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Control of interjoint coordination in the performance of manual circular movements can explain lateral specialization

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ABSTRACT

Between-arm performance asymmetry can be seen in different arm movements requiring specific interjoint coordination to generate the desired hand trajectory. In the current investigation, we assessed between-arm asymmetry of shoulder-elbow coordination and its stability in the performance of circular movements. Participants were 16 healthy right-handed university students. The task consisted of performing cyclic circular movements with either the dominant right arm or the nondominant left arm at movement frequencies ranging from 40% of maximum to maximum frequency in steps of 15%. Kinematic analysis of shoulder and elbow motions was performed through an optoelectronic system in the three-dimensional space. Results showed that as movement frequency increased circularity of left arm movements diminished, taking an elliptical shape, becoming significantly different from the right arm at higher movement frequencies. Shoulder-elbow coordination was found to be asymmetric between the two arms across movement frequencies, with lower shoulder-elbow angle coefficients and higher relative phase for the left compared to the right arm. Results also revealed greater variability of left arm movements in all variables assessed, an outcome observed from low to high movement frequencies. From these findings, we propose that specialization of the left cerebral hemisphere for motor control resides in its higher capacity to generate appropriate and stable interjoint coordination leading to the planned hand trajectory.

1. Introduction

Between-arm performance asymmetry can be seen in different arm movements requiring specific interjoint coordination to generate the desired hand trajectory. In typical right-handers, testing the capabilities of motor control of the right and left arms has been made mostly in aiming tasks, requiring reaching for spatial targets through rectilinear hand movements. The results have shown that right-handed aiming is characterized by high linearity toward the target from movement onset (Bagesteiro & Sainburg, 2002; Mutha, Haaland, & Sainburg, 2012; Sainburg, 2002; Schaffer & Sainburg, 2017) and adaptation either to novel inertial dynamics (Duff & Sainburg, 2007; Sainburg, 2002) or to a predictable external force field (Yadav & Sainburg, 2014), associated with reduced muscular effort (Poirier, Papaxanthis, Mourey, Lebigre, & Gaveau, 2022). Left-handed movements, on the other hand, have been found to be characterized by an increased capability of generating feedback-based online movement corrections to errors of hand displacement

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toward a spatial target (Bagesteiro & Sainburg, 2003; Schaffer & Sainburg, 2017). Focusing on the properties of the right arm, these results have supported the "dynamic dominance model", proposing that the left cerebral hemisphere is specialized for feedforward (predictive) control mechanisms, leading to better coordination of dominant arm muscle torques across joints, and then more accurate control of the desired hand trajectory (Sainburg, 2002; Sainburg & Kalakanis, 2000). Findings from neurotypical individuals have been substantiated by evidence that lesions to the left, but not right, cerebral hemisphere lead to poor modulation of movement acceleration amplitude (Schaefer, Haaland, & Sainburg, 2007), reduced control of arm trajectory (Schaefer, Haaland, & Sainburg, 2009; Schaefer, Mutha, Haaland, & Sainburg, 2012), and deficient coordination between the two arms (Schaffer, Maenza, Good, Przybyla, & Sainburg, 2020). From a coordination perspective, these results can be thought to support the assumption that in right-handers the left cerebral hemisphere is specialized for predictive control of interjoint coordination leading to accurate production of the desired hand path (for contradictory evidence, see Maurus, Kurtzer, Antonawich, & Cluff, 2021; Takagi, Maxwell, Melendez-Calderon, & Burdet, 2020).

While looking at kinematics and joint torques of linear arm movements has revealed consistent asymmetries between the right and left arms, a deeper evaluation of between-arm asymmetries of within-limb interjoint coordination could be achieved by testing cyclic movements performed at different frequencies (cf. Bosga, Meulenbroek, & Swinnen, 2003; Buchanan & Kelso, 1993; Fink, Foo, Jirsa, & Kelso, 2000; Kelso, 1984). By testing performance on bimanual cyclic circle drawing at two frequencies, Dounskaia, Nogueira, Swinnen, and Drummond (2010) found that right-handed movements were unaffected by motion frequency, while left-handed movements were featured by reduced circularity, taking an elliptical shape, at the higher movement frequency. Further analysis showed that poorer drawing circularity of left-handed movements at a higher frequency was associated with decreased capability to predictively control interactive torques between the shoulder and elbow joints (see also Aoki, Rivlis, & Schieber, 2016; Dounskaia, Ketcham, & Stelmach, 2002; Ketcham, Dounskaia, & Stelmach, 2004; Pfann, Corcos, Moore, & Hasan, 2002; Tseng, Scholz, & Valere, 2006). Additional investigation has shown that intermanual asymmetries in movement circularity can be seen not only in lower circularity shape but also in increased movement variability over cycles of left- in comparison with right-handed movements (Cattaert, Semjen, & Summers, 1999; Zhou et al., 2022). The latter results may express increased motor output variability as a fundamental characteristic of control of left arm movements (Roy & Elliott, 1986). A possible increased variability of left arm movements is a point left untouched in the dynamic dominance model, deserving further investigation.

It becomes apparent from the aforementioned findings that fundamental distinctions of control between the right and left body sides reside in the ability to convert the intended movement trajectory into appropriate and stable interjoint coordination. Although previous evidence of improved circularity shape (Dounskaia et al., 2010) and low movement variability (Zhou et al., 2022) of right-handed movements can be thought to support the assumption that intermanual asymmetries in generating the desired hand path are inherently due to distinct within-limb interjoint coordination patterns and their stability, scarce information has been provided on this matter. Additionally, lack of comparisons between increasing movement speeds prevents a deeper understanding of the effects of progressive requirement of predictive control on interjoint coordination. In the current investigation, we aimed to compare shoulder-elbow coordination patterns and their variability between the right and left arms when performing intended circular movements at different frequencies ranging from low to individual maximum (after Dounskaia et al., 2002). Our hypothesis was that with increasing movement frequency the left arm is controlled through a distinct and more variable interjoint coordination pattern in comparison with the right arm.

2. Method

2.1. Participants

Participants in this research were 16 male university students with a mean age of 20.06 years (*SD* = 1.53). They were right-handers,

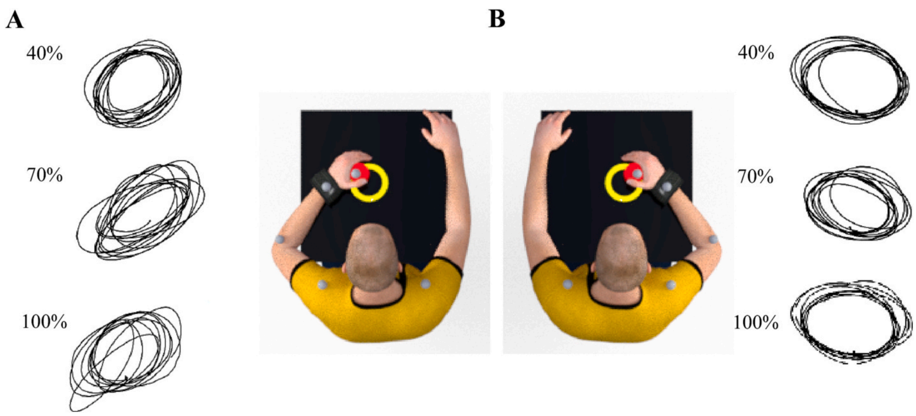

Fig. 1. Schematic representation of the experimental task performed with the left and right arms and respective markers used for analysis of interjoint coordination; representative shapes of left- and right-handed movements are shown for the lowest (40%), intermediate (70%) and the highest (100%) frequencies.

as assessed by the Edinburgh Inventory (Oldfield, 1971), with laterality indexes above 0.5. The inclusion criteria were absence of neurological or musculoskeletal disorders. The research protocol was approved by the local university ethics committee and conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki, with provision of informed consent by all participants prior to their inclusion in the study.

2.2. Task and equipment

The task consisted of performing serial cyclic circular motions with either the dominant right or the nondominant left arm at different movement frequencies. Employing a palmar grasp to support a pen-like cylinder (2-cm diameter), red colored extremity pointing downward, the participant's goal was to make aerial movements (not touching a surface) on the horizontal plane outlining as accurately as possible a 13-cm diameter circle template (1-cm diameter) positioned on a regular table surface under the task space. To ensure perceptual salience, the table surface was black colored, and the circle template was printed in yellow. The circle template was positioned 10 cm from the table edge. As movements were performed without touching the surface (keeping approximately 4 cm over the table), the circle drawing was virtual. This implies that no visual feedback existed from traces, as would be the case of real drawing on a sheet of paper, while the aerial path of the cylinder extremity could be compared to the circle template on the table surface by means of vision. To assess the coordination of the two main joints for this movement, shoulder and elbow, the wrist was immobilized through an orthosis.

Movements were made clockwise for the left arm and anti-clockwise for the right arm. Fig. 1 displays a schematic representation of the task layout. Movement frequency was paced through auditory beeps emitted by a metronome (Boss, Dr. Beat DB-60), with instruction of synchronizing each beep with the near body midline. Participants sat comfortably with their back supported on a chair, keeping 5 cm of anterior distance from the table edge. The arm contralateral to that used to perform the task was supported on the table and used to stabilize the trunk.

Six passive reflective markers were attached to the following anatomical points, on the right and left body sides: wrist (radius styloid process), elbow (upper part of the epicondyle of the humerus) and shoulder (acromion). The line connecting adjacent markers formed the segments (forearm = wrist-elbow; arm = elbow-shoulder; trunk = right shoulder-left shoulder). Additional reflective markers were attached to the top of the grasped cylinder and on the table at the near body midline (reference for circular movement onset/end). Recordings of displacement of the reflective markers were performed through an optoelectronic system (Vicon, Nexus 1.4), with three cameras positioned overhead, for off-line three-dimensional kinematic analysis.

2.3. Experimental procedures

Data acquisition was conducted on two separate days. On the first day, participants were informed about the experimental procedures, had their handedness assessed (Oldfield, 1971), and were tested for maximum frequency of the experimental task individually for each hand based on the wrist marker. Participants performed three trials of 15 cycles outlining the circle template at their maximum speed, using each arm alternately with a 2-min. rest between trials. Average frequency of the three trials was computed as the maximum frequency for each arm. With the purpose of having the two arms evaluated at the same absolute movement frequencies, the lowest maximum value between the two arms was considered for calculation of all movement frequencies equally for the right and left arms individually for each participant.

On the second day, participants were tested at five individualized movement frequencies of the experimental task: 40%, 55%, 70%, 85%, and 100%. Examiners verbally instructed participants to make aerial circular movements outlining the circular template on the table as accurately as possible, trying to make parallel movements to the table top, and timing each movement cycle to the beeps emitted by the metronome. To perform the movements at the appropriate frequency, participants were provided with two familiarization trials for each movement frequency immediately before the main trials. Evaluation was initiated only when the examiner considered through subjective evaluation that the correct movement frequency was achieved by the participant. On the main trials, the metronome was activated 5 s before trial initiation so that movements could be initiated at the right frequency from trial onset. The trial was canceled and immediately repeated either if the participant touched the table with the grasped cylinder or if the performed frequency was perceived by the examiner to be distinct from that specified by the metronome. To prevent fatigue, participants rested 1 min. between trials. The sequence of evaluation of the right and left hands was counterbalanced, and the sequence of movement frequencies was randomized across participants.

2.4. Data acquisition and processing

Data sampling frequency was set at 240 Hz. Following preliminary visual inspection of individual trial signals, raw data were processed through MATLAB (MathWorks, Inc., Natick, MA, USA) routines. Data were filtered by applying a recursive low-pass fourth-order Butterworth filter with frequency set at 10 Hz. Movement onset was determined automatically as the first increasing value 3 standard deviations above the average speed of the wrist marker in the horizontal plane during rest, where small hand displacements occurred as participants held their performing arm in the air. To minimize initial and final movement variability on data analysis, the first two and last three cycles were excluded, averaging the values of the 10 middle cycles of each trial for analysis.

2.5. Variables

2.5.1. Movement circularity index

This variable was calculated as the fraction between the shorter divided by the longer axis of the wrist marker displacement in the three-dimensional space during the movements. In this way, the ideal circle is indicated by a ratio equal to 1, with lower values indicating elliptical-shaped movements; the lower the value, the more elliptical the movement was performed (Fig. 2A).

2.5.2. Amplitude of shoulder and elbow motion

The angular amplitudes of the shoulder and elbow were calculated from the average of the differences between the largest and smallest angular values in each movement cycle (peak to peak of each joint in Fig. 2B).

2.5.3. Shoulder-elbow amplitude ratio

This is a relational variable in the space domain, representing the relative participation of each joint in the circular movements. It was calculated as the ratio of the angular amplitude of the shoulder to the angular amplitude of the elbow across cycles. Thus, if the two joints have the same movement amplitude, the ratio would be equal to 1, while lower values indicate movements with increased amplitude of the elbow (ratio between joint amplitudes in Fig. 2B).

2.5.4. Relative phase

This is a relational variable in the time dimension that is representative of interjoint coordination. It is given by the time of elbow flexion peak relative to the duration of the respective shoulder cycle multiplied by 360. In Fig. 2B, relative phase is given by the equation (b/a)*360. The values are given in polar coordinates, with values near zero indicating in-phase and near 180^{o} anti-phase interjoint coordination.

2.5.5. Movement variability

For all evaluated variables, intraindividual variability was calculated by means of the standard deviation across the 10 movement cycles of each trial.

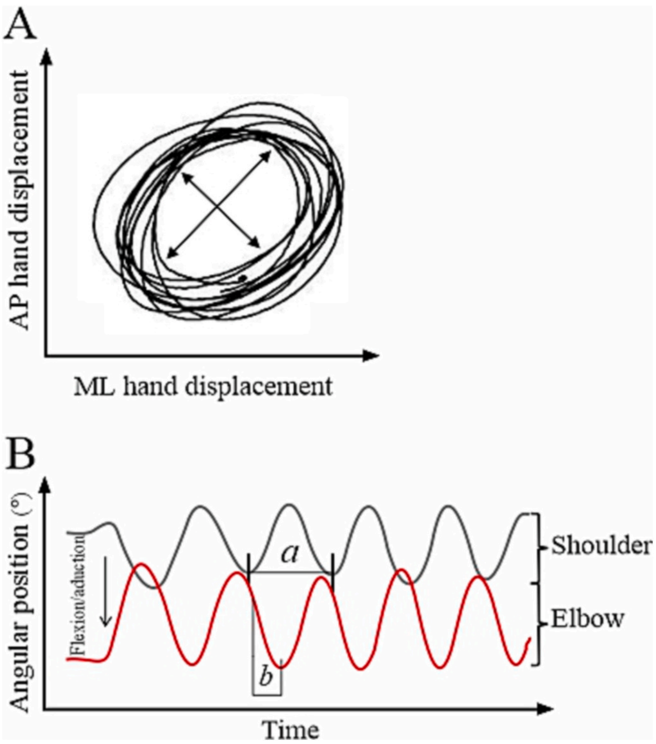

Fig. 2. Representation of the analyzed variables: (A) movement circularity, showing the longitudinal and transversal axes considered in the computation of the circularity index; (B) variation of angular position over time for the shoulder and elbow, with joints' peak to peak indicating amplitude, ratio between joint amplitudes were used for calculation of the shoulder-elbow amplitude coefficient, and temporal markers (a/b) were used for calculation of relative phase.

2.6. Statistical analysis

Individual values were calculated as the average of the three trials for each experimental condition. Normality of data distribution was tested by applying Shapiro–Wilk's test. To compare performance between the right and left arms across the different movement frequencies, we used two-way 2 (arm) x 5 (frequency) ANOVAs with repeated measures on both factors. Post hoc comparisons were made through the Bonferroni test, with effect sizes given by partial eta-squared (η_p^2) or Cohen's *d* (Cohen, 1988). Statistical significance was set at 5%.

3. Results

Approximately 5% of the trials across participants were repeated due to performing the movements at a frequency different from that specified through the metronome. Shapiro–Wilk's test indicated normal data distribution across variables. Average maximal frequency in the performance of the cyclic circular movements was 4.04 Hz for the left arm and 4.80 Hz for the right arm, with all participants reaching the highest movement frequency with their right arm. Table 1 shows the observed mean and standard error for the actual movement frequency for both the left and right arms in each experimental condition.

3.1. Movement circularity index

Analysis of movement circularity indicated significant main effects of arm, $F(1, 15) = 20.01$, $p < 0.001$, $\eta_p^2 = 0.57$, and frequency, $F(4, 60) = 6.05$, $p < 0.001$, $\eta_p^2 = 0.29$, and a significant arm by frequency interaction, $F(4, 60) = 8.53$, $p < 0.001$, $\eta_p^2 = 0.34$. Post hoc comparisons for the interaction showed a lower circularity index for the left arm than for the right arm at the two faster movement frequencies (*p* values < 0.001, $d = 0.98$ and 1.57, respectively, for 85% and 100%). For the within-arm comparisons, the left arm had a significantly lower movement circularity at the highest frequency compared to the frequencies of 40% ($p < 0.001$, $d = 1.18$), 55% ($p < 0.001$, $d = 0.98$) and 70% ($p = 0.025$, $d = 0.56$), and at the 70% and 85% frequencies compared to the lowest frequency, as indicated by closed round markers in Fig. 3A (*p* values < 0.025, $d = 0.84$, 1.01, respectively). For the right arm, the circularity index was not significantly different across movement frequencies.

Analysis of variability of movement circularity indicated significant main effects of arm, $F(1, 15) = 31.97$, $p < 0.001$, $\eta_p^2 = 0.68$, and frequency, $F(4, 60) = 12.37$, $p < 0.001$, $\eta_p^2 = 0.46$, and a significant arm by frequency interaction, $F(4, 60) = 2.29$, $p = 0.044$, $\eta_p^2 = 0.21$. Post hoc comparisons for the interaction showed significantly higher variability for the left than the right arm at the four higher movement frequencies (*p* values < 0.001, *d* range = 0.95-1.12). In within-arm comparisons for the left arm, the three higher movement frequencies (70%, 85% and 100%) led to significantly higher variability than the lowest frequency (40%) (*p* values < 0.001, *d* range = 1.21-1.25) (Fig. 3B).

3.2. Joints' motion amplitude

Analysis of shoulder motion amplitude indicated lack of statistically significant effects (*F* values < 1, *p* values > 0.05, Fig. 4A). For the elbow motion amplitude, results indicated a significant main effect of arm, $F(1, 15) = 78.42$, $p < 0.001$, $\eta_p^2 = 0.74$, and a significant arm by frequency interaction, $F(4, 60) = 3.14$, $p = 0.020$, $\eta_p^2 = 0.30$. The main effect of frequency fell short of statistical significance, $F(4, 60) = 0.29$, $p > 0.1$. Post hoc comparisons for the interaction showed significantly higher values for the left than the right arm at all movement frequencies (*p* values <0.001, *d* range = 0.91-1.52). For within-arm comparisons, the left arm presented lower values at the highest than at the lowest movement frequency ($p = 0.012$, $d = 0.85$) (Fig. 4B).

Analysis of variability of shoulder motion amplitude indicated significant main effects of arm, $F(1, 15) = 32.12$, $p < 0.001$, $\eta_p^2 = 0.65$, and frequency, $F(4, 60) = 19.14$, $p < 0.001$, $\eta_p^2 = 0.52$, and a significant arm by frequency interaction, $F(4, 60) = 2.80$, $p = 0.048$, $\eta_p^2 = 0.14$. Post hoc comparisons for the interaction showed significantly higher values for the left than the right arm at the two higher movement frequencies (*p* values < 0.005, $d = 1.23$ and 1.19, respectively for 85% and 100%). Within-arm comparisons for the left arm showed significantly higher variability at the three higher frequencies in comparison with the two lower frequencies (*p* values < 0.010, *d* range = 0.74-1.45) (Fig. 4C).

For amplitude of elbow movement variability, results indicated significant main effects of arm, $F(1, 15) = 71.03$, $p < 0.001$, $\eta_p^2 = 0.72$, and frequency, $F(4, 60) = 6.02$, $p < 0.001$, $\eta_p^2 = 0.18$, and a significant arm by frequency interaction, $F(4, 60) = 3.18$, $p = 0.025$, $\eta_p^2 = 0.14$. Post hoc comparisons for the interaction showed significantly higher values for the left than the right arm at all movement frequencies (*p* values < 0.001, *d* range = 1.29-1.89). For within-arm comparisons, the left arm showed significantly higher variability

Table 1
Average and standard error (in parentheses) of actual movement frequencies (Hz) for the left and right arms.

	Movement frequency (%)				
Arm	40	55	70	85	100
Left	1.62 (0.22)	2.22 (0.31)	2.83 (0.39)	3.44 (0.47)	4.04 (0.55)
Right	1.60 (0.17)	2.18 (0.22)	2.77 (0.18)	3.49 (0.21)	4.15 (0.23)

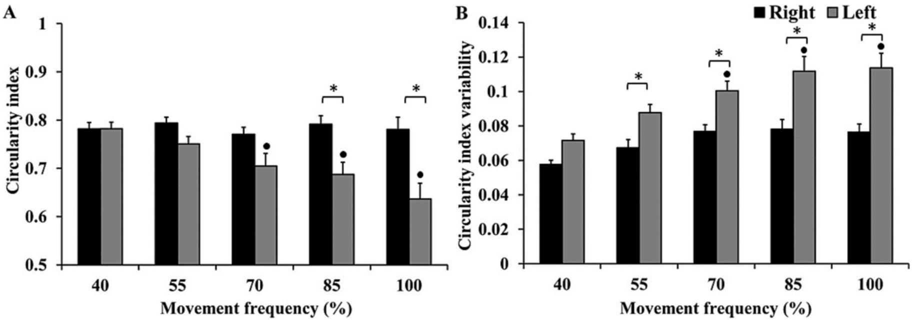

Fig. 3. Average and standard errors (vertical bars) for (A) movement circularity index and (B) respective variability for the right and left arms as a function of movement frequency; significant between-arm differences are marked by asterisks, and intra-arm significant differences from the 40% frequency are indicated by closed round markers.

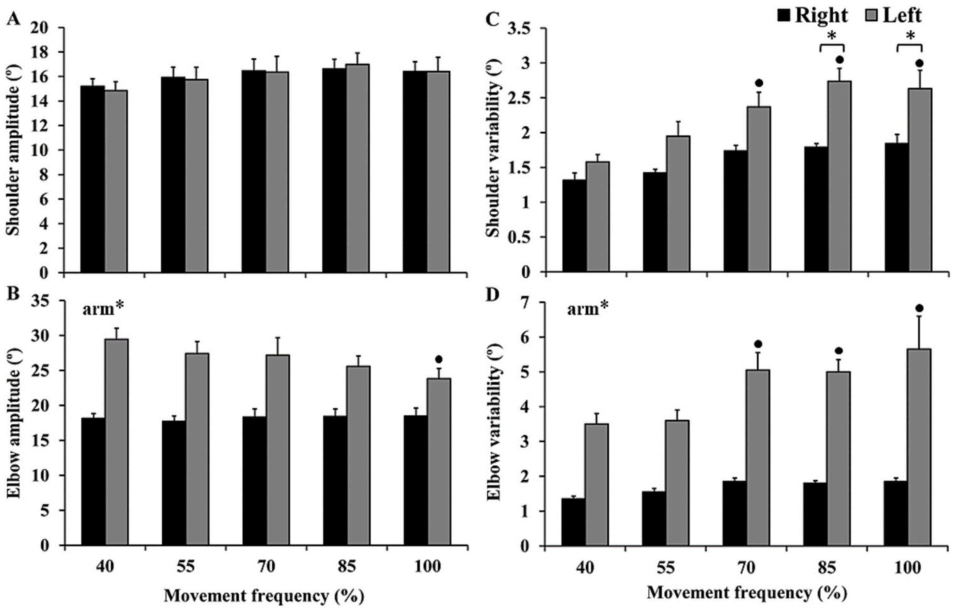

Fig. 4. Average and standard error (vertical bars) of angular amplitudes for the (A) shoulder and (B) elbow, and (C–D) respective intraindividual variability for the right and left arms as a function of movement frequency; significant frequency-specific between-arm differences are marked by asterisks, significant between-arm differences across all frequencies are indicated by "arm*", and intra-arm significant differences from the 40% frequency are indicated by closed round markers.

at the three higher frequencies in comparison with the two lower frequencies (p values < 0.005, d range $= 0.96$-1.15) (Fig. 4D).

3.3. Shoulder-elbow amplitude ratio

Fig. 5A depicts the distinction between the right and left arms over movement frequencies of shoulder-elbow coordination in the spatial domain by showing mean trajectories across participants. Analysis of the coefficient of shoulder-elbow movement amplitude indicated significant main effects of arm, $F(1, 15) = 94.80$, $p < 0.001$, $\eta_p^2 = 0.77$, and frequency, $F(4, 60) = 4.14$, $p < 0.001$, $\eta_p^2 = 0.15$, and a significant arm by frequency interaction, $F(4, 60) = 5.62$, $p < 0.001$, $\eta_p^2 = 0.16$. Post hoc comparisons for the interaction showed significantly lower coefficients for the left arm than for the right arm at all movement frequencies (p values < 0.001, d range $= 1.28$-1.74). Within-arm comparisons for the left arm showed significantly higher values at the three higher movement frequencies compared to the lowest frequency (p values <0.050, d range $= 0.33$-0.42) (Fig. 5B).

Analysis of variability of the coefficient of shoulder-elbow movement amplitude indicated significant main effects of arm, $F(4, 60) = 31.56$, $p < 0.001$, $\eta_p^2 = 0.64$, and frequency, $F(4, 60) = 12.48$, $p < 0.001$, $\eta_p^2 = 0.49$. The arm by frequency interaction fell short of statistical significance, $F(4, 60) = 0.55$, $p > 0.1$. The arm effect was due to higher variability values in the left arm than in the right arm, while the frequency effect was due to increased values at the three higher frequencies in comparison with the lowest frequency, as indicated by double closed round markers in Fig. 5C (p values < 0.050, d range $= 0.31$-0.67).

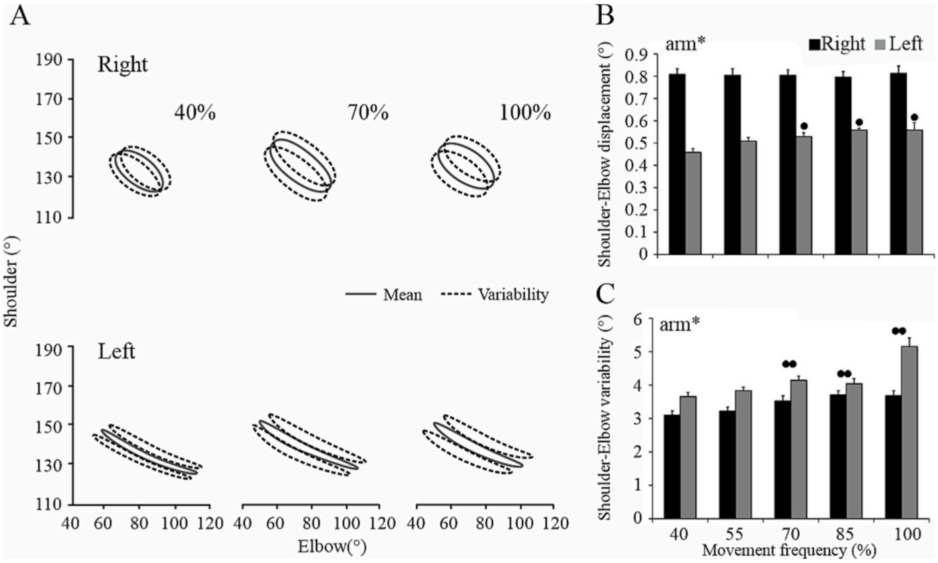

Fig. 5. Left-sided panels: Mean (solid line) and variability (dashed lines) of the spatial relationship between shoulder and elbow angular displacement in movements performed with the right and left arms at the lowest (40%), intermediate (70%) and the highest (100%) movement frequencies. Right-sided panels: Average and standard error (vertical bars) of the (B) shoulder-elbow amplitude coefficient and (C) respective intraindividual variability for the right and left arms as a function of movement frequency. Significant between-arm differences across all frequencies are indicated by "arm*", intra-arm significant differences are represented by single closed round markers compared to the 40% frequency, and significant differences due to the main effect of frequency are represented by double closed round markers.

3.4. Relative phase

Left-sided panels of Fig. 6A depict the distinction between the right and left arms of shoulder-elbow coordination in the temporal domain. Relative phase analysis indicated significant main effects of arm, $F(1, 15) = 256.70, p < 0.001, \eta_p^2 = 0.95$, and frequency, F(4,

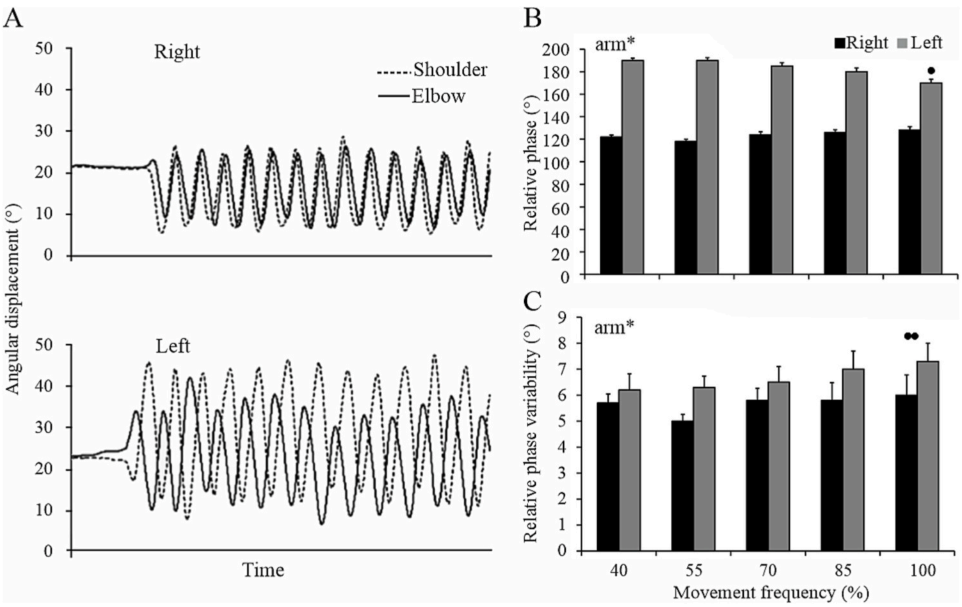

Fig. 6. Left-sided panels (A): Representative kinematic signals showing the distinction of the temporal relationship between shoulder and elbow angular displacements for the right and left arms. Right-sided panels: Average and standard error (vertical bars) of (B) relative phase and (C) intraindividual variability for the right and left arms as a function of movement frequency. Significant between-arm differences across all frequencies (either arm main effect or across pairwise comparisons) are indicated by "arm*", an intra-arm significant difference from the 40% is indicated by a single closed round marker, and a significant main effect of frequency is indicated by double closed round markers (compared to the 55% frequency).

60) = 5.27, $p < 0.001$, $\eta_p^2 = 0.15$, and a significant arm by frequency interaction, $F(4, 60) = 13.76$, $p < 0.001$, $\eta_p^2 = 0.45$. Post hoc comparisons for the interaction showed significantly higher relative phase values for the left arm than for the right arm at all movement frequencies (p values < 0.001, d range = 1.59-1.84). Within-arm comparisons for the left arm showed a significantly lower value at the highest movement frequency compared to all other frequencies (p values <0.050, d range = 0.38-0.64) (Fig. 6B).

Analysis of intraindividual variability of relative phase indicated significant main effects of arm, $F(1, 15) = 18.18$, $p < 0.001$, $\eta_p^2 = 0.33$, and frequency, $F(4, 60) = 3.73$, $p < 0.001$, $\eta_p^2 = 0.27$. The arm by frequency interaction fell short of statistical significance, $F(4, 60) = 0.66$, $p > 0.1$. The arm effect was due to higher relative phase variability for the left arm than for the right arm. Post hoc comparisons for the frequency effect indicated a significantly higher value at the highest frequency compared to the 55% frequency ($p = 0.038$) (Fig. 6C).

4. Discussion

In the current investigation, we compared shoulder-elbow coordination patterns and their stability between the right and left arms when performing circular movements at different movement frequencies. We hypothesized that with increasing movement frequency the left arm is controlled through a distinct and more variable interjoint coordination pattern in comparison with the right arm. The results confirmed the hypothesis by showing that circularity of left arm movements diminished and respective variability increased as movement frequency was augmented, becoming significantly different from the right arm at movement frequencies higher than the lowest one. For most variables, we also found significant between-arm asymmetries at the slowest movement frequency. This was the case for elbow amplitude, shoulder-elbow amplitude ratio, relative phase, and the respective variability for these variables. Intra-arm comparisons across movement frequencies showed that increment of speed led to metric and coordinative changes in the left arm, while the right arm movements seem to have been unaffected. Then, the results showed that asymmetries of interjoint coordination in the performance of circular movements can be seen even in slow movements, and that increment of movement speed can lead to magnification of performance asymmetries between the right and left arms.

4.1. *Circularity*

To examine between-arm asymmetries of interjoint coordination to produce the desired circular hand trajectory, we employed the experimental strategy of testing the coordination pattern stability by going from low to high movement frequencies (cf. Bosga et al., 2003; Buchanan & Kelso, 1993; Fink et al., 2000; Kelso, 1984). Our global behavioral outcome confirmed the expected decreasing circularity of the left-hand trajectory for faster movements, taking an elliptical shape as movement frequency was increased (cf. Ketcham et al., 2004; Pfann et al., 2002). Generation of an elliptical shape while intending to produce circular movements has been proposed to be due to poor predictability by the central nervous system of the interaction between muscular and extramuscular forces defining the hand trajectory (Pfann et al., 2002), with ill-controlled movements being explained by an inability to anticipate and modulate interjoint interactive torques (Dounskaia et al., 2010; Ketcham et al., 2004). Movement circularity of the right hand, conversely, seems to have been unaffected by movement frequency, reaching similar high circularity indexes across the tested frequencies (Fig. 3). As the circularity indexes were equivalent between the right and left arms at lower movement frequencies, a possible interpretation for this behavioral outcome is that as the demand for predictive control of shoulder-elbow interactive torques increases at higher movement frequencies, between-arm asymmetry of predictive control becomes more evident (cf. Dounskaia et al., 2010; Zhou et al., 2022). This result is consistent with the proposition made in the dynamic dominance model that the left cerebral hemisphere is specialized for predictive control, manifested in more accurate desired movement trajectories (Sainburg, 2002; Sainburg & Kalakanis, 2000; Schaffer et al., 2020; Yadav & Sainburg, 2011, 2014). At low movement frequencies, conversely, more erratic hand paths in producing circular movements due to a low predictive control capability in the performance with the left hand may have been corrected through sensory feedback mechanisms, which is proposed in the dynamic dominance model to be a specialization of the right cerebral hemisphere (Bagesteiro & Sainburg, 2003; Duff & Sainburg, 2007; Jayasinghe, Sarlegna, Scheidt, & Sainburg, 2020).

4.2. *Coordination in the spatial dimension*

For a deeper understanding of between-arm asymmetries in producing the desired hand trajectory, we selected coordination variables as the main outcome. The hand path in the experimental task was achieved by coordinating amplitude and timing of the simultaneous and interactive motions of the shoulder and elbow joints. Assessment of individual joint motions showed equivalent shoulder amplitudes between the two arms, while for the elbow we found greater amplitudes for the left arm than for the right arm throughout movement frequencies (Fig. 4). Between-arm asymmetry, particularly at the elbow, may be related to previous results showing that drawing movements are regulated through adjustments of amplitude and timing of elbow motion, generating muscle torques as required by the interaction with the shoulder (Dounskaia et al., 2002; Ketcham et al., 2004). The increased amplitude of elbow movements in the left arm was reflected in the shoulder-elbow amplitude ratio (Fig. 5), with higher values for the right arm across movement frequencies indicating more similar angular amplitudes between the shoulder and elbow motions than those observed for the left arm. The shoulder-elbow amplitude ratio represents a coordination variable in the spatial dimension, suggesting that the plan to produce the circular hand trajectory at the higher volitive control level is converted by the lower executive level into arm-specific muscular activation in the right and left cerebral hemispheres to deal with the interactive torques continuously varying throughout joint excursion as the movement is performed (cf. Cattaert et al., 1999). From this conceptualization, it can be thought that each cerebral hemisphere converts the abstract movement plan into different parameters in the neural drive to produce muscular activation leading to joint motion. This between-arm asymmetry of interjoint coordination in the spatial dimension can be thought to partially explain the distinct trajectories found between the right and left hands. This proposition is in agreement with the conceptualization that the left cerebral hemisphere is specialized for the dynamic control of voluntary movements (Sainburg, 2002; Sainburg & Kalakanis, 2000).

4.3. Coordination in the temporal dimension

In the temporal dimension, interjoint relative phase was distinct between the right and left arms across all movement frequencies, with a stable value near 120^{o} for the right arm and values in the range of approximately 160-180^{o} for left arm movements (Fig. 6). The results revealed that shoulder-elbow relative phase was stable across movement frequencies for the right arm (cf. Bosga et al., 2003), while for the left arm the coordination pattern varied across frequencies. This finding of spontaneous modulation of relative phase as a function of higher movement frequencies indicates a less stable interjoint coordination pattern for left arm movements (cf. Buchanan & Kelso, 1993; Fink et al., 2000; Kelso, 1984). Although relative phase became more similar between the right and left arms at higher frequencies, the combination of high relative phase and increased amplitude of elbow motion can be thought to explain increasing elliptical rather than circular movements of the left hand with increasing movement frequencies. A similar change of a circular hand trajectory into an elliptical shape with increased movement frequency associated with changes in relative phase between distal joints (wrist and finger movements) was reported previously (Dounskaia et al., 2002), suggesting that this effect is not specific to the analyzed joints. Despite coordination variability across movement frequencies, a near-antiphase interjoint coordination for the left arm suggests the adoption of a naturally easier and more stable coordination pattern than that adopted with the right arm (Tuller & Kelso, 1989). This may represent a coordination strategy to address the limited capacity of the right cerebral hemisphere to convert the intended hand trajectory into well-coordinated joint motion (see Cattaert et al., 1999). Taking performance with the right hand as a reference for appropriate coordination to generate circular hand trajectories, our data of decreased shoulder-elbow amplitude ratio associated with increased relative phase for left arm movements suggest that failure to achieve the desired hand trajectory with the left arm is due to a deficit of the right cerebral hemisphere to control interjoint coordination in the nondominant left arm. This between-arm asymmetry was observed throughout movement frequencies, but it seems to have been particularly critical to achieving the behavioral outcome at higher movement frequencies when predictive control of muscular and extramuscular forces becomes mandatory for achieving the desired circular hand path due to the limited time for online feedback-based corrections. This interpretation is supported by previous results showing that compared to the right arm, left arm movements are featured by decreased reliance on feedforward control (Bagesteiro & Sainburg, 2002, 2003) and less effective feedforward adaptation to intersegmental dynamics (Duff & Sainburg, 2007; Schabowsky, Hidler, & Lum, 2007; Yadav & Sainburg, 2014). In neurologic patients, Schaffer et al. (2020) showed that left hemisphere damage led to poor predictive control of between-arm coordination, while right hemisphere damage seems to have not affected between-arm coordination. Additionally, Schaefer et al. (2009) found that left hemisphere damage was associated with deficits in controlling the desired arm trajectory due to poor interjoint coordination. These findings support the assumption that the left cerebral hemisphere is specialized in predictive mechanisms governing interjoint coordination to generate the desired hand trajectory.

4.4. Coordination variability

A point left untouched in the dynamic dominance model (Sainburg, 2002; Sainburg & Kalakanis, 2000) is between-arm asymmetry of movement variability. Previous results have shown that the left arm is more variable than the right arm both in spatial accuracy of aiming movements (Carson, Goodman, Chua, & Elliott, 1993; Roy & Elliott, 1986; Roy, Kalbfleisch, & Elliott, 1994) and in temporal regularity of fast tapping tasks (Todor & Kyprie, 1980; Todor, Kyprie, & Price, 1982). Analysis of intermanual asymmetries in the performance of circular movements has also shown increased radius variability for the nondominant arm compared with the dominant arm (Zhou et al., 2022). Our results confirmed the greater variability of the left compared to right arm movements. This between-arm asymmetry was observed across the whole set of the assessed variables, leading to more variable shoulder-elbow coordination in the spatial and temporal dimensions for left arm movements, associated with more variable left hand trajectories. For coordinative variables, increased variability for the left arm was found not only at high but also at low movement frequencies. Thus, variability of interjoint coordination over a series of repeated circular movements seems to be fundamentally asymmetric between the control of the right and left arms. These results support the assumption that the specialization of the left cerebral hemisphere is manifested not only in the generation of more effective interjoint coordination to produce the desired hand trajectory but also in more consistent interjoint coordination over a series of repetitive movements in cyclic actions. Schmidt, Zelaznik, Hawkins, Frank, and Quinn (1979) have argued that a potential source of motor output variability is neural noise in the translation of movement parameter selection into executive motor commands to the muscular system. From this proposition, we suggest that the higher output variability found at all movement frequencies for the left arm in comparison with the right arm can be due to greater neural noise in the right than the left cerebral hemisphere during the executive phase of the generation of motor commands controlling interjoint coordination to produce the desired hand path.

As a major limitation of this investigation, we employed equal absolute movement frequencies for the right and left arms based on the maximum frequency of left arm movements. This experimental strategy prevented testing the right arm at its actual maximum movement frequency as done for the left arm. In this regard, it is possible that between-arm asymmetries might have been attenuated if movement frequency was set relative to the individual arm's maximal frequency. We suggest that in future studies addressing between-arm asymmetries of interjoint coordination calculation of movement frequencies be made individually for each arm with reference to its maximum.

As concluding remarks, we showed results supporting the proposition that specialization of the left cerebral hemisphere for motor control resides in appropriate regulation of interjoint coordination with the purpose of producing the desired hand trajectory. While the reported between-arm asymmetry of interjoint coordination was found at different movement frequencies, greater disruption of movement circularity in the left arm at higher movement frequencies is in consonance with the proposition made in the dynamic dominance model of left cerebral hemisphere specialization for feedforward (predictive) control (Sainburg, 2002; Sainburg & Kalakanis, 2000). As an additional original finding, our results revealed greater variability of left arm movements in all variables assessed, an outcome observed from low to high movement frequencies. From this finding, we propose that consistency in generating the planned hand trajectory in cyclic movements is part of left cerebral hemisphere specialization leading to asymmetric performance between the left and right arms.

Author contributions

CFP Monfredini: experimental design planning, data collection, statistical analysis, and interpretation of results.
DB Coelho: data collection, data interpretation, participation in manuscript writing; elaboration of figures.
AJ Marcori: participation in manuscript writing.
LA Teixeira: experimental design planning, interpretation of results, manuscript writing, research supervision.

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Ethics approval

This investigation received study-specific approval by the local university ethics committee for research involving humans, and all participants provided informed consent before inclusion in the experiment.

Declaration of Competing Interest

The authors declare to have neither financial nor non-financial interests that are directly or indirectly related to this work.

Data availability

Data will be made available on request.

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