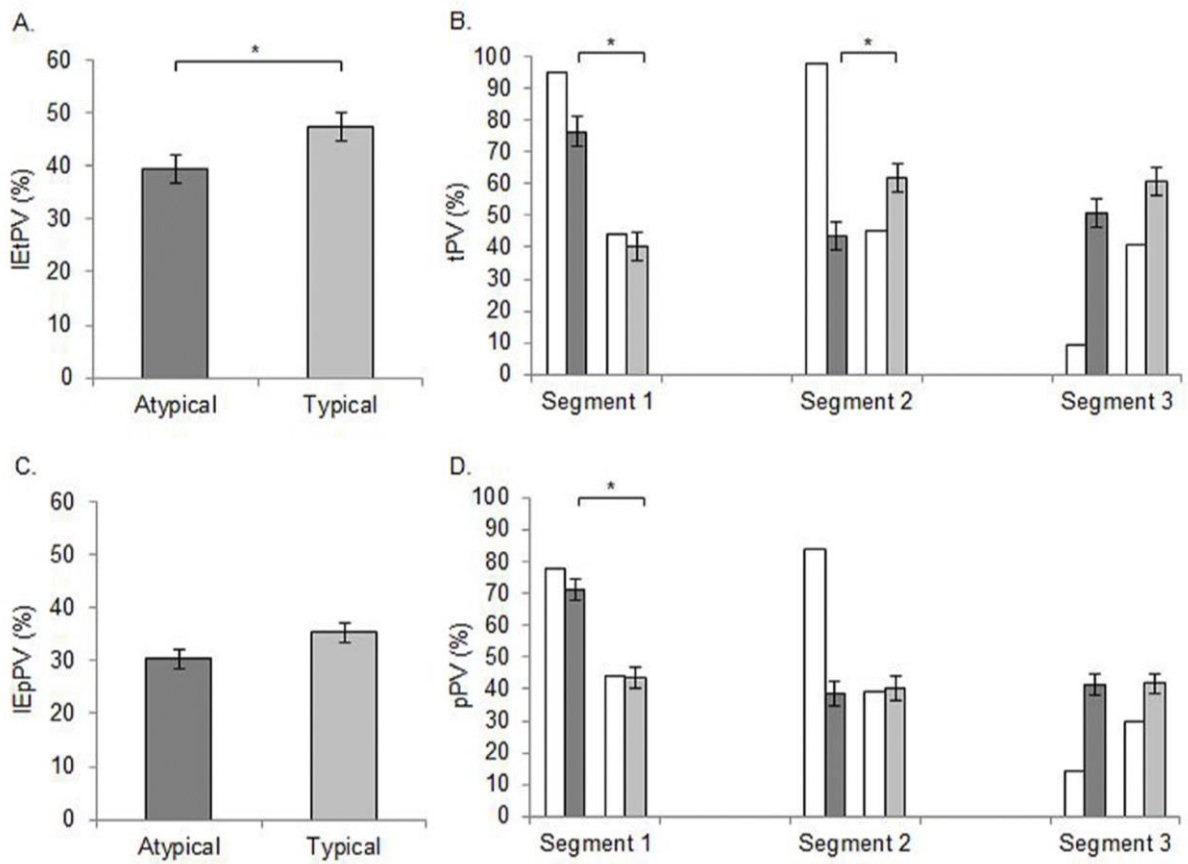


Figure 4

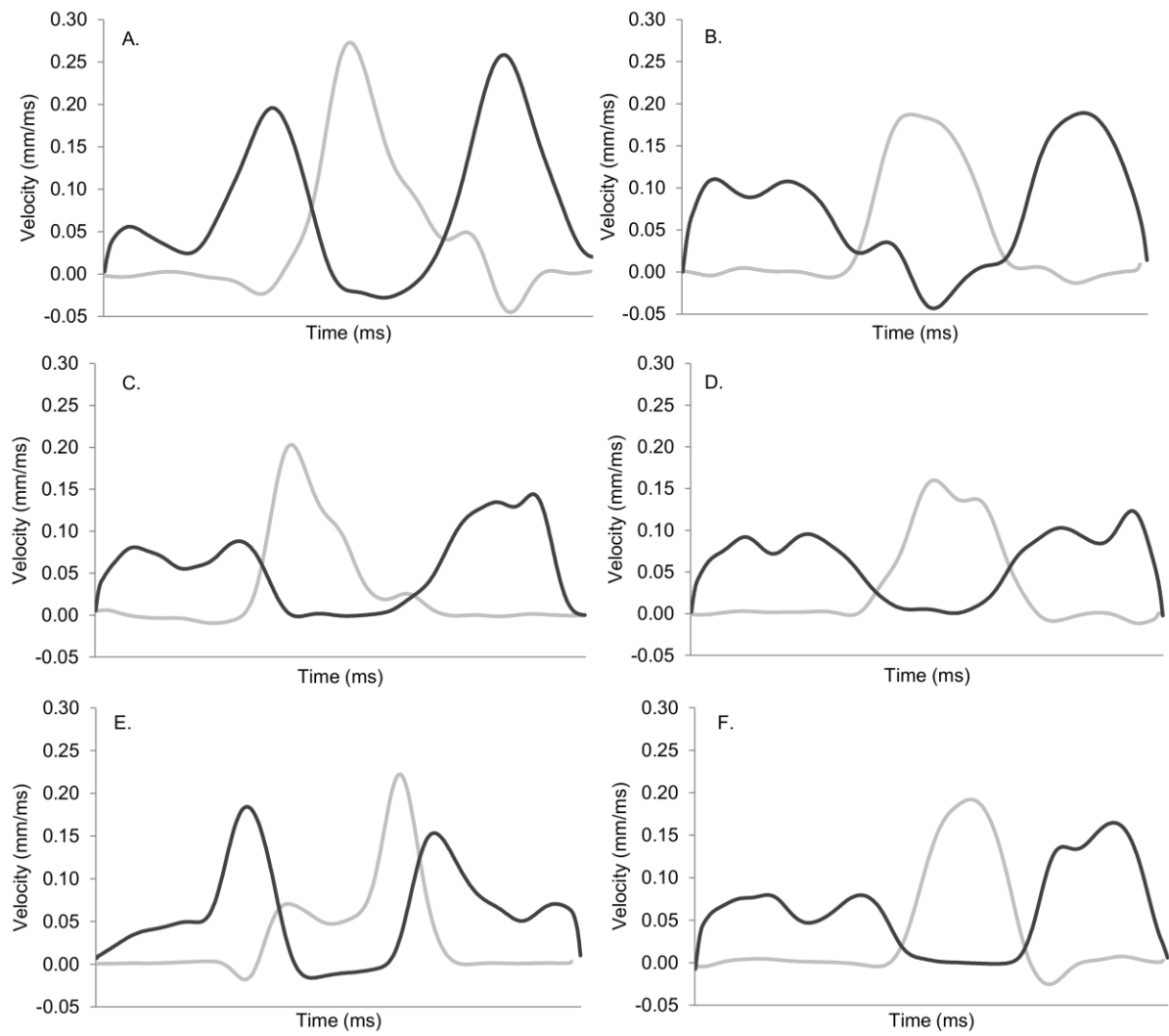


Figure 5

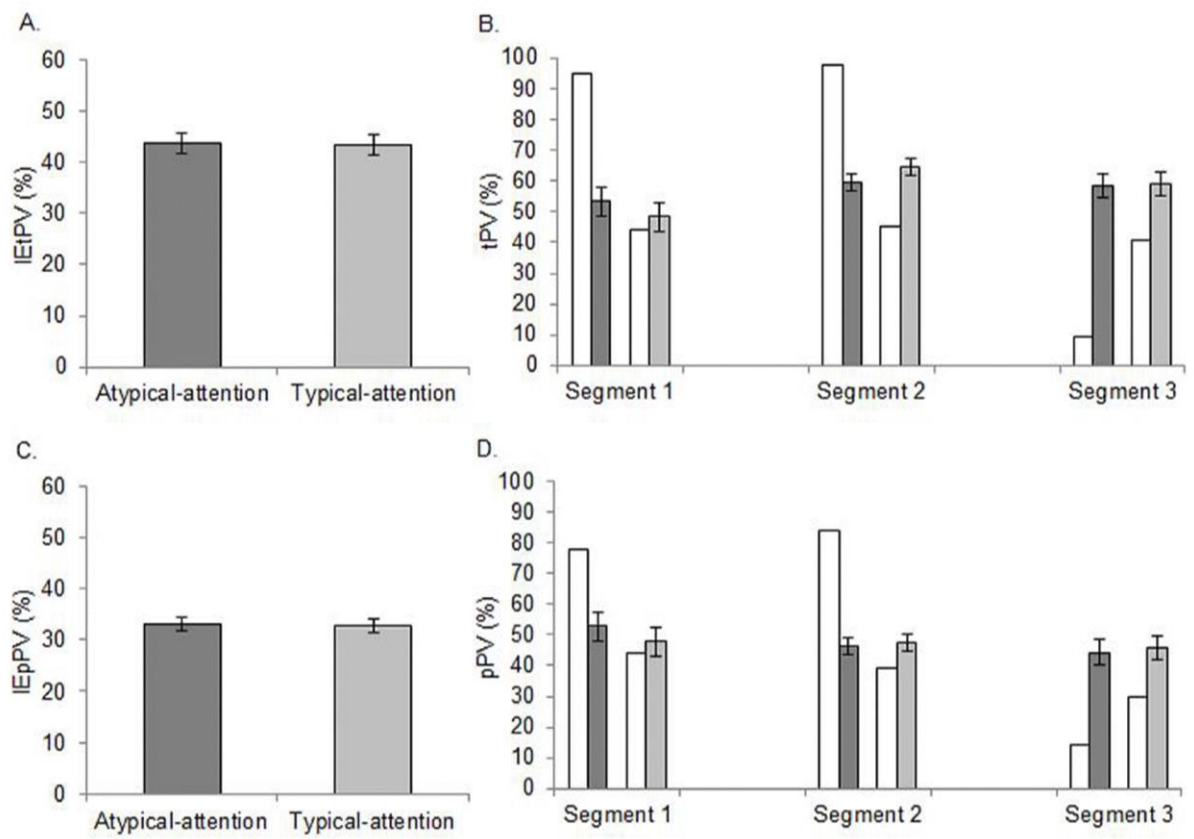


Figure 6

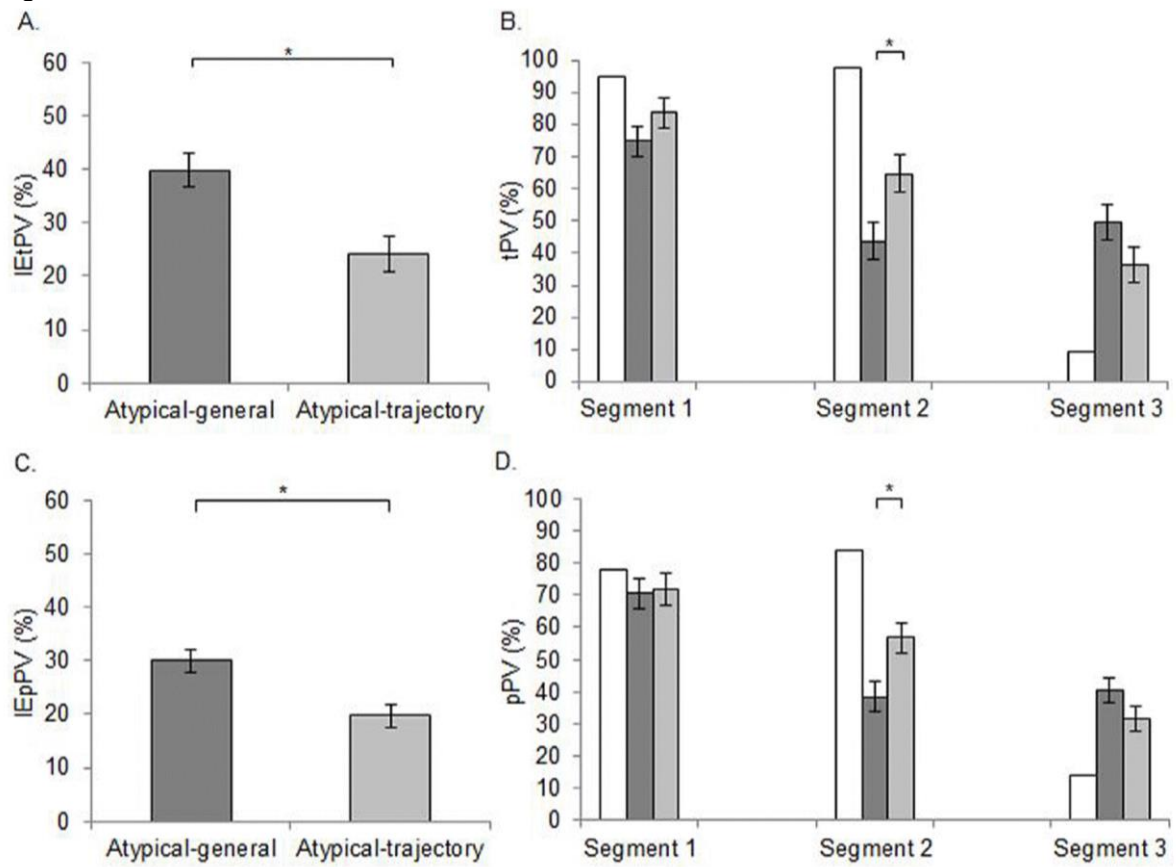


Figure 7

