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7	Action imitation via trajectory-based or posture-based planning
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Abstract

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Movement imitation is a significant daily activity involved in social interaction and motor 2 3 learning. Although imitation remains poorly understood, recent research suggests that it may be 4 achieved in two distinct ways. In posture-based imitation, movements reproduce how the body 5 should look and feel, and are sensitive to the relative positioning of body parts. In trajectory 6 imitation, movements mimic the spatiotemporal motion path of the end effector. We 7 hypothesized that people can imitate via either mechanism. If true, we would expect to see a 8 switch cost when individuals change from one mechanism to the other. To test this, twenty-five 9 healthy young adults performed a sequential multitasking imitation task. Participants were first 10 instructed to pay attention to the limb postures or the hand path of a video-recorded model. They 11 next performed an intervening motor task that was neutral, congruent, or incongruent with the 12 instructed imitation type. Finally, participants imitated the modeled movement. Spatiotemporal 13 imitation accuracy was greatest after a neutral intervening task, and worst after posture matching. 14 When the primary task involved imitating trajectories, we observed a switch cost: movements 15 following the posture-matching intervening task were less consistent with baseline (neutral) 16 performance, suggesting performance was disrupted by the incongruence. Incongruent primary 17 and intervening tasks also reduced cross-subject consistency. Such effects were not observed 18 when imitating limb postures. In summary, we observed a partial dissociation between posture 19 matching and trajectory imitation as a result of instructions and intervening tasks that is 20 nevertheless consistent with the existence of two computationally distinct imitation mechanisms. 21

22 Keywords: Posture matching imitation, trajectory imitation, task-switching

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1. Introduction

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2 The capacity to imitate another individual's actions is critical to many daily social 3 interactions, and is a key component of motor learning and recovery. For instance, reaching up to 4 return a high-five, learning ballet, or rehabilitation of functional movement after stroke can all 5 involve observing and imitating another's movements. Despite the prevalence of imitation in our 6 day-to-day lives, there is no consensus regarding how humans imitate. Two proposed 7 mechanisms include imitation via matching limb postures, and imitation via matching motion 8 trajectories. However, as these mechanisms have thus far not been studied in the context of a 9 single experiment, it unknown whether individuals can and do imitate using both of these 10 methods. 11 A large body of prior research suggests that we imitate movements by matching the postural configurations of our own limbs to the limb configurations of the individual-to-be-12 13 imitated [1,2]. When performing a high-five, for instance, one might seek to match the shoulder-14 elbow-forearm-hand positioning of the other person in order to successfully complete the 15 required response. That is, imitation by posture matching involves a body-dependent process of 16 generating goal representations specifying how the limbs should look and feel while performing 17 the action [3]. Indeed, one well-supported theory proposes that, in general, we plan movements with the intent to achieve desired postures [4,5]. Much of the evidence for posture-based 18 19 imitation stems from research in individuals with limb apraxia, a disorder that commonly results 20 from stroke lesions to the left hemisphere. People with apraxia experience difficulties with 21 imitating gestures [6,7] [1,2] – especially when the relative positions of body parts is critical [8]

22 – despite having otherwise intact motor control. Apraxia is often thought to be related to an

23 inability to form a spatial-configural representation of the body [9], effects which can be

1 observed when individuals imitate postural configurations with their own body or by positioning 2 the limbs of a mannequin [10]. In fact, imitation impairments in these patients have been found 3 to correlate with impairments of the "body schema" [6,11], a representation supporting the 4 ability to represent the spatial relationships between body parts [12,13]. This relationship 5 between imitation deficits and impaired body schema representations in patients with apraxia has 6 been cited as evidence supporting the idea that imitation can occur by matching limb postures. 7 Recently, we proposed another mechanism for imitation that instead involves matching 8 the dynamic trajectory of the end-effector [14]. To imitate a high-five using this method, an 9 individual may specify their desired movement in terms of an arcing motion of the hand to 10 mirror the motion trajectory of the other individual's hand. In this case, the configuration of the 11 individual limb segments to achieve this trajectory are not directly specified as in posturematching imitation, but are simply those most amenable to producing the desired hand motion. 12 13 Thus trajectory imitation is body-independent, as it requires only specifying the motion path of 14 the hand in space [15]. Indeed, when observing others in preparation for imitation, individuals 15 often focus primarily on the end-effector [16]. Our recent study demonstrated that individuals 16 with apraxia are impaired at imitating motion trajectories even when they are presented with no 17 associated body-posture information [14]. In that study, participants with left-hemisphere stroke and neurotypical controls were asked to imitate motion trajectories cued by a human model or 18 19 via the movement of a cursor. While neurotypical controls could successfully imitate the 20 movement regardless of how they were cued, imitation performance in participants with stroke 21 was equally impaired in both conditions, revealing that it is not necessary to observe body-22 configuration information when imitating. However, while suggestive, the previous study did not 23 definitively demonstrate that participants were planning motion trajectories during imitation (i.e.,

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they could have specified their motor plans in terms of postural configurations that satisfy the
desired trajectory). As such, the previous study leaves open the question of whether people
actually directly plan imitative movements by specifying end-effector trajectories; i.e., whether
people actually imitate using both mechanisms.

5 While in many cases imitating postures and trajectories will result in the same gross 6 behavior, some situations seem likely to favor the use of one mechanism over the other. For 7 instance, when learning classical ballet, a student must focus on matching the correct arm, torso, 8 and leg positions of the teacher, which results in enhanced posture matching imitation abilities 9 over years of training [17-19]. On the other hand, when reaching around obstacles the primary 10 concern is to control the trajectory of the hand [15]. Some previous research has even suggested 11 that an observed action may be represented in terms of both postural forms and motion trajectories [20]; this may be possible as different neuroanatomic structures have been associated 12 13 with posture matching (left inferior parietal lobe) and trajectory imitation (left dorsolateral 14 premotor cortex) [7,14]. Thus we hypothesized that individuals should able to use either 15 proposed imitation mechanism depending on the specific task goals.

16 To test this hypothesis, we manipulated the goal of an imitation task by changing the task 17 instructions. Task instructions have been previously shown to strongly modulate how individuals complete a given task. A large body of prior research, for example, has shown that instructions 18 19 can modulate where people focus their attention while completing various activities, 20 consequently affecting task success. Across a variety of motor activities (from balance and 21 jumping to tennis and golf), instructions to focus on internal features such as how an individual's 22 body is moving (e.g., arm postures during a tennis swing) tends to result in worse performance 23 compared to instructions directing focus toward external features associated with how the

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environment is affected by the movement (e.g., the motion of the racket and ball) (for reviews,
see [21–25]. Thus task instructions can have a surprisingly strong effect on the way in which
people perform motor tasks, and suggest the importance of attending to body-independent
motion trajectories when body position is not explicitly critical (for a similar effect in stroke
patients, see [26]).

6 Here, we used an instruction manipulation to encourage neurotypical individuals to focus 7 on either imitating postures or trajectories in the same paradigm with the same stimuli. To assess 8 whether participants used both forms of imitation as instructed, we employed a sequential 9 multitasking paradigm designed to create interference in the form of a switch cost associated 10 with transitioning from one mechanism to the other. Often observed in cognitive tasks, switch 11 costs can also impair motor planning [27]. Switch cost effects occur in the sequential 12 multitasking paradigm when an intervening task inserted in the midst of a primary task relies on 13 distinct computational processes [28,29], requiring a large "switch" between tasks and 14 subsequently impairing performance of the primary task. Sequential multitasking paradigms 15 have often been used in action observation studies to assess memory for whether an action has 16 been previously observed or not (for a review, see [30]), showing that memory for static postures 17 and dynamic full movements rely on distinct working memory processes [31]; however, 18 sequential multitasking paradigms have not yet been applied to imitation. 19 In the current study, participants first observed a meaningless upper arm movement 20 demonstrated by a model on video and were instructed that they would either have to match body

21 postures or match hand trajectories. Participants then completed an intervening task that was

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designed to be either congruent (no switch cost), incongruent (inducing a switch cost), or neutral

23 with respect to the primary imitation task instructions. We assessed accuracy of movement and

1	timing between the participant and the model, and additionally conducted post hoc analyses
2	comparing participant's movement consistency in the congruent and incongruent conditions
3	against their own performance in the neutral condition, as well as with the other participants'
4	performance in the same condition. We predicted that in all cases, performing incongruent
5	primary and intervening tasks (e.g., trajectory imitation instructions and the posture-matching
6	intervening task) would induce a larger performance decrement compared to performing
7	congruent primary and intervening tasks (e.g., trajectory imitation instructions and the trajectory
8	intervening task). Such findings would provide evidence in support the existence of two
9	computationally distinct means of imitating – by matching postures or copying trajectories – and
10	suggest that individuals are able to employ either mechanism depending on the task goals.
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12	2. Methods
13	2.1 Participants
14	We recruited participants from Salus University through email solicitation with
15	recruitment procedures approved by the Salus Institutional Review Board. Participants were
16	graduate students or faculty in a healthcare field, such as Occupational Therapy or Optometry.
17	Twenty-five young adults completed the experiment across two sessions (22 female). The
18	average age was 25.0 years (SD=4.8, range 22 to 41 years). Participants were right-handed, had
19	full range of motion of the arm, normal or corrected-to-normal vision, and no known
20	neurological disorders. All participants provided written informed consent with procedures
21	approved by the Einstein Healthcare Network Institutional Review Board. Participants
22	completed two sessions; the first session lasted approximately 1.5 hours, and the second session

occurred a minimum of one week later and lasted approximately 1 hour. Participants were
 compensated \$15 per hour for their time.

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4 2.2 Materials

5	For the imitation experiment, participants were seated in a stationary chair 176 cm in
6	front of a 42.5" 4K LG monitor (refresh rate, 60 Hz) mounted on the wall directly in front of the
7	chair, where videos of an actor or static images were displayed using custom experiment scripts
8	written in C++ (<u>https://github.com/CML-lab/DualTaskImitation</u>).

9 Movement kinematics were recorded using a magnetic motion tracking system

10 (TrakSTAR, Northern Digital Inc., Ontario, CA) with a wide-range transmitter (range, 6 feet)

and 4 standard (8mm) sensors. Sensors were placed on the top of the right hand near the wrist,

12 the right elbow joint, and on each shoulder. Movement was recorded at an effective sampling

13 rate of 420 Hz. A piece of tape on the participant's right thigh, near the knee, served to indicate a

14 home position where the participant should return his or her hand between movements.

15 Following the imitation experiment, participants were seated at a desk in front of a

16 desktop computer (23.8" Acer R240HY widescreen monitor, 60 Hz refresh rate) and completed a

17 computerized Corsi Block Tapping Task in the Psychology Experiment Building Language

18 (PEBL; <u>http://pebl.sourceforge.net/battery.html</u>).

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20 2.3 Procedure

The imitation experiment consisted of a sequential multitasking paradigm [28,29] in which participants were asked to watch videos of an actor generating a movement with what appeared to be his left arm, complete an intervening task, then imitate the movement they had

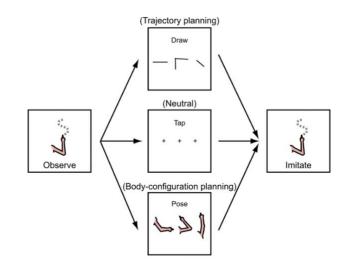
1 watched using their right arm (i.e., imitating as if the movement was observed in a mirror, which 2 is considered a more automatic and natural form of imitation; [32,33]; see Figure 1). Movements 3 of the actor were in fact recorded using the actor's right arm to ensure greater comparability to the participants' own movements; videos were then mirror-reversed to make it appear as if the 4 actor was using his left arm. For the imitation portion of the task, movements consisted of two or 5 6 more static postures (with a ~1 second hold at each posture) with dynamic transitions between 7 those postures, and were designed to have no obvious meaning associated with the movement. 8 For example, one movement would consist of lifting the arm off the lap and bending it into a 9 raised "L" shape out to the side (posture 1), a brief pause, extending the arm out to the side to a 10 low diagonal (transition to posture 2), a brief pause, and then returning the arm to the lap (see 11 Figure 2). Postures and transitions involved motion about the shoulder and elbow, but did not 12 include flexion/extension at the wrist or movement of the fingers; the hand remained in a fist 13 throughout the motion. Movements were selected to range in difficulty based on whether they 14 included 1 or 2 dynamic transitions (2 or 3 static postures, respectively), with the transition 15 movements being either straight or curved. After watching the movement and completing an 16 intervening task (see below), participants were instructed to wait until the go cue, in which the 17 word "Imitate!" was displayed on the screen along with an auditory tone, to begin imitating. The go cue appeared 500 ms after the end of the intervening task. If participants moved before the go 18 19 cue (detected as movement of the hand more than 5 cm from the home position), the trial 20 restarted. 21 On each day (Fig. 1b), participants were given a specific set of instructions for the entire

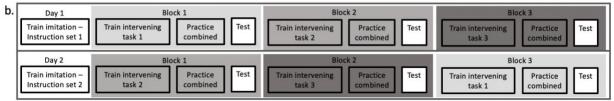
22 session about what movement features to focus on during imitation (see Instructions

23 manipulation below). They then completed 4 imitation-only practice trials in which they watched

1 a video of the model performing the movement, and were immediately instructed to imitate the 2 observed movement with no intervening task present. Next, participants completed 3 blocks in 3 each session, one for each of the 3 intervening tasks described below. Each block began with 10 4 familiarization trials of the intervening task to be performed in that block. This was followed by 5 4 combined practice trials, where they first watched the model movement without moving their 6 hand, completed the same intervening task they had just practiced, then performed their imitation 7 of the model movement upon seeing a go cue. Finally, participants completed 20 test trials 8 (analogous to the combined practice trials) to finish the block, and received a brief (~30 seconds) 9 break before beginning the next block. Following the completion of all blocks in the session, 10 participants completed the Corsi task.

a.





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12 **Figure 1.** Overview of experimental paradigm.

1	2.3.1 Primary task: Instruction manipulation. The primary task (PT) was to imitate
2	gestures. Instructions were used to manipulate the focus of attention during imitation on either
3	limb postures or end-effector trajectories. That is, participants received a different set of
4	instructions in each session (order counterbalanced between subjects). For each instruction, the
5	practice videos were edited to emphasize the relevant set of instructions. In the Posture
6	Matching instructions (Posture Matching PT), the experimenter instructed participants to: "Pay
7	attention to the position of the body parts-for example, how the elbow, shoulder, and wrist are
8	positioned." In the practice videos, when the model reached each static posture, the movement
9	was momentarily paused and straight red lines appeared on the model's forearm and upper arm
10	to encourage participants to pay attention to the positions of the body parts relative to each other
11	(Fig. 2, top panel). In the Trajectory instructions (Trajectory PT), the experimenter instructed
12	participants to "Pay attention to the path that the hand takes through space." In the practice
13	videos, the model's hand was encircled by a red circle that followed the movement of the hand;
14	upon completion of the movement, the full path of the movement was displayed as a red line on
15	the screen to encourage participants to attend to the path of the end effector (Fig. 2, bottom
16	panel). The experimenter also verbally reminded participants to either "focus on the position of
17	the body parts" or to "pay attention to the path the hand takes through space" at 7 points during
18	each session: prior to the instruction-only practice videos at the very beginning of the session,
19	prior to the combined practice trials (one for each of the three intervening tasks described below),
20	and prior to the test trials for each intervening task. In all cases, participants were instructed to
21	imitate the movement at the same speed as the model.

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2 Figure 2. Snapshots of Instruction videos. The top panel is an example of the instruction video provided in the Posture Matching PT. Participants watched the model perform a two-posture 3 4 movement, pausing at each position. Emphasis lines appeared to draw attention to the position of 5 the body parts (wrist, elbow, shoulder). The bottom panel is an example of the instruction video 6 provided in the Trajectory PT. Participants watched the model perform a two segmented 7 movement with the circle tracking the movement of the hand (bottom left and bottom middle). 8 Upon reaching the end position, a "trace" of the movement appeared, which represented the path 9 the hand took through space (bottom right). Emphasis lines were only present during the initial four practices on each day of testing. Photos of author M. Isaacs used with the author's 10 11 permission.

13	In order to minimize learning effects, we randomized the order of the movements within
14	easy (the first 8 trials, consisting of 2 static postures each) and hard (the second 12 trials,
15	consisting of 3 static postures each) trials between blocks so that participants did not view the
16	movements in the same order each time. We also created forward and reversed videos of each
17	movement, which contained equivalent kinematic information but allowed us to minimize the
18	number of repeated exposures to the exact same movements. Reversed videos were generated by
19	running time backwards in the videos. Participants saw either the forward or the reversed videos

1 in the first session (paired with either Posture Matching or Trajectory PTs), and then the other set 2 of videos in the second session, paired with the other set of instructions. We hypothesized that 3 the direction of movement would not significantly influence imitation accuracy. For trials where 4 the video was reversed, we also inverted time in the kinematic recordings from the participants 5 such that in our analyses the recorded gestures from all trials and all participants were compared 6 to the kinematics of the forward-in-time model movement. Note that the model kinematics were 7 the exact kinematics recorded from the model during filming of the movement videos for this 8 experiment, using the same trakSTAR and placement of trackers.

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10 **2.3.2 Intervening tasks.** We included three intervening tasks (IT), which were 11 manipulated within-subjects. The order of ITs was randomized and counterbalanced between participants and between sessions. These tasks were meant to evoke processing interference with 12 13 the primary imitation task; as such one task was related to planning limb postures and a second 14 was related to planning trajectories. The third task served as a control for the working memory 15 demands associated with remembering the PT while performing an IT. In these three ITs, 16 participants were required to produce a movement once every 1200 ms in time with a metronome 17 for 6 iterations before returning their finger to the home position.

In the Posture Matching IT, participants were asked to reproduce three body postures presented in pictures on the screen, from left to right, in time with the metronome (see Figure 3). In the Trajectory IT, participants saw three meaningless shapes on the screen, and were asked to extend their right arm directly in front of them and draw the shapes in the air using their whole arm in time with the metronome. Examples of these shapes include a straight horizontal line, a

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rotated "L", and a diagonal line. Drawing movements were to begin at the dot in each image (see
 Figure 3).

3 To control for working memory demands associated with the delay that the intervening 4 tasks created between watching the action and performing the imitation, we included a neutral 5 intervening task in which participants saw 3 fixation crosses presented side by side on the screen 6 and simply had to tap their hand on their thigh in time with the metronome -a motor response 7 that does not preferentially invoke the planning of either body configurations or trajectories. 8 Fixation crosses were used to provide an analogous amount of visual cuing information across 9 conditions. When tapping, participants were instructed to slide their hand up their leg away from 10 the home position, and keep the heel of their hand on their leg.



Figure 3. Intervening Tasks. Participants completed each of three ITs for both sets of 1 2 Instructions. In the Posture Matching IT (top row), participants matched the arm positions in the photographs of the model from left to right in time with a metronome that presented a tone once 3 4 every 1200 ms. They heard 6 tones and were asked to match the postures from left to right twice through. Posture Matching IT is congruent with Posture Matching PT, but incongruent from 5 6 Trajectory PT. In the Trajectory IT (middle row), participants raised their hand in front of them 7 into the air and drew the shapes one at a time from left to right in time with the metronome. They 8 completed the row of shapes twice for 6 metronome tones. We instructed participants to start the 9 drawing movement at the circle on each shape. The Trajectory IT is congruent with Trajectory PT, but incongruent from Posture Matching PT. In the Neutral IT (bottom row), participants 10 11 tapped their hand on their upper leg in time with the metronome, 6 times. We expected the 12 Neutral IT to be unrelated to either Posture Matching or Trajectory PT and to serve as a control for working memory demands. Photos of author M. Isaacs used with the author's permission. 13 14

2.3.3 Corsi task. As our task required individuals to hold a multi-segment movement in 15 16 mind while performing an IT, we wanted to control for potential individual differences in spatial 17 working memory abilities. To assess spatial working memory, participants completed a standard computerized Corsi block tapping task at the end of each session. Participants viewed a layout of 18 19 nine blue squares on a black background. Blocks briefly turned yellow one at a time in sequence, 20 and after the last block in the sequence returned to blue, participants were instructed to reproduce 21 the sequence by clicking on the boxes in the same order. Participants first completed 3 practice trials, then began the experimental trials. Sequences progressed in difficulty starting with 3 22 blocks. If participants correctly reproduced at least one of the two sequences at that length, the 23 sequence became longer. When participants failed both attempts, the task ended. The maximum 24 25 number of blocks correctly reproduced was used as that individual's Corsi block span. For each individual, we took the average of their two Corsi span assessments. The average Corsi span 26 27 across individuals was 6.68 (SD=1.11, range 5 to 9).

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29 2.4 Data Analysis

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1 Kinematic data were analyzed in Matlab using custom scripts. Movement start and end 2 were automatically identified according to a velocity threshold of 5 cm/s. These points were 3 verified by visual inspection and manually adjusted if necessary by one researcher, then they 4 were independently confirmed by a second researcher. The start of each movement was identified as the point at which participants initiated a movement away from the first static 5 6 posture, and the end of each movement was the point at which participants arrived at the final 7 static posture; that is, we only included the "core" portion of the movement from the first to the 8 last target postures, excluding motion to and from the home position. As a preliminary analysis, 9 we counted the number of movement segments executed on each trial using the same velocity 10 threshold method to mark the movement segments. Segment-count errors were identified when 11 there were more than or fewer than the correct number of movement segments generated during 12 that trial. We observed a greater likelihood of producing movement segment errors after the Posture Matching or Trajectory ITs compared to the Neutral IT, suggesting that the Neutral IT 13 14 was indeed "neutral" with respect to the primary imitation task¹. 15 **2.4.1 Primary task performance.** Accuracy in the primary task (imitation performance) 16 was measured by quantifying the degree of dissimilarity between the participant's kinematics

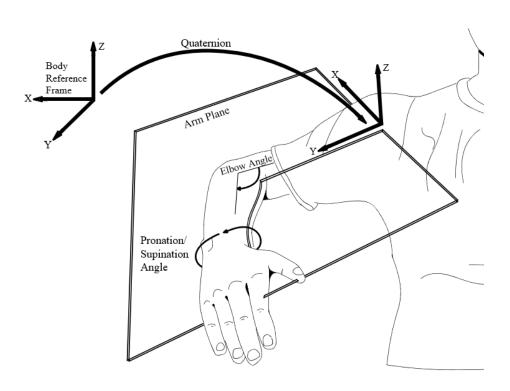
and the model's kinematics (analysis 1). We also performed two *post hoc* analyses to assess
within-subjects' and between-subjects' consistency of movement. We compared the participant's
kinematics in one condition to their own kinematics for the same movement in another condition
(analysis 2), and the participant's kinematics on a given movement compared to the kinematics

¹ Segment-count errors comprised 3.33% of the data. Neither Instruction ($\chi^2(3)$ =.97, p=0.8) nor the Instruction*Intervening Task interaction ($\chi^2(2)$ =0.78, p=0.7) had a significant effect on segment-count error trials according to a binomial generalized linear model, but Intervening Task explained significant variance in the data ($\chi^2(4)$ =15.50, p=0.004). Both Posture Matching (z = -3.26, p=0.003) and Trajectory (z = -3.18, p=0.004) ITs increased the likelihood of a segment-count error compared to the Neutral IT, but there was no difference between Posture Matching and Trajectory ITs (z = 0.08, p=0.9).

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1 of the other participants for that same movement, for each condition (analysis 3). For these three 2 analyses we used a Procrustes Distance (PD) metric, which is a measure of dissimilarity between 3 two geometric shapes after accounting for any affine transformations (i.e., translation, rotation, 4 and scaling) [34]. A larger PD indicates greater dissimilarity, or error, compared to the referent. 5 To describe the motion of the entire arm throughout the movement, we projected all data 6 into a coordinate system defined by the orientation of the participant's body in space (where x 7 points to the participant's right, y points forward, and z points up). We then developed a novel 8 method of summarizing the configuration of the arm by treating the arm as a plane rotating in 3D 9 space, with its origin at the shoulder, y axis directed along the shoulder-elbow vector, z axis 10 directed along the normal to the plane, and containing the elbow-hand vector (Figure 4). We 11 calculated the instantaneous orientation of the plane as a quaternion relative to the body-centered 12 coordinate frame. Two additional angles were needed to define arm orientation fully; these 13 consisted of the elbow angle (the angle from the shoulder-elbow to the elbow-hand vector), and 14 the roll angle of the hand within the plane (reflecting pronation/supination of the forearm, 15 defined as the angle between the normal to the hand sensor and the normal to the plane). These 16 latter two angles were normalized by 360 degrees to put them on a comparable scale to the arm-17 plane quaternion. This six-element vector was computed at every time step, and the entire highdimensional trajectory was then time-normalized to have 200 equally spaced points. Finally, we 18 19 compared this time-normalized arm representation against a similarly constructed one for the 20 model. For this comparison we used a modification of the PD algorithm in which movements 21 could be scaled differently in each dimension, as it improved the quality of the fits [35].

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Figure 4. Arm configuration at each time step was described using six values: a quaternion that
described the rotation of the axes of an "arm plane" (defined as the plane containing the
shoulder-elbow and elbow-wrist vectors) relative to a body-centered reference frame (4 values);
the angle of the elbow within the arm plane (1 value); and the pronation/supination angle of the
forearm (1 value). The latter two angles were normalized by 360 degrees to be of a similar scale
as the individual elements of the quaternion.

8

9 PD measures are typically bounded between 0 and 1, where 1 reflects maximal 10 dissimilarity [34,36]. However, when the algorithm is modified to allow each dimension to scale 11 differently as suggested by Rohlf and Slice [35], PD values may exceed 1. Nevertheless, even in 12 such cases PD values remain relatively constrained to the range 0-1 such that PD values greater 13 than 1 reflect unusually large behavioral outliers; we therefore removed these outliers in our 14 analyses. This resulted in the removal of 0.03% of our data (8 trials) for our primary analyses, 0.3% of the data for our first post hoc analysis (69 trials), and 0.03% of the data for our second 15 16 post hoc analysis (123 trials). **2.4.2 Movement time.** As participants were instructed to imitate movement speed as well 17

as spatial position, we also assessed temporal accuracy errors. Timing errors were computed as

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the absolute difference between the time taken for the participant and the model to produce a
 given movement. Larger values indicate a greater difference between participant and model
 movement times, suggesting more timing dissimilarity.

- 4 2.4.3 Statistical analysis. All statistical analyses were performed in R [37]. We used the 5 *lme4* package [38] to fit generalized linear mixed effects models, with significant effects of 6 interest identified by calculating likelihood ratio tests between models with and without the 7 factor of interest. Because the PD data are bounded and non-normally distributed, we used a 8 generalized linear model with a log link to analyze imitation accuracy. For the Movement Time 9 data, we used a square root link, which normalized the data to resemble a more normal 10 distribution. Because of experimenter or technical error, 86 of 3000 trials (2.87%) were missing. 11 Our hypothesized models included fixed effects of Instruction (2 levels), Intervening Task (3 levels), and the Instruction*Intervening Task interaction (2x3), along with a random effect of 12 13 Participant. We also checked for an effect of instruction Order and video Direction (forward or 14 reverse) in our models; we hypothesized *a priori* that neither of these factors would have a significant impact on our data. Finally, we tested whether performance was influenced by spatial 15 16 working memory span. For all statistical models, we performed pairwise contrasts with the 17 emmeans package [39] using a Tukey adjustment for multiple comparisons.
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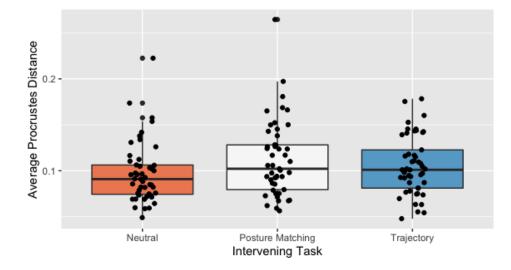
3. Results

20 **3.1 Imitation is disrupted by an imitation-related intervening task**

In our first analysis we compared participants' imitation to the model to assess the extent of spatial dissimilarity using the Procrustes Distance algorithm. We first checked if there were any effects of video Direction and instruction Order. As hypothesized there was no significant

1	effect of Direction ($\chi^2(1)=0.38$, $p=0.5$) or Order ($\chi^2(1)=0.38$, $p=0.5$), so we removed these terms
2	from the model. The resulting model suggested a trending effect of Intervening Task ($\chi^2(4)$ =8.60,
3	$p=0.07$) but no effect of Instruction ($\chi^2(3)=0.97$, $p=0.8$). There was also no significant interaction
4	($\chi^2(2)=0.92$, $p=0.6$). Planned pairwise contrasts revealed that imitation following the Neutral IT
5	was significantly more accurate (lower PD) compared to imitation following the Posture
6	Matching IT (z =-2.97, p =0.008; see Figure 4). PD following the Trajectory IT did not differ
7	significantly from Neutral (z =-1.91, p =0.1) or Posture Matching (z =1.06, p =0.5) ITs. Adding
8	average Corsi block span to the model did not improve model fit ($\chi^2(1)=1.29$, p=0.3), suggesting
9	that imitation accuracy was not significantly related to spatial working memory. See Table 1 for
10	means in each condition.

11



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Figure 5. Boxplot of participant's average PD across the 20 trials in each condition.

15 Table 1. Average imitation performance compared to the model.

Posture Matching Primary Task			Trajectory Primary Task			
Intervenin g Task	Posture Matching	Trajectory	Neutral	Posture Matching	Trajectory	Neutral
	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)	M(SD)

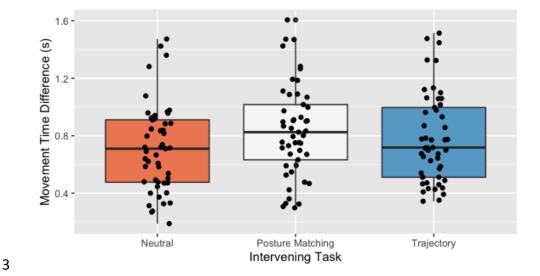
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PD	.111 (.137)	.103 (.119)	.099 (.122)	.114 (.145)	.108 (.130)	.096 (.128)
Movement Time	.831 (.623)	.777 (.608)	.724 (.594)	.844 (.625)	.785 (.614)	.696 (.564)

1 Note.

2 Participants were also instructed to imitate movement timing (movement speeds and 3 static posture hold times) as well as position; thus we additionally examined how well 4 participants were able to imitate total movement time by comparing the absolute difference 5 between the time taken for the participant and the model to produce a given movement (Fig. 5). 6 Larger values indicate a greater timing dissimilarity (i.e., more error) between participant and 7 model movement times. 8 We first checked if there were any effects of video Direction and instruction Order. There was a significant effect of Direction ($\chi^2(1)=50.29$, p<0.0001) but not of Order ($\chi^2(1)=0.85$, 9 10 p=0.4). We therefore retained Direction as a nuisance variable in our analysis. Using this model, 11 we observed a significant effect of Intervening Task ($\chi^2(4)=25.57, p<0.001$), but no significant effects of Instruction ($\gamma^2(3)=0.82$, p=0.8), nor was there an Instruction*Intervening Task 12 13 interaction ($\chi^2(2)=0.81$, p=0.7). Planned pairwise contrasts revealed that imitation movement 14 time errors following the Neutral IT were significantly smaller than Movement Time errors 15 following the Posture Matching (t=-7.29, p<0.0001) and Trajectory ITs (t=-4.16, p=0.0001). 16 Movement time errors following the Posture Matching IT were significantly larger than 17 following the Trajectory IT (t=3.13, p=0.005). See Table 1 for means. These data reveal that 18 individuals were more accurate at imitating movement timing following the Neutral IT than the 19 two interference conditions, and moreover that imitating movement time was more accurate after 20 Trajectory than Posture Matching ITs. Taken together with measures of spatial imitation 21 accuracy, these results suggest that in general, having to perform an intervening task related to 22 either of the hypothesized mechanisms supporting imitation is disruptive to the ability to

- 22
- 1 reproduce both spatial and temporal movement features. We also note that the Trajectory IT may



2 be a little less disruptive compared to the Posture Matching IT.

- 4 Figure 6. Boxplot of participant mean movement time errors in each condition.
- 5

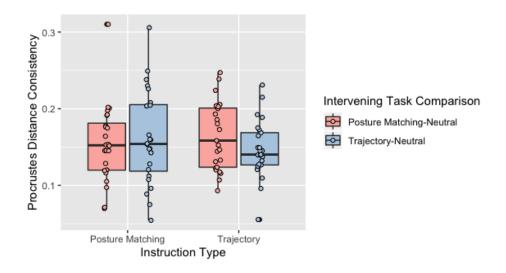
6 *3.2 Post hoc analyses*

7 3.2.1 Within-subjects consistency reveals a switch cost for imitating trajectories

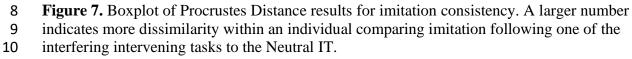
8 In the prior analysis, we assessed how accurately people imitated in contrast to the ideal 9 (model) movement. While we did not observe the expected interaction between primary and 10 intervening tasks, this may have been due to a large amount of noise or variance unrelated to our 11 manipulations. That is, because it may be challenging in general to exactly reproduce the 12 kinematics of an observed model, our measure of accuracy compared to the model may not have 13 been sufficiently sensitive to detect any additional behavioral variance arising from the IT 14 manipulation. Thus as an additional, potentially more sensitive measure of imitation performance, 15 we also examined the ability for any given individual to repeatedly produce the same movement 16 consistently in all conditions. In other words, the disruption induced by an intervening task might 17 be better detected by comparing each participant's performance for a given movement shape and

1 condition to their own performance of the same movement shape in a different condition (i.e., a 2 measure of variance versus a measure of bias). Specifically, since the same set of movements 3 were imitated in every block, and because in our prior analyses we confirmed that the Neutral 4 condition is least disruptive of imitation accuracy, we calculated a PD value that represented a 5 participant's performance dissimilarity following the Posture Matching and Neutral ITs, and 6 following the Trajectory and Neutral ITs, within each Primary Task instruction condition. A 7 higher PD value indicates less imitation consistency with reference to the neutral condition, 8 suggestive of greater disruption due to the IT. 9 We again ran a generalized linear mixed effects model with fixed effects of Instruction 10 (Posture Matching or Trajectory) and Intervening Task Comparison (Posture Matching vs. 11 Neutral or Trajectory vs. Neutral) as well as the Instruction X Intervening Task Comparison interaction. There was no significant effect of Order ($\chi^2(1)=0.98$, p=0.3) but there was a 12 significant effect of video Direction ($\gamma^2(1)=5.33$, p=0.02). We dropped Order and retained 13 14 Direction as a nuisance variable in the model. With this model, there was no significant effect of Instruction ($\chi^2(2)=4.95$, p=0.08), and no significant effect of Intervening Task ($\chi^2(2)=4.94$, 15 p=0.08), but there was a significant interaction ($\chi^2(1)=4.52$, p=0.03). Planned contrasts revealed 16 17 a significant difference between Intervening Task comparison types for the Trajectory PT (z=1.97, p=0.049) but not for the Posture Matching PT (z=-1.01, p=0.3). As depicted in Figure 6, 18 19 for the Trajectory PT, there was greater consistency between performance following a Neutral IT 20 and Trajectory IT than there was between performance following a Neutral IT and Posture 21 Matching IT. In other words, the combination of Trajectory PT and Trajectory IT resulted in 22 performance that was relatively less disrupted (i.e., more consistent with performance following 23 the Neutral IT) compared to other combinations. This effect was present regardless of the spatial

working memory span of individual participants: adding Corsi block span to the model did not
 improve model fit (χ²(1)=0.41, *p*=0.5). In summary, we observe a switch cost effect due to
 Intervening Task within the Trajectory PT, but not within the Posture Matching PT. That is, the
 goal of what participants are trying to imitate affects how consistent individuals are across
 repeated imitation attempts, and moreover, participants typically imitate less consistently when
 the intervening task is incongruent with the instruction type (at least for Trajectory instructions).



7



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12 **3.2.2** Switch costs reduce cross-subject consistency

13 Finally, as an additional *post-hoc* exploratory analysis we asked how consistently

14 participants performed with respect to each other. This analysis allowed us to examine whether a

- 15 particular combination of instruction type and intervening task resulted in less consistent
- 16 behavior across individuals (i.e., more disrupted imitation leading to greater inter-subject
- 17 variability), which could again suggest the presence of a switch cost. For this analysis, we
- 18 calculated a PD value for every participant compared to every other participant on each trial
- 19 within a specific PT and IT condition (e.g., Participant 1's imitation of movement 1 in the

1	Posture Matching PT + Posture Matching IT condition compared to participants 2-25 for that
2	same movement and condition). We ran a generalized linear model to assess for effects of
3	Instruction, Intervening Task, and the Instruction*Intervening Task interaction on between-
4	subjects' consistency. Based on this model, we observed significant effects of Instruction
5	$(\chi^2(3)=11.27, p=0.01)$, Intervening Task ($\chi^2(4)=144.52, p<0.0001$), and the interaction
6	($\chi^2(2)=8.26$, <i>p</i> =0.016). Planned contrasts again revealed a task switching effect when the primary
7	task was to imitate Trajectories. Critically, for the Trajectory PT, PDs after the Posture Matching
8	IT were higher than PDs after the Trajectory IT ($z=3.31$, $p=0.003$). This same task switching
9	effect was not observed for the Posture Matching PT (z =-0.64, p =0.8) (See Fig. 8). We also
10	noted that for both instruction types, PDs after the Neutral IT were significantly lower than PDs
11	after either the Posture Matching IT (Trajectory PT: z=-8.29, p<0.0001; Posture Matching PT:
12	z=-7.11, p<0.0001) or the Trajectory IT (Trajectory PT: z=-4.99, p<0.0001; Posture Matching
13	PT: z =-7.74, p <0.0001), again demonstrating that the neutral IT was least disruptive in general
14	and therefore resulted in the greatest performance consistency across individuals. These results,
15	combined with the within-subjects consistency findings above, are consistent with our hypothesis
16	that participants exhibit greater imitation performance decrements (i.e., larger switch costs) when
17	the instructions and intervening task are incongruent, particularly when imitating trajectories.

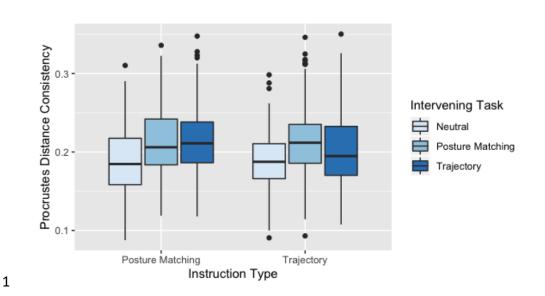


Figure 8. Boxplot of the average PD of the 20 trials in each condition for every subject pairing.
A point represents a subject pairing (e.g., subject 1 and 4) and how consistent their performance
was across the trials in that condition.

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4. Discussion

7 In the current study we aimed to test whether individuals could imitate via either posture 8 matching or trajectory mechanisms using a sequential multitasking paradigm. We reasoned that 9 if people can imitate using both mechanisms, we should observe a cost when switching from one mechanism to the other, such as when performing an intervening task that requires a different 10 processing mechanism compared to the primary task. Our primary task was to imitate gestures 11 12 by attending to either the limb postures or path of the hand of the model. In tandem, participants 13 also completed one of three motor intervening tasks: two that were congruent/incongruent with 14 the instructions and designed to potentially create interference, and one that served as a neutral 15 baseline. In our primary analysis, we saw no overall effect of the primary task, but did observe 16 that the neutral intervening task was least disruptive to imitation as suggested by better 17 spatiotemporal imitation accuracy (i.e., lower spatial dissimilarity and smaller movement timing errors) when comparing individuals' behavior against the model. Once we better controlled for 18

1 individual subjects' variability by measuring within-subjects consistency, however, we were able 2 to observe a task switching effect in the trajectory primary task condition. Specifically, when 3 participants had to complete a posture-matching intervening task that was incongruent with the 4 primary trajectory imitation task, their performance was less consistent with their own baseline 5 performance. Finally, in our analysis of consistency between subjects, we also observed a task-6 switching effect for trajectory imitation such that consistency decreased when the intervening 7 task was posture based, and thus incongruent with the primary imitation task. These effects were 8 unrelated to any potential individual differences in spatial working memory as assessed by Corsi 9 span (for similar lack of working memory effect, see [40]). Each result is discussed below in turn. 10 Together these results suggest that switching between trajectory and posture matching imitation 11 tasks is computationally burdensome and induces a switch cost, supporting our hypothesis that 12 people can imitate via either of these two distinct methods.

13 In our primary analysis of spatiotemporal accuracy compared to the model, our results 14 were only partially consistent with our hypothesis. While we expected an interaction between 15 primary and intervening tasks that would provide evidence of a switch cost, we only observed an 16 effect of intervening task. The posture matching and trajectory intervening tasks were intended to 17 be cognitively and motorically disruptive of the primary task, whereas the neutral intervening task was intentionally designed to obviate these spatio-motor and cognitive demands. Our results 18 19 suggest that indeed, performance of the primary imitation task following the neutral intervening 20 task was most similar to the model, regardless of the task instructions. In contrast, the posture 21 matching and trajectory intervening tasks both elicited a "cost" compared to the neutral 22 intervening task in the form of decreased spatiotemporal accuracy, suggesting that these 23 intervening tasks were indeed disruptive of imitation. Additionally, imitation following the

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trajectory intervening task was more temporally accurate than imitation following the posture
matching intervening task. While this same pattern was not observed for spatial accuracy, this
result suggests that the trajectory intervening task may be a little less disruptive compared to
matching postures.

5 In our first *post hoc* analysis we then compared participant's performance in each 6 intervening task to their own baseline (neutral) performance. Unlike in our measures of imitation 7 accuracy, this measure of consistency yielded clear evidence of a switch cost when the primary 8 task was to imitate trajectories. Switching to a posture matching intervening task elicited a "cost" 9 that impaired performance of the primary task. We suspect that the reason this effect may not 10 have been observed in our original accuracy measures is because we were actually measuring 11 two kinds of errors in that case: errors related to imitation more generally, and errors related to 12 potential disruptions by the intervening task. The former source of error could arise from needing 13 to attend to and perform a mirror mapping of the model's movement to one's own body, 14 maintain the components of the movement in working memory, and execute the movement – each of which would introduce "noise" that would be relatively independent of the specific 15 imitation condition. By comparing each person's performance to their own "baseline" 16 17 performance (i.e., by assessing movement consistency), we could account for these sources of error and instead more directly examine specific disruptions arising from the intervening task. 18 19 Thus by adopting a within-subjects analysis, we were better able to detect a task-switching effect 20 in the form of a switch cost when participants had to switch between trajectory imitation and a 21 posture matching intervening task [28].

Intriguingly, we observed similar effects when examining between-subjects consistency
in our second *post hoc* analysis, such that consistency across participants decreased when

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1 switching between incongruent tasks. Although seemingly counterintuitive, we propose that in 2 contrast to the previous within-subjects analysis that sought to remove variability from one 3 individual to the next, this analysis relied upon that variability. That is, we used the variance across individuals following the neutral intervening task as a baseline level of variance in our 4 5 population, and assessed whether the intervening task introduced additional between-subjects 6 variability over and above that baseline. We again saw that incongruent imitation tasks elicited a 7 task-switching cost resulting in less consistency between individuals, while congruent imitation 8 tasks led to greater consistency (at least for the trajectory primary task). Moreover, when taken 9 alongside our finding of temporal imitation accuracy, this suggests that imitating trajectories may 10 be an overall easier form of imitation as people tend to produce more accurate movements and 11 are more similar to each other, consistent with the notion that planning trajectories may be less 12 computationally burdensome [15]. However, this result is curious given that trajectory plans do not constrain the position of the limb segments, and yet our consistency measures examine 13 14 similarity across arm configurations. We speculate that requiring individuals to focus on the 15 greater number of degrees of freedom required to control all the joints may actually impair 16 movement accuracy (particularly if different individuals emphasized control of different joints), 17 in line with prior studies [22].

Our findings are consistent with prior research that has posited the existence of at least two distinct ways to imitate, with evidence for both posture matching [1,2,7] and trajectory matching [14] mechanisms. These two dissociated processes are hypothesized to emphasize different aspects of the movement-to-be-imitated: posture matching requires the ability to represent how the body should look and feel during performance of the movement, whereas trajectory matching instead requires the ability to represent how the end-effector motion should

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1 look in a body-independent manner. As these are both useful but distinct means of imitating 2 movements, we hypothesized that people may be able to make use of both mechanisms. Our 3 current study is the first to our knowledge to directly compare these two mechanisms in the same 4 paradigm (and using the same stimuli) to determine whether people can indeed imitate in both 5 ways. There are clearly conditions in which body posture and joint angles are critical to imitation 6 success, such as in learning ballet or modern dance [17-19], or in the static posture imitation 7 tasks that are often used with clinical neurological populations to test for apraxia (e.g., [1,2,10]). 8 However, a trajectory-matching method of imitation may be more ubiquitous, as the action need 9 not be contingent on body-specific properties. Thus this mechanism may not only support 10 imitation using a different effector, but also imitation between species who have different 11 effectors (a human and a dolphin), or species that differ vastly in size and proportion (a human 12 and a monkey; [41]).

13 Trajectories are also a more computationally compact way of representing a movement, 14 as they need only specify spatiotemporal parameters of the end-effector rather than information 15 about all of the joints. Indeed, our timing data are consistent with this claim that trajectory 16 imitation may be less computationally burdensome. Furthermore, a combined trajectory 17 primary/intervening task resulted in the closest performance to an individual's own baseline 18 performance, suggesting that this combination has a lower computational burden compared to 19 combinations of primary/intervening tasks that include posture-matching. These findings are also 20 consistent with prior research demonstrating that focusing on external, body-independent 21 movement features (potentially akin to end-effector trajectories) is less attentionally demanding 22 and yields greater movement automaticity compared to focusing on internal body-based 23 movement features (e.g., [25,42]). Finally, we note that trajectory representations seem to be

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1 readily accommodated by existing theories of motor command generation [15,43,44]. Thus, 2 while it seems that individuals are capable of imitating by matching postures or copying 3 trajectories, future research will be necessary to further explore the conditions under which each 4 method of imitation is most accurate and least computationally costly. 5 In our primary imitation task, aside from the instructions everything about the actual 6 movements-to-be-imitated was exactly the same between conditions; our use of visual emphasis 7 lines to direct attention to postures or trajectories was only present during practice trials. Our 8 findings therefore suggest that in accordance with the primary task, participants were attending 9 to different features of the movement during observation and specifying their motor commands 10 in a way that was unique to those particular movement features. These results are concordant 11 with research on internal and external focus of attention, which similarly demonstrate that task 12 instructions can influence (and improve) motor behavior [22,24,42]. Our results also suggest that 13 where individuals attend when observing a movement is important for how that behavior is 14 produced. Prior research has suggested that attention during imitation may be focused on the 15 end-effector or the arm posture [41,16]. While our study did not allow us to ascertain what 16 participants were actually looking at during movement observation, it would be interesting for 17 future studies with eye tracking methods to assess differences in visual behaviors in the different imitation conditions. One might hypothesize, for instance, that fixations will be directed towards 18 19 the end effector when imitating trajectories and toward other joint segments when imitating 20 postures (although the location of fixations does not seem to greatly affect general imitation 21 ability; [45]).

It is important to note an asymmetry in our results, in that we observed a switch costwhen participants were instructed to imitate trajectories but not when instructed to imitate

1 postures. Interestingly, this partial dissociation is consistent with another action observation 2 study that demonstrated interference from an intervening task only in one condition [31]. We 3 speculate that this asymmetry could have arisen for two potential reasons. The first is that there is an inherent asymmetry between the control of postures and the control of trajectories: in 4 5 trajectory matching, multiple postures can be associated with a given trajectory, but in posture 6 matching, only one trajectory can be associated with a set of postures. In other words, when 7 imitating end-effector trajectories, due to redundant degrees of freedom at the joints it is possible 8 to produce the same trajectory using different arm postures. Hence an intervening task that biases 9 the use of different joint configurations is more likely to influence exactly how the arm is 10 configured (analogous to how observed kinematics unintentionally bias one's movement; 11 [46,47]), and may thus introduce imitation errors when movements are compared at the level of arm configurations as we do here. That is, the constrained joint positions required to complete 12 13 the posture matching intervening task could carry over into the trajectory primary task, 14 disrupting performance. In contrast, moving one's arm to achieve specific postures necessarily 15 constrains the trajectory of the end-effector (i.e., if one generates a series of postures, only one 16 resulting trajectory of the end-effector is possible). As such, when the primary task was posture 17 matching, there was a limit to how much a trajectory intervening task could bias future behavior 18 since the trajectory produced in the primary imitation task was inherently constrained by the 19 intended postures. Hence even if trajectories are not explicitly planned when the goal is to match 20 postures, it may not be possible to observe a switch cost as long as nothing disrupts the 21 representation of the desired postures themselves. This inherent asymmetry in how movements 22 are controlled may be reflected in our findings.

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1 The second potential explanation for the observed switch cost only when participants 2 were instructed to imitate trajectories (which is not mutually exclusive with the first explanation) 3 is that the posture-matching primary and intervening tasks were much more similar compared to 4 the trajectory primary and intervening tasks. Specifically, both the posture matching primary and 5 intervening task presented images of an actor to be imitated (i.e., they were both clearly imitation 6 tasks), while the trajectory intervening task involved only viewing and tracing abstract shapes 7 with no body information present. Thus in some sense, the trajectory intervening task could be 8 considered less of an imitation task compared to the posture matching intervening task. If the 9 trajectory intervening task invoked a different set of computations than those required during 10 imitation more broadly, it could explain why the trajectory intervening task was potentially less 11 disruptive of imitation performance relative to the other three conditions. That is, there may be 12 an inherent asymmetry in the similarity between primary and intervening tasks. 13 As we note above, the effectiveness or tendency to imitate via posture or trajectory

14 matching is likely contingent on the task. In our paradigm we attempted to constrain the type of 15 imitation used by participants in each condition using task instructions, but it is interesting to 16 consider what type of imitation people would choose to use by default depending on the particular movement or context (and whether that preference changes across repeated exposure 17 18 or practice). Nevertheless, evidence for the ability to employ two distinct methods of imitation is 19 exciting because it suggests that imitation can be modulated depending on the demands of the 20 task and how that task is delineated, indicating that it may be possible to modulate imitation 21 impairments in individuals with apraxia by manipulating the focus of the task. In particular, an 22 individual who is differentially impaired in using these two planning mechanisms could 23 potentially be taught to strategically utilize the relatively intact planning mechanism in order to

- 1 achieve the desired movement outcome. This is particularly intriguing as these two mechanisms
- 2 are thought to be supported by different brain regions [1,6,7,14], such that lesions (e.g., as a
- 3 result of stroke) could differentially spare one mechanism over the other. We are currently
- 4 exploring this idea in a similar experiment with patients.
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