

Corrective jitter motion shows similar individual frequencies for the arm and the finger

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Abstract A characteristic of visuomotor tracking of non-regular oscillating stimuli are high-frequency jittery corrective motions, oscillating around the tracked stimuli. However, the properties of these corrective jitter responses are not well understood. For example, does the jitter response show an idiosyncratic signature? What is the relationship between stimuli properties and jitter properties? Is the jitter response similar across effectors with different inertial properties? To answer these questions, we measured participants' jitter frequencies in two tracking tasks in the arm and the finger. Thirty participants tracked the same set of eleven non-regular oscillating stimuli, vertically moving on a screen, once with forward–backward arm movements (holding a tablet stylus) and once with upward–downward index finger movements (with a motion tracker attached). Participants' jitter frequencies and tracking errors varied systematically as a function of stimuli frequency and amplitude. Additionally, there were clear individual differences in average jitter frequencies between participants, ranging from 0.7 to 1.15 Hz, similar to values reported previously. A comparison of individual jitter frequencies in the

two tasks showed a strong correlation between participants' jitter frequencies in the finger and the arm, despite the very different inertial properties of the two effectors. This result suggests that the corrective jitter response stems from common neural processes.

Keywords Visuomotor tracking · Jitter · Intermittent control · Submovements · Motor control · Mirror game

Introduction

When individuals are asked to imitate non-regular oscillatory motion, the observed responses are often not smooth, but rather exhibit abrupt changes in their velocity profiles. These high-frequency motions, oscillating around the tracked stimuli, are presumed to be the result of intermittent motor control (Miall et al. 1986, 1993). Intermittent control refers to control signals given by the central nervous system (CNS) at discrete points in time rather than on a continuous basis (Navas and Stark 1968; Miall et al. 1986, 1993; Burdet and Milner 1998; Morasso et al. 2010; Gawthrop et al. 2011). Intermittent control is typically attributed to time delays inherent in receiving feedback (Navas and Stark 1968) as it guarantees stability over a larger range of parameter space (Doeringer and Hogan 1998; Morasso et al. 2010). Karniel (2013) suggested that intermittent control is used as a way of minimizing the number of transitions necessary in high-level motor commands. Each generation of an intermittent control signal can be considered as execution of an open-loop motor plan, or a *submovement* (Flash and Henis 1991; Doeringer and Hogan 1998). The rate of submovement production reduces as children develop (Von Hofsten 1991), during recovery from stroke (Krebs et al. 1999), and with motor learning (Sosnik et al. 2004). Recently, evidence

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that intermittent corrective movements rather than continuous control are used has been observed in single-cell recordings from motor and premotor cortices of rhesus macaques (Dickey et al. 2013) and from event-related potentials in humans (Dipietro et al. 2014). Intermittency is also observed in the use of perceptual information, for example, in studies of continuous tracking of constant isometric force (Slifkin et al. 2000; Sosnoff and Newell 2005).

In a recent study, we used intermittency as a marker of reactive control in a joint improvisation task—the mirror game—in which two actors imitate each other with or without a designated leader (Noy et al. 2011, and see similar approaches in Dumas et al. 2010; Konvalinka et al. 2010; Watanabe and Miwa 2012; Yun et al. 2012; Masumoto and Inui 2013, 2014; Arueti et al. 2013). In a one-dimensional version of the game, a follower often exhibits a characteristic jittery motion, presumed to result from intermittent corrective control. We termed this marker of followership a jitter response (or simply jitter). In certain periods in the game, players enter a state where both players produce smooth and synchronized motion without jitter. We suggested that in these periods, players create the motion together by agreeing on future motion. In a follow-up study, we examined the relationship between individuality and togetherness in the mirror game (Hart et al. 2014). We found that players show idiosyncratic ‘motor signatures’ in their basic strokes. However, these individual patterns converge to a universal symmetric and maximally smooth pattern when players create the motion together. These studies sparked our interest in the mechanism of the jitter response.

In the current work, we aim to better understand the nature of the jitter response. Specifically, we were intrigued by the observation that participants show individuality not only in the shape of their velocity profiles but also in the frequency of their jitter response (unpublished data from Hart et al. 2014). However, these data come from open-ended games that varied in their motion parameters (e.g., average velocity and frequency of the motion). Thus, the observed individuality can be the result of this variance. Moreover, this data did not enable studying the properties of the jitter response as a function of the stimuli properties. In the present work, we overcome this limitation by studying jitter response when different people track the same set of stimuli.

The frequency of the jitter response can be the result of several factors. It can be task specific, perhaps mostly determined by properties of the stimuli such as frequency and amplitude, or it can be the result of peripheral considerations such as the inertia of the body part. Similar to other individual differences like reaction times (Schmiedek et al. 2007), it might result from common neural processes across different tasks and body parts.

The time delay between submovements must have a lower bound. This may be governed by the psychological refractory period (Smith 1967), which is the minimum time

needed to perform two sequential actions. Gawthrop et al. (2011) noted that this minimal time could be related to physiology (e.g., conduction times of the neurons) or a soft limit chosen by the CNS. Also, there appears to be an upper bound to the duration of submovements. For example, when participants were required to make 30 cm movements to the left and right over different durations of time, the number of peaks in the velocity profile (that is, the number of submovements) increased as the movements became slower, with an upper bound of approximately 500 ms (2 Hz) on submovement duration (van der Wel et al. 2009).

A considerable body of work comparing inter- and intra-individual differences in movement timing suggests that jitter frequency might be similar between effectors. In a series of studies, timing variability was found to be correlated between effectors (e.g., finger, foot, arm) in tasks requiring explicit representations of time, such as tapping (Franz et al. 1992; Keele and Hawkins 1982; Keele et al. 1987; Keele and Ivry 1987). However, the correlation of timing variance between effectors was not observed in tasks that did not demand an explicit representation of time, for example, in continuous circle drawing (Ivry et al. 2002; Spencer et al. 2003; Zelaznik et al. 2005; Zelaznik et al. 2000). As the tracking task in this study is similar to the aforementioned tapping tasks (in particular when tracking fixed frequency stimuli), we expected to see similarities in the timing behavior between effectors in this study, in particular in the jitter frequency.

To test this hypothesis, we measure the jitter response using two different body parts (whole arm and finger) and apparatuses (drawing movements on a graphics tablet, and extension and flexion of the index finger). We predict that the jitter frequency will vary as a result of stimuli amplitude and frequency, as these changes will result in differences in the difficulty of the tracking task, which will change the nature of the response. As in many other tasks (Fleishman 1967; King et al. 2012), we expect to see individual differences between participants in the rate of their jitter response to the same stimuli. We expect that the timing of the jitter response will be a function of common neural processes between effectors. This will be manifested by similar jitter response across the two conditions. Our operational prediction is that while the jitter frequency will vary across individuals and as a function of the stimuli, the jitter frequency will be correlated across the two tracking tasks, when the same stimuli are tracked with different effectors.

Methods

Participants

Thirty right-handed participants participated in the experiment, from the student population at Tel Aviv University

(22 females, average age 26). Ethics approval was received from the Tel Aviv University human ethics committee, and participants signed an informed consent form before starting the experiment. Each participant performed the tracking task with the two response devices: drawing with a pen, and moving the index finger. Half the participants performed the pen task first and the other half the index task first. The duration of the experiment was approximately 30 min; the participants were paid 40 NIS (approximately \$11) for their participation.

Tracking tasks

The participant sat approximately 40 cm away from a 23.6" computer monitor (522×296 mm, $1,920 \times 1,080$ resolution, 60 Hz refresh rate), which was placed at the far end of the table. The participants were shown a red rectangle on a computer monitor (see Fig. 1a). The base of the rectangle did not move, while the height of the rectangle constantly changed in a smooth manner (maximum height of 756 pixels = 20.5 cm). The movement of the pen or finger changed the height of a blue rectangle, shown next to the red rectangle, with the same base height, and of equal width. The height of the blue rectangle was controlled either by moving a stylus (held in the right hand) forward or backward on the graphics tablet (Wacom Intuos tablet, sampling at 100 Hz, 1 cm pen movement = 35 pixels = 0.95 cm of rectangle height), or by moving the right index finger up or down (recorded using a Polhemus Liberty system, sampling at 240 Hz, 1 cm index finger movement = 360 pixels = 9.8 cm of rectangle height). We chose these motions in order to match the complexity of the perception-to-action mapping in the two conditions. We tried to produce two mappings which were similarly natural: (1) a perceptual 'up' corresponding to a forward motion of the arm (the familiar computer–mouse to screen mapping), and (2) a perceptual 'up' corresponding to an upward motion of the finger, a natural mapping which is easier to imitate than rotated mappings (Noy et al. 2009). This finger motion, similar to a tapping, is also easier ergonomically than other types of finger motions.

The different ranges of movement of each effector corresponded approximately to the comfortable ranges of movement of the index finger in extension/flexion and of forward/back pen movements. The participants were instructed to imitate the movement of the red rectangle with the blue rectangle. The pen movements of the graphics tablet were constrained to only be forward–backward by creating a thin 2-mm channel for the pen to move in between two 40-cm rulers. For the finger movements, the wrist of the right hand rested on a piece of foam, but the finger was otherwise unconstrained.

Eleven trials were performed with each response device, and each trial was 60 s long, with a break of 10 s between

trials. The stimuli (i.e., the height of the rectangle), available online (Friedman et al. 2014), consisted of half sine waves (i.e., with a single peak or trough), alternating from positive to negative (see Fig. 2), with varying amplitudes and durations (see Fig. 1b) for four examples). For the first three trials, the parameters of the stimuli were selected by the experimenters, to create relatively simple stimuli with few transitions. For the other eight trials, the stimuli were based on stimuli generated by the leader in the mirror game experiment (Noy et al. 2011). The stimuli from the mirror game were altered so that they consisted of a series of half sine waves, which we expect to be easier to imitate. In a previous study (Hart et al. 2014), we found that when two participants experience togetherness, their movements are similar to half sine waves. Additionally, half sine waves are maximally smooth; the lack of abrupt changes should make them easier to copy. Further details of the stimuli are provided in Table 1.

All experiments were run using the "Repeated Measures" software (Friedman 2014), MATLAB (Mathworks Inc) software that runs on top of the Psychophysics Toolbox (Brainard 1997).

Data analysis

The kinematic data were filtered using a low-pass fourth order two-way Butterworth filter with a cutoff of 5 Hz. Only one dimension of the data was used in the analysis (forward–backward for the tablet, and up–down for the finger). Velocities and accelerations were calculated using finite differences. The data from both experiments were resampled to 100 Hz for the remainder of the analysis.

Jitter frequency

We have defined "jitter" as being corrective movements that weave around the required movement (Noy et al. 2011). Each half sine wave will have a zero-crossing in the acceleration profile at the start and end of the half cycle (because the second derivative of a sine wave is a sine wave with the same phase, but opposite sign). If the participant produces perfect sine waves, then zero-crossings in the acceleration will only be observed when each half cycle starts (or ends, which occur at the same time). We interpret other zero-crossings in the acceleration profile (which indicate inflection points in the position) as indicators that a corrective movement has been generated (jitter, see Fig. 2b). We note that other techniques, such as fitting minimum jerk submovements (Friedman et al. 2013; Rohrer and Hogan 2006), are not feasible for this data due to its length, and also because these techniques are typically designed for discrete rather than rhythmic movements. To remove the zero-crossings that correspond to the start and end of half

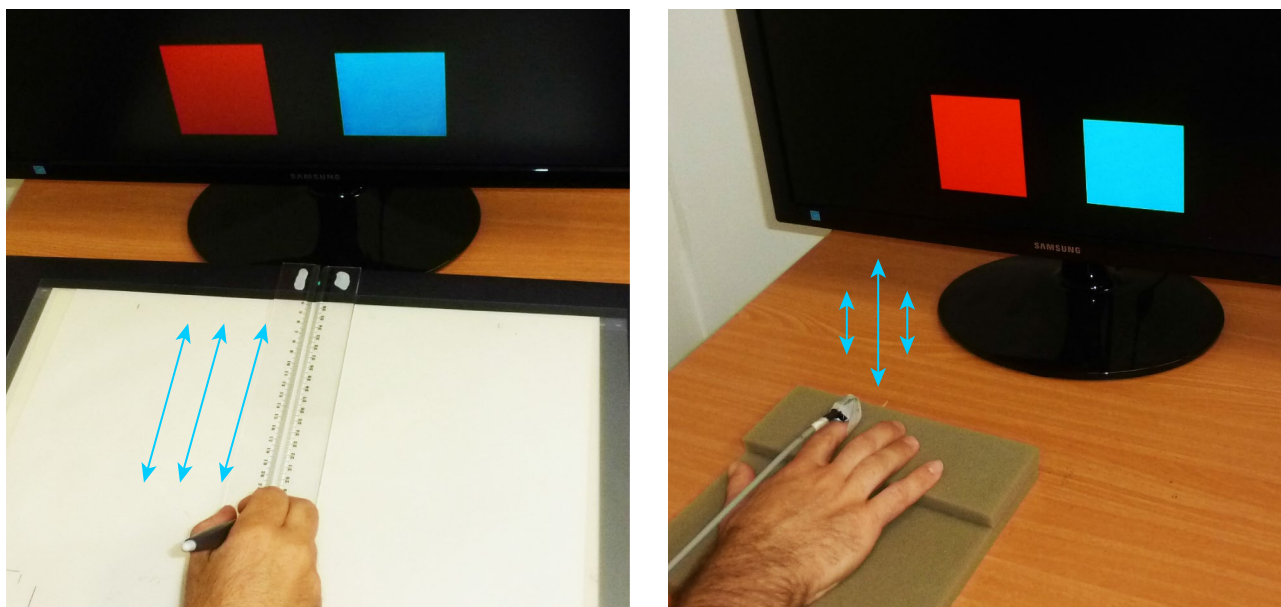
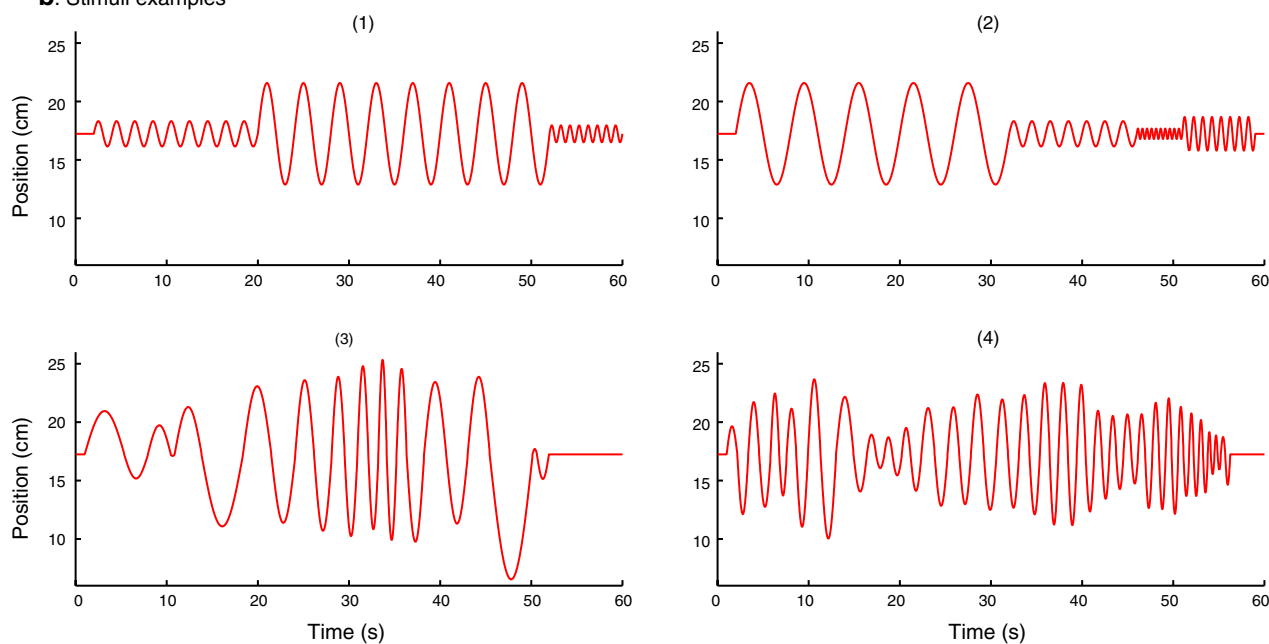
a. Measuring tracking of the same stimuli with the arm (left) and the index finger (right)**b.** Stimuli examples

Fig. 1 Methods. **a** The two effectors used in the experiment—moving a pen back and forth on a tablet with the arm, and moving the index finger up and down. By moving their arm or finger, the participant could control the height of the *blue rectangle* (on the right).

They are told to imitate the movements made by the *red rectangle* (on the left). **b** Examples of the stimuli, (1) and (2), are artificially generated, and (3) and (4) are based on the performance of a leader in the mirror game (Noy et al. 2011) (color figure online)

cycles, we found the best registration of the data with the stimuli (Tang and Müller 2008) and then removed the zero-crossings that occurred in both the stimuli and response. Figure 2a shows an example of the registration process, and Fig. 2b demonstrates the points that are identified as jitter. After finding the zero-crossings in the acceleration, we only use those zero-crossings that are more than 200 ms

apart (i.e., 5 Hz), as it is unlikely that separate movements could be produced in such a short time. We compute the frequency of these movements as half the reciprocal of the duration between the remaining zero-crossings. We divide the reciprocal by two in order to get the frequency of a whole wave, which would consist of two zero-crossings. This allows us to compare the frequencies obtained with

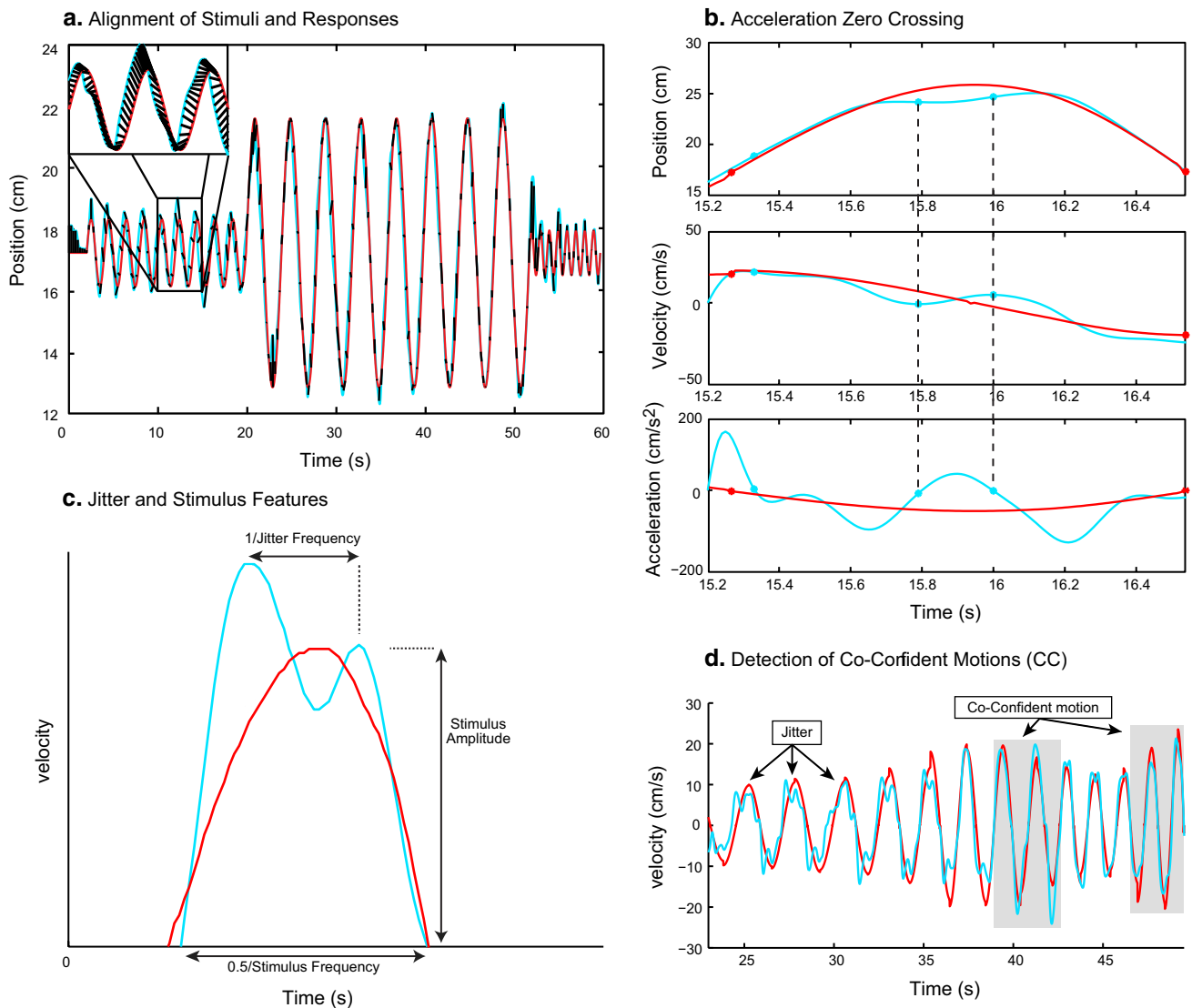


Fig. 2 Kinematic analysis. **a** Example of alignment of stimuli (*red*) to experimental data (*blue*). The *black lines* indicate corresponding points in the stimuli and experimental data. **b** Example of how the jitter points are identified. The *blue lines* correspond to experimental data and the *red lines* to the stimuli (after registration). The *top graph* shows position, the *middle graph* velocity, and the *bottom graph* acceleration. The *stars* correspond to zero-crossings in the accel-

eration profile. Zero-crossings found in the experimental data that are close to zero-crossings in the stimuli are removed (e.g., the first zero-crossing in this example). **c** Schematic diagram showing how the stimulus frequency and amplitude and the jitter frequency are calculated. **d** Example of classification of CC segments. The *highlighted* half sine waves are the segments that are classified as CC (i.e., synchronized and without jitter) (color figure online)

other studies (e.g., Miall et al. 1993). We also computed the jitter frequency, half the reciprocal distance between two jitter points, as shown in Fig. 2c.

Co-confident periods

Co-confident (CC) periods are defined as periods of time when little or no jitter is shown, and the participant moved in synchrony with the stimulus (Noy et al. 2011). These periods imply that the participant was successfully able to predict the stimuli during this time and so did not need to make corrective

movements. To detect CC periods, we first identified segments of motion as periods between zero-crossings of the velocity signals (that is, corresponding to one point-to-point motion of the arm/finger). Valid segments have a minimum duration of 200 ms (thus, considering each two segment as a full motion cycles, allowing for a maximal frequency of 2.5 Hz) and maximal duration of 8 s. On average, 6.2 % (± 5.2 %) of each round was removed with these thresholds. These thresholds were only applied for the CC calculations. Segments belong to a CC period if they matched two conditions: (1) They contained exactly one acceleration zero-crossing (that is, no

Table 1 Stimuli properties

Stimulus number	Experimenter/ mirror game	Mean frequency (\pm SD) Hz	Number of half sine waves	Mean amplitude (\pm SD) cm
1	Experimenter	0.37 (\pm 0.13)	38	6.8 (\pm 1.4)
2	Experimenter	0.58 (\pm 0.31)	50	5.8 (\pm 1.7)
3	Experimenter	1.08 (\pm 0.71)	60	7.2 (\pm 2.6)
4	Mirror game	0.34 (\pm 0.26)	24	11.8 (\pm 8.4)
5	Mirror game	0.60 (\pm 0.27)	58	16.0 (\pm 5.6)
6	Mirror game	0.66 (\pm 0.45)	41	11.0 (\pm 4.3)
7	Mirror game	0.59 (\pm 0.30)	29	19.4 (\pm 15.8)
8	Mirror game	0.55 (\pm 0.25)	48	15.4 (\pm 5.0)
9	Mirror game	0.34 (\pm 0.21)	28	12.6 (\pm 7.0)
10	Mirror game	0.46 (\pm 0.27)	40	21.3 (\pm 10.1)
11	Mirror game	0.98 (\pm 0.48)	64	4.5 (\pm 4.1)

“Experimenter” indicates that the stimuli are wholly generated by the experimenters, whereas “mirror game” are based on movements recorded from participants playing the mirror game (Noy et al. 2011). In both cases, the stimuli consist of a number of concatenated half sine waves. The frequencies and amplitudes of the half sine waves varied across the stimuli.

jitter), and (2) the stimuli and the response were fairly similar ($dV < 0.95$, $dT < 0.15$ s, see below). Isolated CC segments were removed (see Fig. 2d). We note that this technique is different from the one used in Noy et al. (2011).

Accuracy measures

To quantify how well the participants imitated the stimuli, we calculated the relative position (dX) and relative velocity (dV) error, and the temporal accuracy (dT), using the definitions from Noy et al. (2011). Relative position error (dX) and relative velocity error are defined by

$$dX = \frac{2}{n} \sum_{i=1}^n \frac{|x_1^i - x_2^i|}{|x_1^i + x_2^i - 2x_c|}$$

$$dV = \frac{2}{n} \sum_{i=1}^n \frac{|v_1^i - v_2^i|}{|v_1^i + v_2^i|}$$

where x_1^i and x_2^i are the positions of the participant and stimuli at time i (after registration) and similarly for velocity v . For position, we subtract the location of the center (x_c), which is the height that all half sine waves start from. When the denominator was small (< 10 pixels for dX , and < 0.01 pixels/s for dV), these values were not included in the sum to prevent instability in the measure. Temporal accuracy (dT) was computed as the absolute time difference between zero velocity events in the stimuli and participant data (before registration).

Relationship of stimulus properties and jitter response

To study a possible relationship between the tracked stimuli properties and the produced jitter response, we

performed an analysis on all jitter response events, over all players and trials. For each detected jitter event, we computed its frequency and the frequency and amplitude of the relevant tracked stimuli (see Fig. 2). We used a binned scatter plot to look for trends in this large dataset. We treated each jitter event as a 2D data point \langle stimulus frequency, jitter frequency \rangle or \langle stimulus amplitude, jitter frequency \rangle . We divided the dataset to 15 equal mass bins in the X -axis. We then plotted for each bin, the median value of the Y values in this bin and an error bar representing the estimated standard deviation of the median computed by bootstrapping the data 1,000 times. This gives a qualitative description of the relationship of the stimuli and the jitter properties. To test an observed trend, we repeated the same analysis for each participant’s data, performed linear regression over the computed bins’ medians, and tested whether the slopes of these lines were different from zero. We performed this analysis for the finger and the arm data separately.

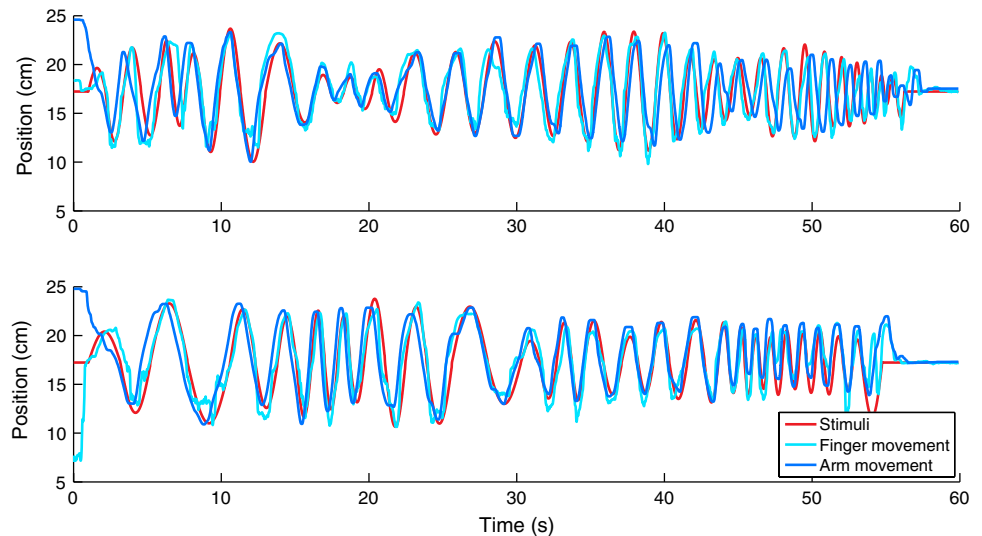
Statistics

We performed a repeated measures MANOVA with the three accuracy measures as dependent variables (dX , dV , and dT) and with independent variables trial (11 levels) and effector (finger or arm). Violations of the assumption of sphericity were tested using Mauchly’s test of sphericity.

Results

Participants were able to successfully track both types of stimuli (experimenter generated and those based on the

Fig. 3 Two examples of the stimuli (red line), shown together with the finger movement (light blue line) and the arm movement (dark blue line), all shown in terms of height on the screen (color figure online)



mirror game), with relatively little error for both effectors (finger and arm). An example of the performance of a single participant for two trials can be found in Fig. 3.

Tracking errors varied between trials and effectors

The mean accuracy of the movements of the participants (in terms of position, velocity, and time) is presented in Table 2. Performance differed between the different tasks and between effectors. A MANOVA showed significant differences for effector [$F(3,27) = 95.7, p < 0.001$], trial [$F(30,870) = 10.43, p < 0.001$], and their interaction [$F(30,870) = 7.43, p < 0.001$]. To determine the cause of differences between the dependent measures, we performed univariate repeated measures ANOVAs for the three dependent variables. For all three measures, there was a significant difference as a function of trial, shown by a main effect [dX: $F(10,290) = 9.98, p < 0.001$; dV: $F(10,290) = 7.22, p < 0.001$; dT: $F(10,290) = 6.67, p < 0.001$]. That is, the error measures varied over different trials, likely as a result of the different stimuli in the trials.

The velocity error (dV) was smaller for the arm (0.64 ± 0.02) compared to the finger (0.90 ± 0.05), shown by a main effect of effector [$F(1,29) = 31.4, p < 0.001$], while the timing error showed the opposite pattern, being smaller for the finger (0.129 ± 0.007 s) than the arm (0.164 ± 0.005 s), shown by a main effect of effector [$F(1,29) = 16.8, p < 0.001$]. There was no main effect of effector for position error [$F(1,29) = 1.59, p = 0.22$]. For the velocity error (dV) and the time error (dT), there was also a significant interaction between trial and effector [dV: $F(10,290) = 6.00, p < 0.001$; dT: $F(10,290) = 14.63, p < 0.001$], see Table 2. We note that for the three error measures, no significant correlation was found between the mean errors (per participant) in the two tasks ($p > 0.05$).

An order effect was observed for the timing and velocity errors of the arm when the finger task was performed first [dT: $t(28) = -2.88, p = 0.008$; dV: $t(28) = -2.25, p = 0.03$], with a reduction in dT from 0.18 ± 0.01 (arm first) to 0.15 ± 0.01 (finger first) and a reduction in dV from 0.69 ± 0.03 (arm first) to 0.60 ± 0.03 (finger first). The effect was not significant for position error [dX: $t(28) = -1.97, p = 0.06$] or for performance in the finger task [dX: $t(28) = -0.92, p = 0.37$; dT: $t(28) = -1.33, p = 0.19$; dV: $t(28) = -0.57, p = 0.57$].

These results demonstrate that the quality of performance varied systematically across trials and is, at least partially, modulated by the effector, with a smaller velocity error observed in arm tracking compared to finger tracking for the same stimuli and a smaller timing error for finger tracking compared to arm tracking.

Participants were able to track some of the motions without jitter

In our previous works, we used jitter-less motion, termed CC motion, as a dyadic marker of agreement in joint improvisation. We were interested to see whether participants are able to produce CC motion when they follow relatively simple motions. We computed the rate of CC motion in each of the trials (Table 2). In some trials, participants were able to produce a considerable amount of CC motion (e.g., ~10 % in trial 5 when tracking with the arm), whereas other trials exhibited no CC motion at all (e.g., trial 1 for both finger and arm movements).

CC rates in many rounds equaled zero, and so, the distribution of %CC was far from normal. To verify that %CC indeed varies systematically, we performed a nonparametric analog of an ANOVA using the Kruskal–Wallis test, with the trial as a factor. For both the arm tracking condition

Table 2 Response properties

Stimulus number	Finger movements					Arm movements				
	Relative position error (dX)	Relative velocity error (dV)	Mean timing error (s) (dT)	Peak jitter frequency (Hz)	%CC	Relative position error (dX)	Relative velocity error (dV)	Mean timing error (s) (dT)	Peak jitter frequency (Hz)	%CC
1	1.33 (± 1.14)	0.92 (± 0.39)	0.15 (± 0.08)	0.99 (± 0.02)	0.0 (± 0.0)	1.45 (± 0.65)	0.74 (± 0.22)	0.16 (± 0.05)	1.00 (± 0.03)	0.0 (± 0.0)
2	1.19 (± 1.44)	0.83 (± 0.46)	0.12 (± 0.04)	0.84 (± 0.02)	1.4 (± 2.1)	1.09 (± 0.73)	0.60 (± 0.25)	0.19 (± 0.04)	0.76 (± 0.03)	4.3 (± 3.3)
3	1.08 (± 1.19)	0.84 (± 0.35)	0.11 (± 0.03)	0.98 (± 0.03)	4.0 (± 3.8)	0.93 (± 0.61)	0.62 (± 0.21)	0.13 (± 0.03)	0.94 (± 0.03)	5.6 (± 3.8)
4	0.78 (± 0.81)	0.93 (± 0.38)	0.16 (± 0.06)	0.92 (± 0.03)	0.0 (± 0.0)	0.49 (± 0.12)	0.50 (± 0.09)	0.14 (± 0.04)	1.02 (± 0.04)	0.3 (± 0.9)
5	0.96 (± 0.94)	0.94 (± 0.34)	0.12 (± 0.04)	0.88 (± 0.03)	3.0 (± 3.2)	0.58 (± 0.15)	0.56 (± 0.13)	0.18 (± 0.04)	0.80 (± 0.03)	10.5 (± 1.0)
6	0.91 (± 1.04)	0.87 (± 0.36)	0.13 (± 0.05)	1.00 (± 0.03)	2.1 (± 2.5)	0.68 (± 0.30)	0.59 (± 0.17)	0.17 (± 0.04)	0.90 (± 0.02)	2.7 (± 7.3)
7	0.97 (± 0.52)	0.90 (± 0.33)	0.12 (± 0.03)	0.90 (± 0.02)	1.0 (± 1.9)	0.90 (± 0.24)	0.80 (± 0.20)	0.17 (± 0.04)	0.79 (± 0.03)	1.4 (± 3.3)
8	0.74 (± 0.35)	0.92 (± 0.30)	0.13 (± 0.04)	0.86 (± 0.03)	2.4 (± 3.0)	0.58 (± 0.21)	0.56 (± 0.12)	0.17 (± 0.04)	0.84 (± 0.04)	7.1 (± 2.2)
9	0.80 (± 1.20)	0.87 (± 0.27)	0.15 (± 0.05)	0.98 (± 0.04)	0.0 (± 0.0)	0.58 (± 0.18)	0.51 (± 0.11)	0.15 (± 0.04)	0.85 (± 0.03)	0.6 (± 4.7)
10	0.84 (± 0.33)	0.99 (± 0.30)	0.14 (± 0.04)	0.95 (± 0.04)	0.1 (± 0.5)	0.67 (± 0.22)	0.62 (± 0.14)	0.18 (± 0.04)	0.86 (± 0.03)	2.5 (± 1.9)
11	1.09 (± 0.56)	0.91 (± 0.31)	0.11 (± 0.02)	0.99 (± 0.05)	2.6 (± 2.5)	1.29 (± 0.47)	0.89 (± 0.31)	0.17 (± 0.03)	0.95 (± 0.04)	2.3 (± 3.2)

All values shown are mean and standard error

Relative position error (dX) and relative velocity error (dV) are unitless. %CC indicates the percentage of time that the participant is performing CC motion, i.e., almost perfectly in synchrony with the stimuli, and without jitter

[$H(10,319) = 151.2, p < 0.001$] and the hand tracking condition [$H(10,319) = 115.4, p < 0.001$], there was a systematic difference between trials. A post hoc analysis, using Bonferroni correction (adjusted p value = 0.0009), showed that 43.6 % of the trials pairs in the arm condition and 40 % of the trial pairs in the hand condition were systematically different.

We next focused on examining how the jitter frequency varies as a function of stimuli properties.

Dependence of the jitter frequency on the properties of the stimuli

To examine the dependence of jitter frequency on stimuli properties (amplitude and frequency), we plotted 2D-binned scatter plots (Fig. 4). As the stimulus frequency increases, the jitter frequency decreases (for both effectors). Likewise, as stimulus amplitude increases, jitter frequency decreases (also for both effectors). To determine whether this effect is significant, we fit a regression line to data binned on a participant-by-participant basis. A t test on the slopes of these regression lines showed that for both measures and effectors, the slope is significantly different from zero [stimulus frequency: arm: $t(29) = -11.7, p < 0.001$; finger: $t(29) = -13.4, p < 0.001$; stimulus amplitude: arm: $t(29) = -12.2, p < 0.001$; finger: $t(29) = -6.7, p < 0.001$]. Thus, we conclude that for both effectors, jitter frequency is at least partially determined by stimulus amplitude and frequency.

As a control, we verified that the reported dependency of jitter frequency on stimulus properties is not the result of our measurement, for example, from a bias added in the registration preprocessing. To test this, we created eight stimuli with constant frequencies (ranging from 0.15 to 1 Hz, at equal intervals) and simulated tracking them with a predictive/reactive controller (described in Noy et al. 2011). The controller is known (shown analytically and in simulations) to produce a constant jitter frequency. We applied the same analysis used to measure the properties of the experimental stimulus and the human responses on these simulated stimuli and responses. The resulting binned scatterplots (equivalent to Fig. 4b, c) show a constant jitter frequency that is not dependent on the stimulus frequency. Hence, the dependency reported above does not result from the measurement method.

The jitter frequency is constant across the different effectors

We next determined whether the distribution of jitter frequency used by an individual participant was comparable between the two effectors. To do this, we computed the peak of the jitter frequency distribution (the peak of the

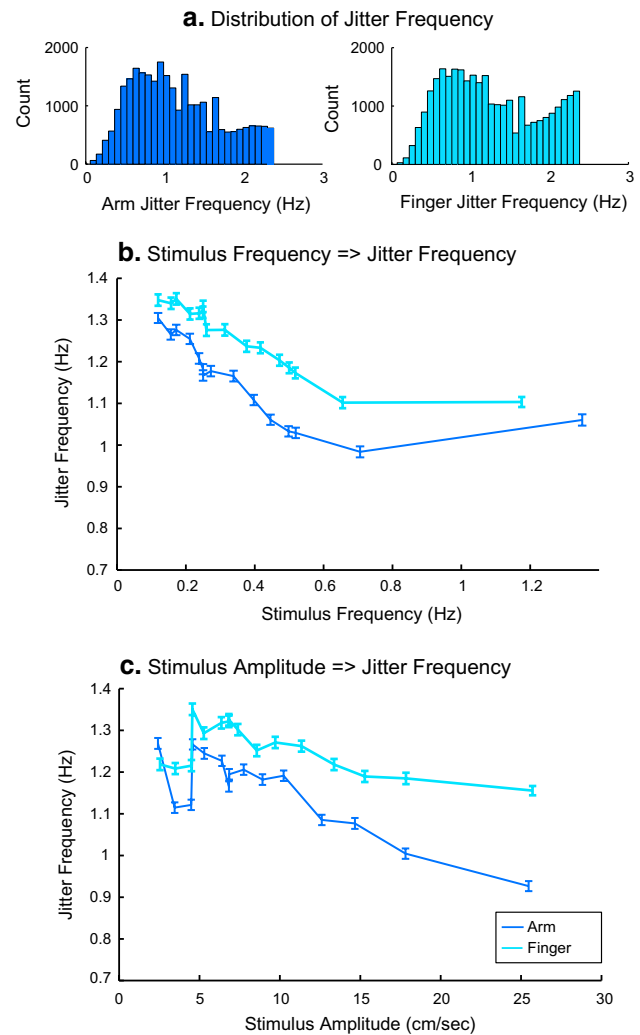


Fig. 4 Jitter frequency properties. **a** Histograms of the distributions of arm jitter frequency and finger jitter frequency. The graphs include all jitter events for all participants and trials pooled together, in screen units. **b, c** Show the relationship between stimulus properties (frequency and amplitude) and jitter frequencies for the finger and arm, based on data pooled from all participants and trials. These graphs are 2D-binned scatter plots, where each of the 15 bins has an equal number of entries, representing the relevant quantiles (from the x -axis values). The values plotted are the mean values (*error bars* are standard error)

kernel density plot) for the two effectors for each trial. We used the peak rather than the mean (or median) because the distributions were non-symmetric and had long tails. A scatterplot of the mean of these peak values for each participant, for the two effectors, can be found in Fig. 5a. A significant correlation is seen between the mean peak jitter for the two effectors ($R^2 = 0.31, p = 0.001$), with values ranging from 0.7–1.15 Hz, similar to the range of 0.8–1.8 Hz observed in Miall et al. (1993). It should be noted that in Noy et al. (2011), the calculations of frequency were performed as the reciprocal of the distance

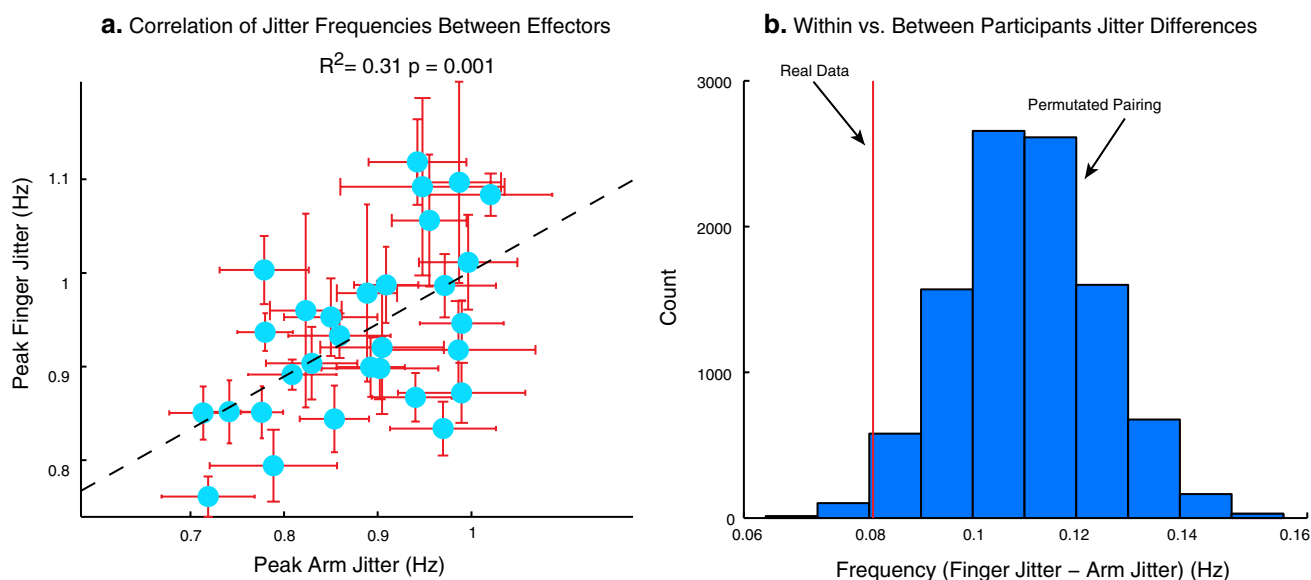


Fig. 5 a Correlation between jitter frequencies of finger and arm. Each point indicates the mean peak jitter frequencies for a single participant, with the error bars indicating the standard error. The dashed line shows the regression line. **b** Distribution of the within-participant

difference between finger and arm jitter frequency resulting from randomly permuting the participant labels 10,000 times. The red line indicates actual difference between frequencies (color figure online)

between two jitter points (and not half the reciprocal as is used here), and so, we expect the values here to be half the values observed in Noy et al. (2011). We also tested using the mean rather than the peak of the distribution, and found that the correlation remains significant ($R^2 = 0.36$, $p < 0.001$).

Overall, jitter frequencies were somewhat higher in the finger than in the arm. We next show that the difference between jitter frequencies in the arm and finger is smaller within an individual than between individuals. For this purpose, we computed the absolute difference (over all trials) between the peak jitter frequency in the finger and in the arm (mean = 0.08 Hz, SE = 0.01). We compare this difference (within an individual) to the distribution of differences between individuals, created by bootstrapping a random pairing of the arm frequency of participant X with the finger frequency of participant Y. This simulated distribution (created with 10,000 repetitions of the random pairing) has a mean of 0.11 Hz, and the within-individual mean difference (0.08 Hz) is smaller than 99 % of the values of this distribution (see Fig. 5b).

We note that in the distributions of finger movements, a second peak is observed for many of the participants around 4 Hz (although smaller than the primary peak of 0.7–1.15 Hz). The source of this additional peak requires further investigation. We also note that the order of performance (finger task first or arm task first) did not have a significant effect on the peak jitter frequency (t test: $p > 0.05$).

Discussion

The participants in the study were able to successfully perform the task of imitating non-periodic stimuli with both forward–backward movements of the arm and upward–downward movements of the index finger. While they succeeded in imitating the movements with relatively small error, clear signs of jitter were observed, that is, relatively abrupt changes of velocity. The mean jitter frequency observed across the 11 trials (0.7–1.15 Hz) was of a similar magnitude to that observed in previous studies (Miall et al. 1993; Noy et al. 2011). As expected, there was some variance between the frequencies of jitter responses of different participants.

Further, we observed that the jitter frequency is not constant, but rather varies as a function of stimuli properties. First, the different amounts of jitter may be partially due to the predictability of the stimuli or the difficulty in tracking. This can be seen, for example, in the different rate of CC motion (%CC) in different trials (corresponding to periods of zero jitter). The %CC in different trials varied systematically, with some trials showing no CC for all participants, whereas other trials showed up to 10 %CC.

We also observed that stimulus amplitude and frequency affect the amount of jitter. Over most of the range of stimulus amplitudes, higher amplitudes were correlated with lower amounts of jitter. Higher stimulus frequencies were also correlated with lower jitter frequencies (in the range 0.1–0.7 Hz, see Fig. 4b). This may be because it is difficult

for participants to smoothly track relatively low-frequency stimuli.

The observed negative relationship between stimulus frequency and jitter frequency is different from the one observed for monkeys' manual tracking of periodic and pseudo-random oscillations (Miall et al. 1986). Miall et al. report a small positive trend (that is, higher stimulus frequency leading to higher jitter frequencies) for periodic (p. 190, Fig. 4c) and pseudo-random oscillations (p. 195, Fig. 9b). The different trends might be the result of a different control strategy used by monkeys and humans when tracking non-periodic oscillations, or due to the different non-periodic signals used in these two studies. Future research can clarify the relationship between stimuli and jitter frequencies in human manual tracking, using systematic variation of the frequencies of tracked stimuli.

Our result resonates with van der Wel et al. (2009), who observed that below a certain frequency, participants always made movements with more than one velocity peak. For example, we note that comparing the three simple stimuli (generated by the experimenters), the first, which had very low stimulus frequencies (0.37 Hz), had zero %CC (that is, more jitter), while the other two, which had higher frequencies (0.58 and 1.08 Hz), had much larger %CC values (see Tables 1 and 2).

The peak jitter frequency observed for the finger and arm was similar on a participant-by-participant basis (Fig. 5), despite the very different inertial properties of the two effectors. This supports our hypothesis that similar neural processes are involved in the production of corrective responses in both cases. We note that this result is not trivial—other kinematic processes do show significant differences as a result of inertial differences, e.g., endpoint trajectory of the arm compared to the finger (Friedman and Flash 2009). Further support for the similarity of control mechanisms of the finger and the arm stems from the similar changes of jitter frequency as a function of stimulus frequency and amplitude in the two effectors (Fig. 4b, c).

The similarity in jitter frequency between effectors is comparable to the similarities observed for reaction times across different tasks. Schmiedek et al. (2007) found latent (hidden) variables that can predict features of reaction time distributions in different tasks and suggested that common processes may explain these correlations. In this study, we found correlations between the jitter frequencies in different tasks and similarly infer that common neural processes underlie this connection. This similarity in jitter frequency suggests that the control model proposed in Noy et al. (2011) to explain the jitter behavior in an arm tracking task (the one-dimensional mirror game) can be generalized to tracking in other effectors (see also Khoramshahi et al. 2014; Zhai et al. 2014).

Although similar jitter frequencies were observed for the finger and the arm, the performance was more accurate

using the arm (as quantified by the velocity error). This shows that while jitter frequency may be similar across the effectors, the effectiveness of corrections is optimized for the arm. Previous studies have shown that motor variability is partly due to signal-dependent noise and partly due to signal-independent noise (van Beers et al. 2004). If the errors were solely due to signal-dependent noise, and assuming this noise was a constant proportion of the movement magnitude, we would observe comparable relative error for the two cases. As this is not the case, it seems likely that the differences are due to signal-independent noise, which appears to be a larger proportion of the range of motion for the index finger compared to the arm. Tremor may also play a role in this difference tremor of the unsupported index finger was shown to be much larger than that of the arm (Morrison and Newell 2000).

A limitation of this study is that there are no conditions where the stimuli amplitude and frequency are matched to the intrinsic dynamics of the effector. This is because we wanted to use identical stimuli for both effectors, and most of the stimuli were based on data recorded from individual performances in a previous experiment. It remains an interesting question whether the jitter properties of the two effectors would have been more similar if the stimuli properties were more closely matched to the intrinsic dynamics of the effector.

A further limitation of this study is that the visual gain is different between the movements of the finger and the arm, because visual gain is known to affect performance in tracking tasks (Vaillancourt et al. 2006). The very different ranges of motion of the finger and the arm necessitated this difference. We purposely selected two effectors with different properties to allow us to determine which properties of the jitter are effector independent. Despite differences between finger and hand performance that may be due to differences in visual gain, we still managed to observe similarities between the jitter properties for the two effectors, suggesting that these properties are independent of the different perceptual properties between the two tasks.

While the participants in this experiment were tracking movements produced by a computer (rather than another person), we observed jitter similar to that found in the two-player mirror game. We also observed some CC periods, assumedly, due to the participants succeeding in predicting the stimuli for a period of time. The controlled nature of the stimuli in this experiment allows us to conclude that the jitter frequency is idiosyncratic (see Fig. 5). In our previous studies, open-ended mirror games were used with resultant stimuli that differed greatly between games. Hence, it was difficult to know whether differences in individual jitter were due to idiosyncratic differences or the differences between the different games. The findings of this study provide evidence that jitter frequency varies across participants

when presented with the same stimuli. These behavioral differences might be the result of differences in neural processing between individuals.

Future studies can further investigate the systematic relationships observed here between jitter frequency and stimulus properties. In the current study, we have reduced the open-ended mirror game, focusing on the behavior of different human followers to the same set of stimuli. However, the stimuli properties still varied considerably as most stimuli were taken from the motions of leaders in real games. A straight forward follow-up experiment can ask participants to manually track stimuli that vary in a controlled way, e.g., in fixed frequency intervals, in order to better understand the relationship between jitter and stimuli properties. Such a study can help in resolving the apparent discrepancy between our results from human tracking and the results in Miall et al. (1986) with monkey tracking. Another possible future direction is studying the development of tracking behavior as a result of learning. For example, Miall and Jackson (2006) showed that the jitter frequency rate decreased 25 % over an intensive training period of 5 days when there is no induced visual delay between stimuli and response (p.82, Fig. 3, Control condition). Such studies can provide further constraints for developing new control models for movements in the mirror game, as well as more generally for other reactor/predictor tracking models.

CC rates varied systematically between trials. CC periods in this study were only observed for some stimuli and not others and were repeated at specific points for different participants. This suggests that some types of motions promote CC behavior, as suggested in Hart et al. (2014), perhaps because these motions are more predictable. However, as most stimuli in the current dataset varied considerably from each other, it is difficult to draw conclusions on the relationship of the tracked stimuli properties and the ease in which participants can track it in a predictive manner. Future studies can explore this question in a more systematic manner in order to better understand the conditions that enable dyads to move together in synchrony by using similar fixed-stimuli experiments.

More generally, the approach used in the current study opens the way to systematically study human behavior in the mirror game. Until now, mirror game data were gathered from open games in which players are encouraged to be playful and creative, which produces datasets that vary considerably between participating dyads. This variability hinders a systematic investigation of skills used during the mirror game, such as the proposed reactive (with jitter) or predictive (jitter-less) tracking. Using the current experimental setup, we can collect large datasets in which different people respond to a partner with known motion properties. In the present experiment, we focused on one feature of the reactive tracking, the jitter frequency, where

the human takes the role of the follower in the mirror game. Future studies can also systematically explore the behavior of leaders in the mirror game, and possibly also human behavior during joint improvisation, playing with a (yet to be developed) realistic simulation of a mirror game partner.

The observed jitter response may be the product of intermittent control, previously reported by other studies examining tracking tasks (Navas and Stark 1968; Miall et al. 1986, 1993), by computational models (Burdet and Milner 1998; Gawthrop et al. 2011; Morasso et al. 2010), and by electrophysiological data (Dipietro et al. 2014). The similar frequencies of jitter used by the same participant despite effectors with very different inertia suggest that this intermittent control is modulated by common neural processes. This correlation is similar to that observed with respect to variability for tapping with the finger and arm (Keele and Ivry 1987). In contrast to the aforementioned study, this correlation is observed here despite the lack of a need for explicit timing in our tracking task.

However, we note that while the peak jitter values were similar between effectors for each individual participant, relatively wide distributions of jitter frequencies were observed (rather than a narrow distribution). This suggests that the movement correction and initiation process is not as simple as generating a new submovement at fixed intervals, but rather is dependent on multiple factors. The question of when a new submovement is generated requires further investigation.

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Conflict of interest The authors declare that they have no conflict of interest.

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