



Atypical inter-hemispheric communication correlates with altered motor inhibition during learning of a new bimanual coordination pattern in developmental coordination disorder

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Abstract

Impairment of motor learning skills in developmental coordination disorder (DCD) has been reported in several studies. Some hypotheses on neural mechanisms of motor learning deficits in DCD have emerged but, to date, brain-imaging investigations are scarce. The aim of the present study is to assess possible changes in communication between brain areas during practice of a new bimanual coordination task in teenagers with DCD ($n = 10$) compared to matched controls ($n = 10$). Accuracy, stability and number of mirror movements were computed as behavioural variables. Neural variables were assessed by electroencephalographic coherence analyses of intra-hemispheric and inter-hemispheric fronto-central electrodes. In both groups, accuracy of the new coordination increased concomitantly with right intra-hemispheric fronto-central coherence. Compared to typically developing teenagers, DCD teenagers presented learning difficulties expressed by less stability, no stabilization of the new coordination and a greater number of mirror movements despite practice. These measures correlated with reduced inter-hemispheric communication, even after practice of the new coordination. For the first time, these findings provide neuro-imaging evidence of a kind of inter-hemispheric 'disconnection' related to altered inhibition of mirror movements during motor learning in DCD.

RESEARCH HIGHLIGHTS

- Accuracy of the new coordination increased concomitantly with right intra-hemispheric fronto-central coherence with practice in both groups.
- Teenagers with DCD presented lower stability, larger number of mirror movements and reduced inter-hemispheric communication than typically developing teenagers after practice.
- Less inter-hemispheric fronto-central communication correlated with larger number of mirror movements after learning

1 | INTRODUCTION

Developmental coordination disorder (DCD) is one of the least understood neurodevelopmental disorders (Gomez & Sirigu, 2015).

Typically, children with DCD have impairments in motor skills that affect their daily living activities and academic performance (Blank, Smits-Engelsman, Polatajko, & Wilson, 2012; Geuze, 2005), which cannot be explained by neurological or intellectual dysfunction (American Psychiatric Association, 2013). These impairments may occur in adolescence (Cousins & Smyth, 2003) and adulthood (Kirby, Edwards, & Sugden, 2011). It is well known that DCD impacts motor control (de Castelnau, Albaret, Chaix, & Zanone, 2007; Geuze & Kalverboer, 1994; Jover, Schmitz, Centelles, Chabrol, & Assaiante, 2010; Smits-Engelsman, Wilson, Westenberg, & Duysens, 2003; Wilson, Ruddock, Smits-Engelsman, Polatajko, & Blank, 2013), but learning new motor skills has rarely been investigated. The few available studies on motor learning in participants with DCD have yielded divergent results: two of them (Wilson, Maruff, & Lum, 2003; Lejeune, Catale, Willems, & Meulemans, 2013), which required participants to learn unimanual motor sequences, did not discern learning impairments in



DCD, whereas another study involving bimanual motor sequences did (Gheysen, Van Waelvelde, & Fias, 2011).

Very few brain-imaging investigations have examined neural mechanisms of motor learning deficits in DCD. Dominant hypotheses focus on dysfunction of cerebellum networks (Zwicker, Missiuna, Harris, & Boyd, 2011), basal ganglia (Lundy-Ekman, Ivry, Keele, & Woollacott, 1991), parietal networks (Kashiwagi, Iwaki, Narumi, Tamai, & Suzuki, 2009) and the corpus callosum (Sigmundsson, Whiting, & Ingvaldsen, 1999; Tallet, Albaret, & Barral, 2013) (for reviews see Bo & Lee, 2013; Peters, Maathuis, & Hadders-Algra, 2013; Zwicker, Missiuna, & Boyd, 2009). In addition to dysfunction of isolated brain areas, possible modifications in communication between brain areas in DCD have yet to be assessed.

Bimanual coordination provides a key opportunity to probe possible dysfunctions in brain communications because it relies on coupling between brain regions, particularly functional coupling between motor areas of both cerebral hemispheres (Serrien, 2008) through the corpus callosum (Gooijers et al., 2013; Gooijers & Swinnen, 2014). Bimanual movements are investigated with a synchronization paradigm requiring tapping with the right and left fingers in synchrony with a timing pattern specified by two stimuli (flashes or beeps). In healthy adults and children, two pre-existing bimanual coordination patterns are accurate and stable without practice (Kelso, 1984; Robertson, 2001): inphase coordination refers to simultaneous activation of homologous muscle groups, and antiphase coordination corresponds to simultaneous activation of antagonist muscle groups. In the framework of dynamic system theory, these two pre-existing bimanual coordination patterns are called attractors because they are preferentially produced when another bimanual coordination is required (Tuller & Kelso, 1989). Moreover, inphase is more stable, hence a stronger attractor, than antiphase coordination (Kelso, 1984).

Using cortico-cortical coherence analysis of electroencephalographic (EEG) signals in healthy adults (for review see Rueda-Delgado et al., 2014), Serrien (2008) showed that antiphase coordination was associated with higher EEG-EEG coherence (i.e., increased inter-hemispheric communication) between frontal regions than inphase coordination. EEG-EEG coherence measures correlations between brain regions, that is, the degree of synchronization of their oscillatory activities (Gerloff et al., 1998), and can be considered to reflect neural communications across brain sites (Fries, 2005). It provides a powerful tool to assess whether functional brain communication is altered in DCD and whether it changes with practice of a new bimanual coordination pattern.

Deficits in the production of bimanual coordination in DCD are well described in the literature (Roche, Wilms-Floet, Clark, & Whittall, 2011; Volman & Geuze, 1998; Volman, Laroy, & Jongmans, 2006; Whittall et al., 2008). In particular, compared to their typically developing (TD) peers, children with DCD make more non-voluntary mirror movements (Licari & Larkin, 2008; Licari, Larkin, & Miyahara, 2006; Tallet et al., 2013), that are defined as symmetric movements of both hands during unimanual voluntary movements (Armatas, Summers, & Bradshaw, 1996). Moreover, children with DCD produce less stable antiphase coordination/parallel movements than their age-related

peers without DCD (Volman & Geuze, 1998; Volman et al., 2006). Considering that antiphase requires more communication between brain areas than inphase coordination (Serrien, 2008), these results could suggest an atypical inter-hemispheric communication in DCD.

Previous studies in healthy adults have demonstrated that learning a new bimanual coordination pattern reveals the attracting power of the pre-existing inphase and antiphase coordination, as expressed by the production of mirror and parallel movements at the beginning of practice (Tallet, Kostrubiec, & Zanone, 2008). Learning a new bimanual coordination pattern results in increased accuracy and stability of coordination (Walter & Swinnen, 1994; Zanone & Kelso, 1992) and is associated with changes in intra- and inter-hemispheric coherence between pairs of EEG signals (Andres et al., 1999; Gerloff & Andres, 2002; Serrien, 2009). In healthy adults, Andres et al. (1999) investigated coupling between the premotor cortex, the primary sensorimotor cortex of the left and right hemispheres, and the mesial fronto-central cortex during learning of a bimanual sequence. They showed that the increased behavioural stability of bimanual sequence with practice is associated with changes in oscillatory activities of the beta band (13–30 Hz), which reflects motor cortical functions (Boonstra, Daffertshofer, Breakspear, & Beek, 2007; Gerloff & Andres, 2002; Houweling, Daffertshofer, Van Dijk, & Beek, 2008; Pfurtscheller & Da Silva, 1999; Pollok, Latz, Krause, Butz, & Schnitzler, 2014; Serrien & Brown, 2003). More precisely, intra- and inter-hemispheric coherence was found to be increased in the early stage of bimanual learning, followed by decreased intra- and inter-hemispheric coherence after bimanual training (around 30 min).

At the behavioural level, the present study aims to test whether teenagers with DCD present difficulties in learning a new bimanual coordination pattern compared to TD controls as revealed by lower increases in accuracy and stability and by a greater number of mirror movements during the production of the required new bimanual coordination pattern despite practice. At the neural level, this study aims to test whether functional brain communication, as assessed by EEG-EEG coherence over the inter- and intra-hemispheric premotor cortex, is altered in DCD, how it changes with the practice of a new bimanual coordination pattern, and how it correlates with behavioural variables.

2 | METHODS

2.1 | Participants

Ten TD teenagers (mean age = 13.49 ± 1.76 years; 7 girls) and 10 teenagers with DCD (mean age = 13.47 ± 1.39 years; 3 girls) aged 12 to 16 years participated in this study. They were all right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971; mean laterality quotient: 88.77 ± 20.33 ; range: 20–100). None of the participants was a musician, and none played videogames intensively. Participants had corrected-to-normal vision and hearing, as verified by pre-experimental questionnaire. Teenagers with DCD were recruited from the paediatric neurology service, and TD teenagers were enrolled from the entourage or peers of DCD teenagers.

Criteria for inclusion the DCD group were: (1) no attention deficit/hyperactivity disorder according to the DSM-5 (American Psychiatric Association, 2013); (2) diagnosis of DCD by paediatrician, and (3) total impairment Movement Assessment Battery for Children score (M-ABC; Soppelsa & Albaret, 2004) less than the 5th percentile. The TD teenagers and their parents reported no perceptual-motor disorder and no psychomotor therapy, and their M-ABC score had to be above the 15th percentile. None of the teenagers had attentional difficulties: the Continuous Performance Test II (CPT-II) (Conners, Epstein, Angold, & Klaric, 2003) revealed that the mean and standard error (SE) of reaction time for all teenagers was in accordance with normative data (Conners et al., 2003). None of the children presented intellectual disability, assessed by two subtests of the Wechsler Intelligence Scale for Children, 4th version (Similarities and Picture Concepts; Wechsler, 2005). The study was in agreement with university guidelines and ethical standards laid down in the Declaration of Helsinki. Informed oral and written consent was obtained from all the teenagers and their parents before the study began.

Participant characteristics are detailed in Table 1.

2.2 | Materials

In the experiment, a computer delivered visual instructions and visual stimuli with Presentation software, version 0.81 (Neurobehavioural Systems, Inc., Albany, CA). This computer was connected to a Xbox360 joystick, with each key pressing recorded by Presentation. Visual stimuli were composed of two identical blue circles (3.2 cm diameter) presented for 40 ms at 5 cm left and right from the centre of a 17" black screen located 80 cm in front of the participants. A second computer recorded EEG signals (Active II, Biosemi Inc., Amsterdam, The Netherlands) at 1024 Hz from 64 active electrodes placed on

the scalp in accordance with the International 10–20 System (Jasper, 1958). Impedance at all electrodes was kept below 5 k Ω .

2.3 | Tasks

Participants were asked to produce three bimanual coordination patterns – 'inphase', 'antiphase' and 'new' bimanual coordination – with thumb-tapping in synchrony with visual stimulus presentation. They had to synchronize tapping of their right thumb on a 'back' key with the appearance of the right circle and synchronized tapping of their left thumb on a 'start' key with the appearance of the left circle. 'Inphase' coordination (INPHASE) corresponded to simultaneous tapping of both thumbs in synchrony with stimulus presentation; 'antiphase' (ANTI) and 'new' (NEW) coordination corresponded to alternate tapping of the right and left thumbs in synchrony with stimulus presentation. The interval between two identical stimuli was 700 ms for the three coordination patterns. The inter-tapping interval between right thumb-tapping and left thumb-tapping was 0 ms for INPHASE, 350 ms for ANTI and 175 ms for NEW coordination.

2.4 | Procedure

Participants were invited to sit in a chair in a dark, quiet room with their head 80 cm from the screen. The armrests were adjusted so that the forearms were comfortably positioned. Participants were required to maintain the same position during the entire experiment for standardization and to avoid EEG artifacts.

The experimental task comprised four tasks:

- First, participants performed the Control task. They were required to hold a glass box in their hands which had a form similar to a joystick, but without buttons which might evoke tapping. A visual stimulus 'Ready?' appeared on the screen until the participants said 'yes'. The experimenter then started the trials, and one of the three conditions was presented (INPHASE, ANTI or NEW). Participants were asked to focus their attention on visual stimulus presentation without moving. An indication 'End of the trial' appeared on screen at the end of the trial. Participants said 'yes' when they were ready and the experimenter started the next trial. Each trial of the Control task lasted 15 s, and each condition consisted of a block of five trials, for a total of 210 stimuli (42 stimuli per trial \times 5 trials). Each condition was counterbalanced between participants to avoid fatigue and order effects.
- Second, participants performed the Pre-test task. They were required to hold the joystick in their hands in the reverse standardized position, to place their thumbs on the 'start' and 'back' buttons and to tap in synchrony with the stimuli. They produced each of the three conditions. A visual stimulus 'Ready?' appeared on the screen until the participant pressed the 'back' key of the joystick. Each experimental trial lasted 15 s, and each condition corresponded to one block of six trials, the first for familiarization. Hence, the five experimental trials corresponded to a total of 210 stimuli and 210 corresponding taps (105 right and 105 left taps) for each condition.

TABLE 1 Participant characteristics of level of motor skills, hand preference, attention and IQ scores of DCD and TD groups

	DCD (<i>n</i> = 10; 3 girls)		TD (<i>n</i> = 10; 7 girls)	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Age (years)	13.47	1.39	13.49	1.76
M-ABC scores	23.45	5.18	2.75	2.17
Edinburgh Handedness Inventory	81.55	26.19	96	8.43
Reaction time (mean, ms); CPT-II	359.67	76.24	370.97	67.66
Similarities; WISC-IV	13.7	3.43	15.4	3.20
Picture Concepts; WISC-IV	8.3	1.76	12	2.62

Note: DCD, developmental coordination disorder; TD, typically developing; *M*, mean; *SD*, standard deviation; CPT-II, Continuous Performance Test II; WISC-IV, Wechsler Intelligence Scale for Children; M-ABC, Movement Assessment Battery for Children.

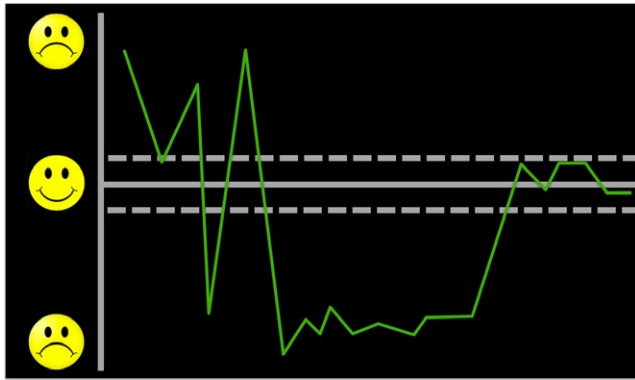


FIGURE 1 Representation of feedback displayed after one trial. Visual feedback consisted of a curve representing 21 relative phase (RP) between both hands during one trial for one participant. The two dotted lines represent the required RP ($90^\circ \pm 15^\circ$ ($75^\circ < RP < 105^\circ$)). The happy smiley in the middle of the figure indicates that the RP produced is near the required RP. The unhappy smiley at the bottom of the figure represents RP near inphase coordination (0°) and the unhappy smiley at the top of the figure represents RP near antiphase coordination (180°)

No feedback was given. Each Pre-test condition was counterbalanced between participants to avoid fatigue and order effects.

- Third, the Practice task was performed. Participants had 25 trials to learn NEW coordination synchronizing with the visual stimuli. Between each trial, visual feedback was presented on the screen in the form of smiley face to inform participants about its accuracy and stability (Figure 1).
- Finally, the Post-test was identical to the Pre-test except that there was no familiarization trial. Participants performed the three conditions with five trials per condition. Each Post-test condition was counterbalanced between participants to avoid fatigue and order effects.

2.5 | Data analysis

2.5.1 | Behavioural data

Behavioural data served to compute:

- The relative phase (RP) for each participant and each condition. RP is the temporal delay between right-left inter-tapping divided by the period of corresponding right taps multiplied by 360 (Kelso, 1984). RP is expressed in degrees and theoretically gives 0° for INPHASE, 180° for ANTI and 90° for NEW coordination.
- Absolute error of RP (RP AE), that is, the absolute difference between required and produced RP, and standard deviation of RP (RP SD) were then computed. RP AE provides information about the accuracy of the produced coordination, and RP SD reflects its stability.
- The number of mirror and parallel movements during the production of required NEW coordination in Pre- and Post-test to assess the tendency to produce movements near pre-existing

coordination, that is, mirror movements (near INPHASE, 0° of RP) and parallel movements (near ANTI, 180° of RP). Mirror movements corresponded to RP between -40° and 40° (around 0°) whereas parallel movements corresponded to RP between 140° and 220° (around 180°).

2.5.2 | EEG data

In the Control task, Pre-test and Post-test, raw EEG data were 3–100 Hz bandpass-filtered with a 4th-order, zero-lag Butterworth filter and then average-referenced. The continuous dataset was segmented into epochs, from -150 to 550 ms, around right visual stimuli to analyse whole epochs containing right and left taps. Hence, each epoch contained the two stimuli with one right and one left tap. Independent component analysis of the EEG data was conducted to detect blink artifacts (Delorme, Sejnowski, & Makeig, 2007) with EEGLAB (Delorme & Makeig, 2004) and to reject epochs contaminated by these artifacts. From a total of 105 epochs in the five trials, 4.11 ± 2.07 epochs were rejected per participant and condition.

After EEG pre-processing, cortico-cortical coherence was calculated in the time-frequency domain for FC3-FC4 (fronto-central cortex), FC3-C3 and FC4-C4 (left and right fronto-central regions, respectively) pairs of electrodes using the *WavCrossSpec* package for wavelet-based time-frequency analysis of the statistical dependence between non-stationary electrophysiological signals (Bigot, Longcamp, Dal Maso, & Amarantini, 2011; http://www.math.u-bordeaux1.fr/~jbigot/Site/Software_files/WavCrossSpec.zip). The above EEG electrodes were chosen in agreement with previous EEG studies showing that the premotor cortex is particularly important for bimanual performance (Sadato, Yonekura, Waki, Yamada, & Ishii, 1997) and plays a dominant role in visuomotor integration processes (Kandel, Schwartz, & Jessell, 2000) and motor learning (Gerloff & Andres, 2002; Hardwick, Rottschy, Miall, & Eickhoff, 2013). In *WavCrossSpec*, the parameters 'nvoice', which determines scale resolution of the wavelet, 'J1', which is the number of scales, and the Morlet mother wavelet parameter 'wavenumber' were set at 7, 50 and 10, respectively, to yield accurate identification of oscillatory activity in the $[0.32 \cdot 10^{-2}; 0.23: 79.97]$ Hz frequency range. As illustrated in Figure 2, magnitude-squared coherence between each pair of electrodes *EEG1* and *EEG2* was computed with:

$$R_{EEG1/EEG2}^2(w, u) = |S_{EEG1/EEG2}(w, u)|^2 / (S_{EEG1}(w, u)S_{EEG2}(w, u)) \quad (1)$$

where $S_{EEG1/EEG2}(w, u)$ is the wavelet cross-spectrum between the two EEG time-series and $S_x(w, u)$ is the wavelet auto-spectrum of signal x ($x = \{EEG1, EEG2\}$) at frequency w and time u (please refer to Bigot et al. (2011) for detailed equations). The magnitude of beta EEG-EEG coherence was defined for each pair of electrodes as the mean of magnitude-squared coherence values in the 13–30 Hz frequency band (Gerloff et al., 1998; Serrien, 2008; Serrien & Brown, 2003), with values set to zero where non-significant correlation between EEG time-series was detected on the wavelet cross-spectrum (Bigot et al., 2011). Finally, Task-Related Coherence (TRCoh) was computed as the

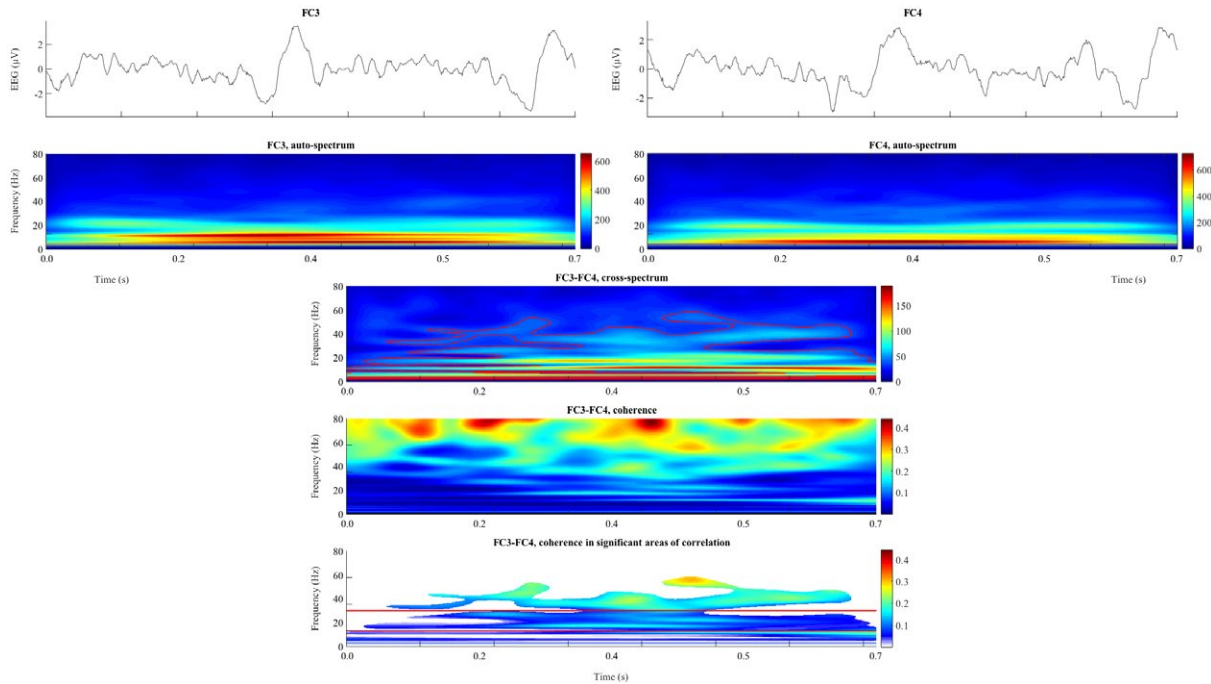


FIGURE 2 Illustration of different steps of time-frequency analysis of cortico-cortical coherence in a representative TD participant executing ANTI coordination in the Post-test condition. First row: mean EEG signals from FC3 (left) and FC4 (right) electrodes. Second row: wavelet auto-spectra of EEG time-series from FC3 (left) and FC4 (right) electrodes. Third row: wavelet cross-spectrum between two EEG time-series; red contours identify areas in the time-frequency plane where correlation between EEG signals is significant. Fourth row: wavelet magnitude-squared coherence between two EEG time-series. Fifth row: wavelet magnitude-squared coherence between two EEG time-series where the correlation between EEG signals is significant; red horizontal lines delimit the 13–30 Hz (beta) frequency band. Beta EEG-EEG coherence was quantified as the mean of magnitude-squared coherence values in the 13–30 Hz frequency band, with values set to zero where a non-significant correlation between EEG time-series was detected on the wavelet cross-spectrum

coherence specifically associated with bimanual tapping in each condition by subtracting the magnitude of beta EEG-EEG coherence of the Control task from that of Pre- or Post-test.

during NEW coordination in Pre-test and Post-test. Finally, according to the data distribution, Pearson or Spearman correlation tests were performed between EEG and behavioural variables. p -value was fixed at $p < .05$ for each analysis.

2.6 | Statistics

Statistical Group (2) \times Test (2) \times Coordination (3) analyses of variance (ANOVA) were carried out with repeated measures on Test (Pre-test; Post-test) and Coordination (INPHASE; ANTI; NEW) on each behavioural dependent variable: RP AE, RP SD and the EEG-dependent variable – TRCoh in the 13–30 Hz frequency band over the fronto-central cortex (FC3-FC4, FC3-C3 and FC4-C4 pairs). Group (2) \times Test (2) analysis was performed on the number of parallel movements performed during NEW coordination. Homogeneity of variance was verified for each ANOVA, and F , df and p -values underwent Greenhouse-Geisser correction, if necessary. η^2 was reported for significant effects on ANOVA. Separate post hoc t -tests were computed for independent groups with a sequentially acceptive step-up Bonferroni procedure (Hochberg, 1988; Keselman, 1994). Moreover, according to the data distribution, comparisons with unilateral Student's t -tests or Wilcoxon Mann Whitney non-parametric tests were carried out on the number of mirror movements performed

3 | RESULTS

Only significant results are reported.

3.1 | Behavioural results

3.1.1 | Standard deviation of relative phase (RP SD)

ANOVA revealed a main Group effect on RP SD ($F(1, 18) = 5.26$, $p = .03$; $\eta^2 = 0.12$). As illustrated in Figure 3a, RP SD was higher in the DCD group ($26.53^\circ \pm 19.58^\circ$) than in the TD group ($15.84^\circ \pm 8.47^\circ$), irrespective of Coordination and Test.

A main effect of Coordination ($F(1.53, 27.54) = 52.30$, $p = .00$; $\eta^2 = 0.32$) was also found on RP SD. Irrespective of Group and Test, RP SD was lower for INPHASE coordination ($9.10^\circ \pm 6.50^\circ$) than for ANTI and NEW coordination ($27.14^\circ \pm 13.99^\circ$ and $27.31^\circ \pm 15.86^\circ$, respectively).

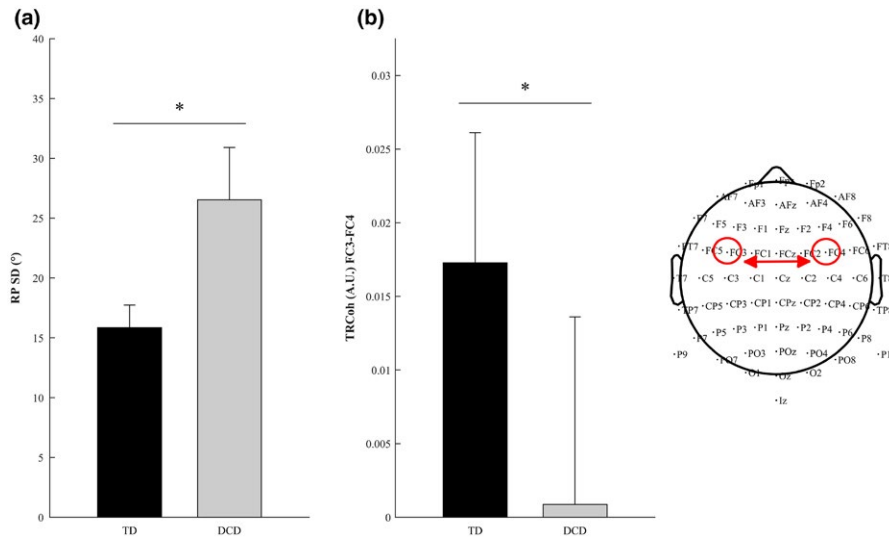


FIGURE 3 (a) Mean RP SD (in °) in TD and DCD groups. (b) TRCoh in the 13–30 Hz (beta) frequency band over fronto-central (FC3–FC4) regions in TD and DCD participants. * indicates significant difference; vertical bars represent inter-individual variability (SE)

3.1.2 | Absolute error of relative phase (RP AE)

ANOVA disclosed a main effect of Coordination on RP AE ($F(2, 36) = 7.71$, $p = .01 \cdot 10^{-1}$; $\eta^2 = 0.15$). Irrespective of Group and Test, RP AE was lower for INPHASE ($10.22^\circ \pm 5.63^\circ$) compared to ANTI and NEW coordination ($21.01^\circ \pm 15.63^\circ$ and $22.15^\circ \pm 13.75^\circ$, respectively).

Significant Test \times Coordination interaction was observed on RP AE ($F(1.45, 26.19) = 12.70$, $p = .00$; $\eta^2 = 0.21$). As shown in Figure 4a, irrespective of Group, for ANTI coordination, RP AE increased between Pre- and Post-test (from $10.39^\circ \pm 9.68^\circ$ to $31.50^\circ \pm 25.61^\circ$; $t(19) = 4.47$; $p = .00$), whereas RP AE decreased for NEW coordination (from $25.81^\circ \pm 21.68^\circ$ to $17.45^\circ \pm 10.65^\circ$; $t(19) = 2.21$, $p = .03$).

3.1.3 | Number of mirror and parallel movements during the production of NEW coordination

Independent analyses indicated that DCD teenagers made more mirror movements than the TD group in Pre-Test ($U(9) = 22$, $Z = -2.22$,

$p = .013$) and Post-Test ($t(9) = 2.76$, $p = .03$) (Figure 5). Moreover independent analyses per group revealed that DCD teenagers produced a greater number of mirror movements after practice ($t(9) = 2.42$, $p = .03$), while the TD group made a similar number of mirror movements in Pre- as in Post-test (ns ; Figure 5).

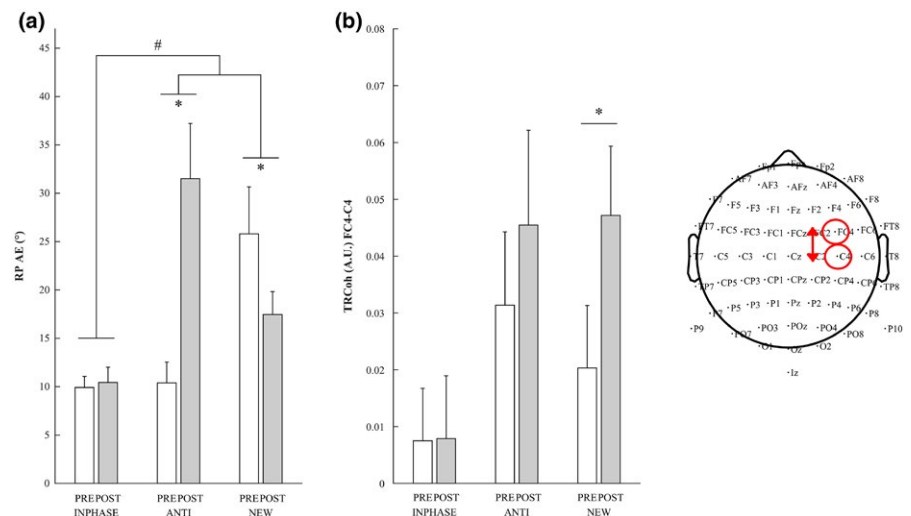
ANOVA revealed a significant Test effect on the number of parallel movements ($F(1, 18) = 19.85$, $p = .03 \cdot 10^{-2}$; $\eta^2 = 0.52$), which decreased with the practice of NEW coordination in both groups (from 15.6 ± 6.29 in Pre- to 5.8 ± 3.84 in Post-test).

3.2 | EEG coherence results

3.2.1 | Inter-hemispheric FC3–FC4 TRCoh

ANOVA disclosed a main Group effect on FC3–FC4 TRCoh ($F(1, 18) = 5.32$, $p = .03$; $\eta^2 = 0.22$). As seen in Figure 3b, TRCoh was lower in DCD ($8.70 \cdot 10^{-4} \pm 0.04$) than in TD teenagers (0.01 ± 0.02), irrespective of Test and Coordination.

FIGURE 4 (a) Mean RP AE (in °). (b) TRCoh in the 13–30 Hz (beta) frequency band over fronto-central (FC4–C4) regions for three coordination patterns (INPHASE, ANTI and NEW) for Pre- and Post-tests, irrespective of Group. # indicates a significant Coordination effect; * indicates a significant difference between Pre- and Post-tests; vertical bars represent inter-individual variability (SE)



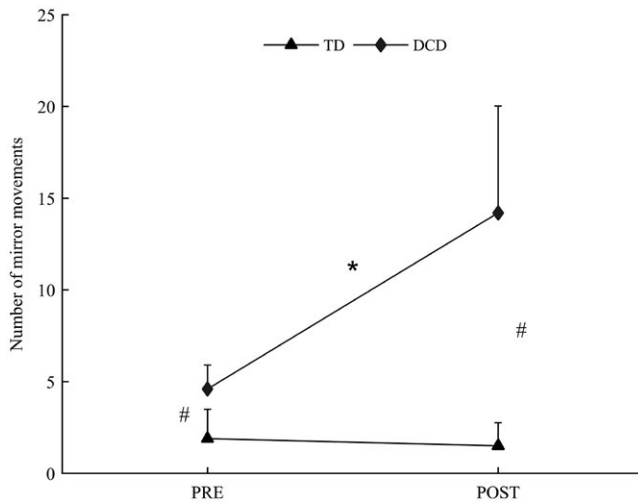


FIGURE 5 Mean number of mirror movements by TD (triangles) and DCD (diamonds) participants during NEW coordination. * indicates significantly increased number of mirror movements by the DCD group between Pre- and Post-tests; # indicates significant difference between TD and DCD. Vertical bars represent inter-individual variability (SE)

3.2.2 | Intra-hemispheric FC4-C4 and FC3-C3 TRCoh

ANOVA revealed Test \times Coordination interaction on right FC4-C4 TRCoh ($F(2, 36) = 3.36, p = .04; \eta^2 = 0.15$). As illustrated in Figure 4b, t-tests revealed that TRCoh increased significantly ($t(19) = 3.01, p = .00$) between Pre- (0.02 ± 0.04) and Post-test (0.04 ± 0.07), irrespective of Group.

No effect or interaction on TRCoh was found over the left fronto-central regions (FC3-C3).

3.3 | Correlations between neural and behavioural variables

First, significant Pearson correlation was found between mean RP SD and mean FC3-FC4 TRCoh of the three coordination patterns produced during Pre- and Post-tests ($r = 0.51; p = .02$): the higher the RP SD, the lower was FC3-FC4 TRCoh.

Second, significant Spearman correlation was noted between the number of mirror movements and FC3-FC4 TRCoh during NEW coordination in Post-test ($r = -0.45; p = .04$). As depicted in Figure 6, the more mirror movements were produced, the lower was FC3-FC4 TRCoh.

4 | DISCUSSION

The aim of the present study was to investigate the behavioural and neural changes associated with the practice of a new bimanual coordination pattern in DCD compared to TD teenagers. As expected, the results show that ANTI and NEW coordination are less stable and less accurate than INPHASE coordination. In addition, the data on NEW

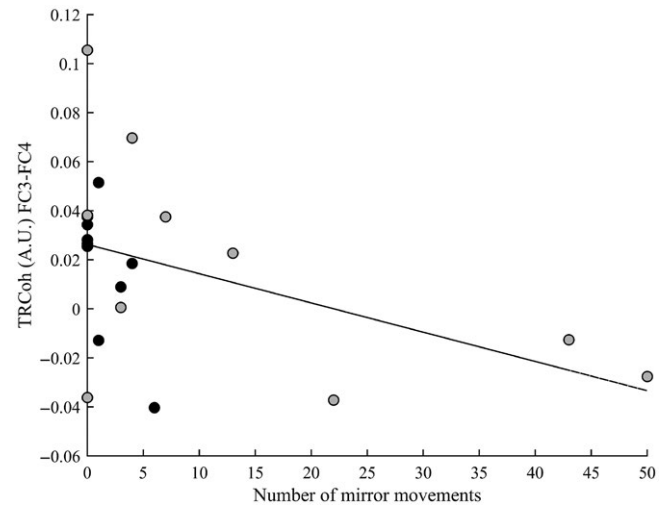


FIGURE 6 Correlation between the number of mirror movements and TRCoh in the 13–30 Hz (beta) frequency band over fronto-central (FC3-FC4) regions in TD (black dots) and DCD (light grey dots) groups during NEW coordination Post-test. The black line represents the best fit linear regression ($r = -0.45$)

coordination suggest that (1) accuracy and right fronto-central intra-hemispheric coherence increased with practice in both groups, but (2) the DCD group presented lower stability, greater number of mirror movements and lower fronto-central inter-hemispheric coherence than the TD group, even after practice of new coordination. Neural and behavioural results are discussed in terms of (1) preserved plasticity of intra-hemispheric communication concomitant with improved accuracy of a new bimanual coordination with practice in both groups and (2) reduced inter-hemispheric communication associated with no stabilization of the new bimanual coordination and no inhibition of mirror movements despite practice in DCD compared to TD teenagers.

4.1 | Accuracy improves and intra-hemispheric coherence increases with practice in both TD and DCD groups

The first findings of this study are specific improvement of accuracy of new coordination after practice by all teenagers and increased neural communication between the right fronto-central regions. The behavioural data are in agreement with previous studies showing increased accuracy of practised coordination in healthy adults (Walter & Swinnen, 1994; Zanone & Kelso, 1992). The RP of new coordination (90°) decreased from 108° to the required value of 90° (which corresponds to an increase in accuracy of the new coordination) whereas the RP of antiphase coordination (180°) regressed from 177° to 149° (which corresponds to a decrease in accuracy of the pre-existing coordination). These results suggest that pre-existing antiphase coordination interfered with new coordination before practice (pre-test) and, conversely, new coordination interfered with antiphase coordination after practice (post-test). Together with the decrease in parallel movements during new coordination after practice, these results are consistent with the idea that learning of a new bimanual coordination



alters pre-existing coordination (Rémy, Wenderoth, Lipkens, & Swinnen, 2008; Swinnen, Walter, Lee, & Serrien, 1993). From the dynamic system theory's perspective, our results confirm that learning a new coordination pattern implies competition with the pre-existing (inphase and antiphase) attractors, leading to the creation of a new attractor between the two pre-existing attractors, at the expense of the antiphase coordination accuracy.

The EEG findings of the present study are also in agreement with previous investigations that reported increased cortico-cortical coherence during the initial phase of practice (Andres et al., 1999; Serrien & Brown, 2003). Andres et al. (1999) supported the idea of different stages in bimanual motor learning: the early stage is associated with fast behavioural improvements and increased neural intra- and inter-hemispheric communication; the later learning stage is linked with slower behavioural improvements and decreased neural communication. Likewise, functional magnetic resonance imaging (fMRI) studies have reported that the early motor skill learning stage is characterized by increased functional connectivity between the frontal and central regions, particularly between the dorso-lateral prefrontal cortex and the premotor cortex (Sun, Miller, Rao, & D'Esposito, 2007). In the present study, participants were required to perform 25 practice trials for a duration of 15 min. It is thus quite possible that the findings reflect the early stage of learning, leading to improved accuracy associated with increased fronto-central communication.

Surprisingly, increased cortico-cortical coherence was only found over the right hemisphere. Such lateralized neural change was not expected in regard to well-known left hemisphere dominance in skilled movement by right-handed humans, especially for bimanual coordination (Serrien, Cassidy, & Brown, 2003; Serrien, Ivry, & Swinnen, 2006). However, the result is less surprising considering that associative areas of the right hemisphere are specifically involved in the selection of spatial responses (Serrien et al., 2006). Given that our task required participants to press the right or left button in synchrony with right or left stimulus, visuo-spatial processes were needed to increase accuracy of the new bimanual coordination. Moreover, it is suggested in the literature that the right hemisphere is particularly recruited for closed-loop motor control, that is, for movements that depend on feedback processing (Haaland & Harrington, 1989). Finally, the right hemisphere is particularly involved in motor learning and related processes, such as attention and inhibition. Using fMRI measures, Debaere, Wenderoth, Sunaert, Van Hecke and Swinnen (2004) found higher involvement of the right hemisphere during initial bimanual motor learning and a more prominent role of the left hemisphere during late learning. Taken together, the present results suggest that teenagers with DCD present a preserved plasticity in intra-hemispheric communication concomitant with practice-related increase in accuracy.

4.2 | The DCD group made more mirror movements correlated with less inter-hemispheric communication than the TD group despite practice

Another interesting finding was that DCD group produced less stable coordination than TD teenagers despite practice. Lesser stability

during bimanual coordination in DCD compared to age-related peers is well documented (Volman & Geuze, 1998; Volman et al., 2006). The present results underscore that, unlike accuracy, stability did not improve with practice in the DCD group. Considering that stability did not improve in the control group because it was already very high at the very beginning of practice, the absence of improvement of stability in the DCD group could reflect a kind of deficit/deviance or immaturity in learning capacity.

Another interesting finding was that DCD teenagers made a greater number of mirror movements during the execution of new coordination, even more so after practice. This result is in line with previous behavioural results showing a deficit of motor inhibition in DCD children who exhibit more non-voluntary mirror movements than TD children (Licari & Larkin, 2008; Licari et al., 2006; Tallet et al., 2013). In addition to the absence of stabilization of new coordination, the deficit in inhibition of mirror movements could be a sign of learning difficulties in DCD. From a dynamic point of view, the increased number of mirror movements and not parallel movements in DCD compared to TD may be explained by the fact that inphase is a stronger competing attractor than antiphase, especially in DCD. Moreover the increase of mirror movements after practice for DCD may reflect the difficulties of learning a new coordination pattern probably due to the attraction of the pre-existing inphase coordination.

Regarding inter-hemispheric transfer, DCD teenagers presented less cortico-cortical coherence in the fronto-central hemisphere than TD teenagers. This result suggests that the transfer of inhibitory information between the fronto-central brain areas of both hemispheres is reduced in DCD teenagers compared to their controls, indicating atypical inter-hemispheric transfer in DCD. It is in accordance with previous behavioural studies, pointing to a deficit in inter-hemispheric transfer in DCD (Sigmundsson et al., 1999; Tallet et al., 2013) and with MRI investigations showing alteration of the corpus callosum in DCD (Langevin, MacMaster, Crawford, Lebel, & Dewey, 2014) or a reduction in functional resting-state connectivity of primary motor cortices (McLeod, Langevin, Goodyear, & Dewey, 2014).

Correlation analyses revealed that the level of inter-hemispheric communication was associated with both the level of stability of the produced coordination and the number of mirror movements produced during new coordination. It is not surprising that inter-hemispheric communication is correlated with both variables, given that the production of mirror movements destabilize new coordination ($r = 0.74$, $p = .01 \cdot 10^{-4}$, not illustrated). It is postulated that less inter-hemispheric coherence is primarily and specifically related to more mirror movements because: (1) no correlation was found between inter-hemispheric coherence and parallel movements, and (2) previous studies showed that inter-hemispheric coherence is not associated with the production of a unimanual synchronization task (de Castelneau, Albaret, Chaix, & Zanone, 2008). For the first time, the present results provide evidence that DCD teenagers incur less inhibition of mirror movements, leading to learning difficulties, probably due to a kind of 'inter-hemispheric disconnection' despite practice.

5 | CONCLUSION

The present results suggest that practice of a new motor coordination leads to improvement of accuracy and intra-hemispheric (right) fronto-central reorganizations in both TD and DCD groups. However, practice does not solve the learning difficulties of DCD teenagers highlighted by a persistent low behavioural stability and difficulties in inhibiting mirror movements, correlated with reduced inter-hemispheric communication. These findings provide innovative neuroimaging evidence of atypical inter-hemispheric transfer of inhibitory information as a marker of altered inhibition during motor learning in DCD. Even if the results need to be generalized to a larger number of participants, especially with larger age-bands, they deliver new, promising insights into neural correlates of motor learning difficulties in DCD. More neuroimaging studies in children with DCD are warranted for better understanding of the neural correlates of DCD, especially by investigating corpus callosum structure that could be implicated in atypical inter-hemispheric communication.

COMPETING INTERESTS

The authors have no conflict of interest to disclose. They confirm that they have read the Journal's position on issues involved in ethical publication and affirm that this report is consistent with those guidelines.

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