

# Neural Correlates of Developmental Coordination Disorder: The Mirror Neuron System Hypothesis

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## ABSTRACT

Primary impairments of developmental coordination disorder (DCD) include impairments in motor skill, motor learning, and imitation. Such difficulties present challenges for individuals with DCD and may persist into adulthood, negatively impacting daily life in school, work, and social domains. A better understanding of the neural correlates of motor and imitation impairments in DCD holds the potential for informing development of treatment approaches to address these impairments. Although the disorder is assumed to be of neurological origin, little is known of the brain-based etiology of DCD. In recent years the discovery of a fronto-parietal circuit—known as the mirror neuron system—has enabled researchers to better understand imitation, general motor functions, and aspects of social cognition. Given its involvement in imitation and other motor functions, we propose that dysfunction in the mirror neuron system may underlie the characteristic impairments of DCD. We review literature pertaining to the mirror neuron system and develop a theory of disordered mirror neuron functioning in DCD. Finally, we review the limited neuroimaging literature available on neural correlates of DCD and show that the findings from those investigations are congruent with a mirror neuron system theory of DCD. Future research in this population should be designed to investigate specifically mirror neuron regions in individuals with DCD during skilled motor tasks and imitation in particular.

**Keywords:** Developmental Coordination Disorder; Dyspraxia; Imitation; Mirror Neuron System; Motor Learning

## 1. Introduction

Developmental coordination disorder is a neurologically based disorder broadly characterized by impaired motor coordination and impaired performance of daily activities requiring motor skill [1]. A similar and perhaps overlapping syndrome, developmental dyspraxia, has been described as impairment of motor planning and execution [2,3] and is frequently tested with tasks requiring imitation [4,5]. Individuals with DCD or developmental dyspraxia may have difficulty learning and imitating skilled or sequenced movements, including object manipulation and tool use, assuming body postures, gesturing, and carrying out multi-step or goal-directed actions [4,6-11]. Functionally, individuals with DCD or developmental dyspraxia have trouble coordinating their movements to learn new fine and gross motor tasks required to perform instrumental daily activities, such as tying shoelaces, dressing, handwriting, playing sports, and using playground equipment [1,3,12,13]. In addition, decreased educational performance and poor social emotional adjustment, perhaps a result of participation limitations, have been found in children, adolescents, and adults with de-

velopmental coordination disorders [14-17].

Historically, a number of labels have been used in describing specific developmental disorders of motor function, such as *clumsiness* [18,19], *physical awkwardness* [20], *minimal cerebral dysfunction* [21], and *congenital maladroitness* (cited by [1] and [9]), with related descriptions like *motor learning impairment* [22], *motor delay* [22], *motor control impairment* [22], *sensory integrative dysfunction* [22] and *hand-eye coordination impairment* [22] sometimes found in the literature. In addition, dyspraxia is sometimes incorrectly used interchangeably with apraxia, a condition in which normal function is disrupted in adults or in previously typically developing children due to an upper motor neuron lesion (e.g., after a stroke; [9,21,23]). Although terminology varies, developmental dyspraxia is a term commonly used by occupational therapists and neurologists in the United States (observation by the authors), whereas DCD is a term widely used by various allied health and medical professionals, movement scientists, and related researchers internationally [24]. DCD is recognized as a diagnosable disorder by the American Psychiatric Association (APA) [25] when specific criteria are met: 1) motor coordination substantially below what is expected for chrono-

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logical age and intelligence; 2) motor difficulties interfere with activities of daily living or academic performance; 3) motor difficulties are not due to a general medical condition, such as cerebral palsy; and 4) motor difficulties are in excess of any mental retardation, if present. Although we will focus on DCD as suggested by an international terminology consensus [24], it is worthwhile also to include in our review the dyspraxia literature with the assumption that the two are likely overlapping with similar features and functional outcomes.

Although DCD is most apparent in childhood when many new skills are acquired and motor milestones are tracked, an increasing body of evidence reveals that many with the disorder continue to have difficulties with coordination and have reduced participation in motor tasks during adolescence and adulthood [15-17,26-29]. In a longitudinal study of children with DCD beginning when the children were 5 years old, Cantell, Smyth, and Ahonen [26] found that a subset of participants with relatively more severe motor impairments compared to other participants continued to have motor difficulties at age 17. Cousins and Smyth [16] documented poor performance on a variety of standardized motor tasks in 19 adults who qualified for a diagnosis of DCD as adults or were previously diagnosed as having DCD as children. Anecdotal descriptions by adolescents, young adults, and parents of young adults with probable DCD corroborate this data with reported sustained motor difficulties and lower performance in other life domains related to their motor impairments [27,29]. There is increasingly more research being conducted with adolescents and adults with DCD; however, only children have participated in the few available neuroimaging studies on the disorder. Conversely, the majority of neuroscience investigations using brain imaging methods in typically developing individuals have been performed with adult or young adult participants. There is somewhat limited data available for comparing the results of any neuroimaging study in children with DCD to typically developing children as well as limited evidence to explicate the neural correlates of DCD in adults and children.

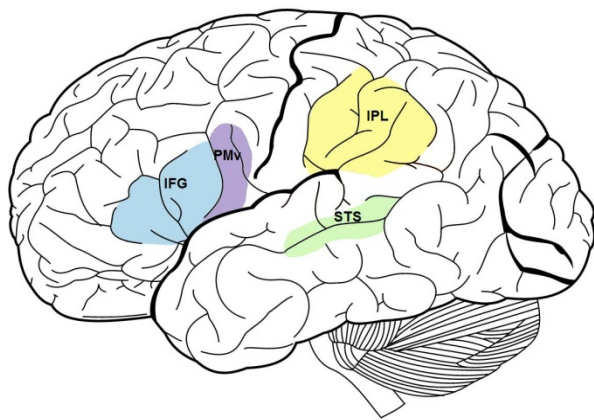
Despite a number of recognizable impairments identified in this population [30,31], DCD is a disorder of largely unknown etiology. Furthermore, the neural correlates of DCD have not been investigated with advanced imaging methods to the extent that they have in adult apraxia [32-35] and other developmental disorders with motor impairments, such as cerebral palsy [36] and autism spectrum disorder [37]. Because impairments in imitation are common in individuals with DCD/dyspraxia [4,10,38,39], we propose that a dysfunction in a fronto-parietal system may underlie the disorder. Known as the mirror neuron system (MNS), this fronto-parietal circuit is thought to be highly involved in imitation in humans [40,41].

The putative human MNS, located in the inferior frontal gyrus (IFG), ventral premotor cortex (PMv), and inferior parietal lobule (IPL), is active during both action execution and action observation [42]. It is thought to be highly involved in action imitation as well as emulation [41]. In fact, evidence from a repetitive transcranial magnetic stimulation (rTMS) study indicated that disruption of the IFG in typically developing adults (aged 19 - 34) during an imitation task significantly interfered with imitation ability [43]. Therefore, hypothetically, individuals with developmental motor impairments may be limited in their ability to imitate, learn new movements, imagine movements, and produce goal-directed and object-oriented actions because they do not accurately perceive or match such actions with neural motor representations the way individuals without coordination disorders can. Mechanisms recruited in addition to MNS areas may be important for understanding the coding of visual input, imitation learning, and action goal understanding, all of which may contribute to imitative ability. We will review functions of the putative human MNS as it is involved in imitation, and propose that its dysfunction may be related to motor impairments in DCD.

## 2. The Mirror Neuron System

Researchers have argued that the MNS is a key element of human imitation [40,41,44-46]. Mirror neurons, originally discovered in macaque monkeys using single-cell recording from surgically implanted microelectrodes, are a particular type of neuron that fire both when a monkey performs an action as well as when the monkey observes another individual performing a similar action [47-49]. In other words, the same neuron has both motor and sensory representations.

In monkeys, mirror neurons have been found in F5 and PF brain regions [48-50]. Based on gyri and sulci topography and evidence from cytoarchitecture, it is thought that the homologous region to F5 in humans is the pars opercularis of the inferior frontal gyrus [51,52]. Single-neuron recording studies are typically not conducted in humans for experimental purposes. Therefore, there is little direct evidence of the existence of mirror neurons at the cellular level [42,53] with the exception of Mukamel *et al.* [54], who reported mirror neurons in humans in the supplementary motor area, hippocampus, parahippocampal gyrus, and entorhinal cortex when recording at sites in the medial frontal and temporal cortices. Brain imaging and neurophysiological studies have provided indirect evidence for a putative MNS in human frontal and parietal brain regions. Specifically, these areas include the IFG and adjacent PMv and the IPL (see **Figure 1**). (For a review of the brain imaging data and how these brain regions were determined to be functionally equivalent to monkey areas F5 and PF, see [42]).



**Figure 1. Lateral view of brain with frontal (IFG & PMv) and parietal (IPL) mirror neuron system regions highlighted. The superior temporal sulcus is also labeled. [IFG = inferior frontal gyrus; PMv = ventral premotor area; IPL = inferior parietal lobule; STS = superior temporal sulcus].**

### 2.1. Properties of Mirror Neurons in Monkeys

Properties of mirror neurons in the macaque brain are described here, as these data provide a framework for our understanding of the MNS. To elicit mirror neuron activity in the monkey, both observed and executed actions must be goal-directed (*i.e.*, hand-object interaction or aiming for a target) [47-49,55]. This means that monkey mirror neurons are not merely responsive for a body part or an object alone, but code the conceptual goal of the action. Second, the majority of mirror neurons in F5 are broadly visuo-motor congruent; they respond to visually similar or conceptually related observed and executed actions. About a third of mirror neurons are strictly congruent in that the observed and executed actions have to match exactly, such as in the type of grasp used to hold an object [47-49]. Third, partial action sequences activate mirror neurons in monkeys who have previously seen the full action sequence, presumably because the animal infers the missing end sequence or goal of the action [56]. This property speaks to the point that mirror neurons are involved in action understanding through an internal motor representation of a full action, even when complete visual information is not immediately present [56]. Finally, many neurons in the monkey frontal mirror area resonate action information from audio as well as visual representation of object-related actions [57,58]. Together these findings in monkeys indicate that mirror neurons may aid in the integrated understanding of action information at a sensorimotor level rather than relying on conceptual interpretation through a semantic transformation process.

Although a number of distinct properties indicate that mirror neurons in monkeys function as a means of understanding the complex actions of others, there is con-

flicting evidence on a monkey's ability to imitate [59-64]. Thus, imitation capability in humans supported by the MNS, as well as possible additional neural regions, probably represents an evolved mechanism from one that served more basic action understanding, such as that in monkeys. More evolved neural systems for learning may have facilitated imitation ability while the evolution of tool use may have helped select for imitation ability.

### 2.2. The Human Mirror Neuron System and Imitation

In recent years, a body of research primarily utilizing functional magnetic resonance imaging (fMRI) has provided evidence that the human MNS is active during action observation, execution, and imitation tasks [40,41,44,46,65-67]. In a seminal study, Iacoboni *et al.* [40] monitored brain function in human frontal and parietal mirror regions while participants in an fMRI scanner were shown finger tapping actions or control stimuli. Participants passively observed the actions, imitated them, or executed a finger movement to a given cue. The researchers predicted that the inferior frontal gyrus and inferior parietal lobule, components of the putative human MNS, would follow an increasing pattern of signal activity. That is, these regions would be active during action observation, more for action execution, and when observation and execution are combined, as in the case of imitation, the highest signal intensity would be observed. The data validated these hypotheses [40].

Research using similar imitation tasks or tasks including object interactions has supported the previous findings that the fronto-parietal mirror network is most active during imitation when compared to observation and execution [66-70]. Furthermore, a re-analysis of data from Iacoboni *et al.*'s [40] study and six others from the same laboratory revealed additional details regarding functional segregation within the IFG for action observation and imitation [71]. This re-analysis indicated that the dorsal pars opercularis within the IFG was specifically active during action observation and imitation, with the most activation during imitation [71]. In addition, disruption of the IFG in either hemisphere with rTMS resulted in a transient impairment of imitation compared to a control movement task, indicating that this region is essential for imitation processing [43].

Together this evidence strongly indicates that these regions have a prominent role in typical human imitation, rendering the fronto-parietal mirror network a likely location of differences in neural activation between individuals with and without DCD. In particular, one may expect decreased signal intensity to correspond with imitation impairments. Although the vast majority of the MNS and imitation literature includes only adult participants, a few investigations have included typically de-

veloping children (such as when comparing to children with ASD) and have reported MNS functioning similar to what has been described in typical adults [72-77]. Such evidence supports the view that a neural mirroring mechanism is present from childhood and that dysfunction in the MNS may contribute to developmental disorders of imitation, motor, and social skills [69].

### 2.3. Coding of Biologic Actions in the Superior Temporal Sulcus

Although not considered a mirror area because it is not active during action execution, the superior temporal sulcus (STS; see **Figure 1**) has been implicated in studies assessing the neural mechanisms of imitation [40,78-80]. The anterior portion of the STS is thought to code visual stimuli for meaningful and goal-directed biological actions [81,82]. In addition, the STS and the fronto-parietal mirror circuit are thought to be connected via the arcuate fasciculus and two tracts running parallel to it [41,45,83]. Thus, it has been proposed that information from the visual cortices undergoes further processing for the visual aspects of observed action by the STS and is then sent to the parietal cortex, which codes the affordances of the action and its kinesthetic qualities [42] via the posterior lateral tract parallel to the arcuate fasciculus terminating in the IPL [83]. Next, it is relayed to the IFG where action goal coding occurs [42] via another parallel tract to the arcuate fasciculus: the anterior lateral tract [83].

### 2.4. Laterality of the Mirror Neuron System

The visuo-motor mirror system is thought to be bilateral [84], and hemispheric differences have been found when comparing the experience of being imitated as opposed to imitating another person. In a study to investigate these differences using positron emission tomography (PET), Decety *et al.* [80] found the *left* inferior parietal cortex, thought to be involved with integrating visual and motor information for sequential processing of goal-directed actions [85,86], correlated with imitating others. The *right* inferior parietal cortex, thought to be involved in body awareness [87,88], correlated with being imitated. Furthermore, in an experiment in which researchers applied rTMS to the inferior parietal lobule, participants were less accurate on a self-other discrimination task when a virtual lesion was created on the right as compared to the left [89]. These results point to a lateralization of the parietal mirror neuron area in particular and general differences between processing self- and other-related visual information. In addition, some have suggested that the fronto-parietal mirror network, especially in the right hemisphere, and cortical midline structures, such as the medial prefrontal cortex, anterior cingulate cortex, and precuneus, work together to process self-

other distinctions [90-92] and that the experience of being imitated is an important aspect of learning to imitate [93].

If differences in inferior parietal regions exist between individuals with DCD and typically developing individuals during imitation or while being imitated, such differences could have implications for understanding the neural etiology of the disorder. Dysfunction in the left inferior parietal cortex may indicate that motor or imitation impairments are related to a specific deficit in visuo-motor integration [85,86], whereas dysfunction in the right inferior parietal cortex may indicate that impairments are due to body awareness and difficulty distinguishing self from others [89]. Hemispheric differences in the MNS, particularly in the posterior parietal cortex, bring to light only weakly supported theories about cerebral laterality in DCD. It has been suggested that left parietal lobe dysfunction may underlie DCD based on the known lesion location usually responsible for acquired apraxia [94,95]. Although it cannot be assumed that the mechanisms of acquired apraxia equate to those of developmental motor impairments (in which there is no notable brain lesion), Zwicker and colleagues [96] found differential activation in the *left* IPL in the direction of higher blood-oxygenation-level dependent (BOLD) signal in children with DCD compared with typically developing peers on a simple motor task. In a follow-up investigation [97], these same researchers found greater signal in the *right* IPL in typically developing children compared with peers with DCD during a motor learning task. More evidence is needed to elucidate the particularities of potential laterality differences to DCD, especially in the context of imitation and imitation learning.

## 3. Imitation Learning

An evident benefit of imitation is the potential for learning novel actions through the copying of actions from others, such as through demonstration of motor acts. Indeed, humans imitate more than any other animal, and much of how humans learn is through imitation [98]. To investigate the neural correlates of imitation learning, Buccino *et al.* [68] asked non-musician participants to observe guitar chords played by a guitarist and, after a pause, imitate each chord. The results revealed the IPL, posterior portion of the IFG, and adjacent premotor region were most active during imitation. During the pause, however, the middle frontal gyrus, thought to be involved in the spatial aspects of working memory, and other motor preparation areas became active in addition to the mirror neuron circuit. Based on these results, Buccino *et al.* concluded that the MNS plays a prominent role in learning by imitation, but other regions, such as the middle frontal gyrus, may be needed as well to orchestrate the selection and organization of motor repre-

sentations needed to learn and imitate a new motor program. Thus, regions beyond the MNS may also be implicated in DCD/dyspraxia.

In a study by Cross, Hamilton, and Grafton [99], expert dancers learned a complex, whole-body dance sequence over a period of five weeks, and researchers recorded their brain activity while watching the rehearsed and control sequences at the end of each week. Participants were asked to imagine themselves performing the movement sequences they observed and rate their perceived ability to perform each. Greater activation was found in the MNS, namely the left IPL and PMv, when participants observed rehearsed movement sequences they judged they could perform well, compared to control movement sequences for which they deemed their performance ability would be poor [99]. Although the participants in this study could not physically imitate the dance sequences while inside the fMRI scanner, the use of imagined movement is commonly used in brain imaging experiments to induce internal representation of motor plans without overt movement.

In a related study, Cross *et al.* [100] demonstrated that neural representations of movement sequences could be acquired by non-dancer participants either physically rehearsing or, to a lesser degree, passively observing actions. The experiment yielded activity in the premotor and inferior parietal regions for physical and observational training, with the dorsolateral prefrontal cortex additionally active for both types of rehearsal and the cerebellum involved during observation. These results, together with those of Buccino *et al.* [68] and Cross *et al.* [99], convey a consistent pattern of MNS activity when participants learned and imitated, or mentally simulated, new movements. However, additional brain regions related to a broad range of sensorimotor tasks appear to be necessary supplements to the core imitation circuit when learning new actions. Because DCD/dyspraxia entails impairment in learning new motor programs, these additional structures (*i.e.*, prefrontal cortex, middle frontal cortex, anterior medial cortex, supplementary motor area, and superior parietal lobule) are important points of consideration for future investigations of the neurologic basis of DCD.

#### 4. Imitation, Empathy, & the Mirror Neuron System

The shared neural representation for action and perception which is thought to underlie imitation and action understanding, the MNS, is also thought to be involved in empathy [41,101-103]. Convincing evidence for this hypothesis comes from experiments showing that self-reported trait empathy and perspective-taking ability (usually measured with a widely-used empathy scale, the Interpersonal Reactivity Index; [104]) correlates with

activity in the MNS [105-111]. In addition, in conditions in which empathy is known to be impaired, such as autism spectrum disorder (ASD), decreased activity in MNS regions has been found to correlate with social symptom severity [112]. Interestingly, individuals with ASD are also thought to have impairments in imitation [113-118].

Evidence points to higher rates of poorer psychosocial adjustment and decreased social skills and empathy in children and adults with DCD/dyspraxia compared to their peers without motor coordination problems [26,119-125]. There is no evidence in the literature to indicate the direction of this relationship. However, given the hypothesis that MNS dysfunction underlies imitation impairments, another question is how imitation ability, empathy, and activity in the MNS regions during imitation interact in individuals with DCD compared with their typically developed peers.

#### 5. Existing Evidence of Brain-Based Differences in DCD

To date, no published fMRI studies have been conducted which examined imitation and MNS functioning in children or adults with dyspraxia, DCD, clumsiness, or other similarly labeled developmental motor coordination disorder. However, a limited number of brain imaging studies have broadly investigated group-level differences in brain activation on motor tasks between individuals with DCD and typically developing (TD) individuals [96,97, 126,127] and are fairly encouraging that a mirror system hypothesis may be supported.

Kashiwagi *et al.* [126] examined direct perceptual-motor mechanisms of DCD via a study of brain activation during a visuomotor tracking task in which participants followed an on-screen moving target with a joystick. The authors report less posterior parietal activation in the DCD group; however, these results appear to be undermined by a skewed results distribution as a consequence of one extreme outlier in the DCD group.

Querne *et al.* [127] examined attention, a corollary of developmental coordination disorder, by examining the attentional brain network in children with DCD and a control group using a go/no-go task in which participants responded when consecutive letters were presented (go) with the exception of "X" (no go). Using structural equation modeling to determine effective connectivity, the authors concluded that middle frontal and anterior cingulate cortex to inferior parietal cortex connectivity was increased in children with DCD, indicating less effective switching between go and no-go tasks in children with DCD and the need for additional recruitment of inhibitory brain responses to compensate.

Of more potential use in understanding the neurological etiology of DCD are a series of brain imaging experiments conducted by Zwicker and colleagues [96,97].

Using fMRI to measure whole-brain activation patterns in 7 children with DCD (aged 8 - 12 years) and 7 age-matched TD peers, Zwicker *et al.* [96] predicted group-wise differences in cerebellar activity when participants performed a fine motor task adapted from the Movement Assessment Battery for Children [128] consisting of trail tracing using a joystick. Although these researchers did not find any significant difference between groups on task performance in the scanner, whole brain exploratory analysis revealed diffuse between-groups differences in a number of brain regions. Significant differences were observed in the left IPL and right supramarginal gyrus (DCD > TD) and left IFG and left precuneus (TD > DCD). In addition, a small cluster of activity was found in the right cerebellar lobule VI that was significantly greater in the DCD than TD group. The authors interpret these results in light of a theory that children with DCD may rely on visuospatial feedback in lieu of somatosensory feedback to guide their movements. Because the experimental task did not include imitation, action observation, or even the presence of another person, no conclusions can be drawn that these differences relate to a mirroring mechanism. However, the results are noteworthy because they include key MNS regions and may be indicative of different functioning in these regions.

In a follow-up study with the same participants as their previous investigation, Zwicker *et al.* [97] broadly hypothesized that the cerebellum, prefrontal cortex, and posterior parietal cortex would differ between DCD and TD groups on a retention test following practice of a fine motor task. Presumably their predictions were derived from a broad array of hypotheses implying large-scale motor and motor-related regional differences in DCD [95]. The same trail tracing task used in their previous study was employed and brain activity was measured at baseline and after three days of practice outside the scanner. In this study, group-wise differences from the initial learning task to retention were found in the bilateral IPL and other regions (DCD < TD). As in the previous study conducted by Zwicker and colleagues, the procedures of this investigation do not provide grounds for making any assumptions about a mirroring mechanism, but still support the potential for broad functional differences in the primary MNS regions when comparing individuals with DCD and TD.

## 6. Conclusion

From the limited neuroimaging experiments in DCD, it is apparent there is a need to conduct more functional imaging studies to further examine direct neural correlates of DCD. In particular, this should be done in regard to MNS areas and their relationship to imitation and motor learning. Furthermore, condition-dependent differential activation (e.g., with novel gestures and during different

time points of action) in regions of the human MNS should be compared between typically developing controls and participants with DCD to inform the contribution of each region to motor planning, motor learning, and imitation in DCD. Given the evidence that the human MNS is highly involved in empathy and social cognition and that individuals with DCD may have impairments in this area, it is also important to determine how traits like empathy may correlate with any differences in function of the mirror system regions in individuals with DCD. Examinations of these types using functional neuroimaging are crucial for increasing the current understanding of neuropathology in DCD.

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