A Perception-Action Approach

to Understanding Typical and Atypical

Motor Development

Jill Whitall

University of Maryland, Baltimore

University of Southampton, England

Jane E. Clark

University of Maryland, College Park

 In this chapter, we ask two questions. First, can the study of the perception-action system across time offer a useful model for understanding motor development? Second, can the study of the perception-action system in children with developmental coordination disorder (DCD) inform our understanding of atypical as well as typical motor development? We begin by describing the conceptual foundations of our work including the dynamical systems perspective and a control-theoretic approach that together frame our paradigms, methodology and interpretation of our experiments. Our experimental strategy has been to perturb one or more sensory systems and observe the effect on the motor system. The majority of the chapter explains how we employed two principal perturbation strategies: 1) removing or adding a static source of sensory information believed to be salient to the task at hand; and, 2) enhancing a dynamic source of sensory information either implicitly or explicitly. These strategies were employed in three different action systems: Posture; rhythmic interlimb coordination, and goal-directed reaching and drawing. After synthesizing our findings, we conclude by addressing the original questions and offering future directions. In brief, we consider that perception-action coupling is an underlying mechanism/foundation/constraint of motor development in the sense that the ongoing processing of sensations and the planning and execution of movements are how the brain produces goal-directed movements. Therefore, a better understanding of how this coupling changes or adapts over time has much to offer as to how motor behavior develops across the lifespan, both typically and atypically.

KEYWORDS: motor development, posture, perception-action, reaching, infants, children, developmental coordination disorder, coordination

In a 2011 Ted talk, the neuroscientist Daniel Wolpert asked the question, “why do humans have a brain?” (Wolpert, 2011). His answer: the brain evolved to produce complex, adaptive *movement*. Indeed, Wolpert argued, our movements are our behaviors. And the development of our behavior is, therefore, the development of our movements (i.e., motor development). We start with Wolpert’s assertion to underscore the argument we make here, namely, that as we look at the development of perception-action relationships, we are looking at the development of behavior. The principles we seek, then, are the principles that would inform our understanding of the development of movement behavior or motor development and, in a consummate sense, human development.

 In this chapter, two questions guide our efforts. First, can the study of the perception-action system across time offer a useful model for understanding motor development? Second, can the study of the perception-action system in children with developmental coordination disorder inform our understanding of atypical as well as typical motor development? We take the opportunity here to concentrate primarily on reviewing our own work, not because we think it is exemplary or definitive, but because it is bound together in a common framework that has informed our work and offers a conceptual framework within which to address our questions about perception-action relationships in motor development, both typical and atypical.

Perception-Action: An Introduction and Definitions

 For decades, perception and action were considered distinct systems that were studied independently. Indeed, since the early 20th century those studying motor development have provided detailed descriptions of how infants and children move their bodies and limbs more accurately, smoothly, and consistently, and with greater speed and force in the service of many activities of daily living and leisure, but rarely did they consider the influence of perception until around the 1970s (Clark & Whitall, 1989).The history of why this was the case and how it came to be replaced by an approach that considers the two systems as integrated has been detailed elsewhere (cf. Schmuckler, 1993; Turvey & Fitzpatrick, 1993). For our purposes here, we view perception and action as comprising a “system” in which perception and action are mutually and reciprocally related. Understanding this system and the nature of the perception-action relationship and its development is our goal and window into typical and atypical development.

 As human infants come into the world, their actions are already modulated by their senses. For example, they turn their eyes toward sound (Muir & Field, 1979), extend their hands toward an object they see (von Hofsten, 1982), and modulate their grasp to different objects placed in their palms (Molina & Jouen, 1996). Indeed, even the movements of the fetus demonstrate the coupling of intrauterine stimuli with fetal actions (Merendonk et al., 2017). These “reflexive-like” actions are not unidirectional, but are modulated right from the start. While much is made of the motor “primitives” that newborns (and for that matter, fetuses) demonstrate, the reality is that these primitives are actions that emerge in unison with the sensory systems and already demonstrate an element of integration.

 At this juncture, it is important that we offer a clarification. Throughout this paper, we will use the terms perception-action and sensorimotor somewhat interchangeably. We recognize, however, that perception-action relationships are built upon sensorimotor relationships. An infant can make nonspecific or spontaneous movements, but are these goal-directed actions? We would argue that they are not. So, a movement is not necessarily an action, whereas an action is, by our definition, movement with a goal. Similarly, sensation is not perception as perception arises from sensation.

Our Approach to Studying Perception-Action Systems

 The challenge for the human is to control and coordinate a multi-segmented body in the service of achieving desired goals or actions whilst doing so in an ever-changing environment. Born unable to manage their complex, unwieldy body, a year after birth (on average), the typically developing human infant rises, stands, and walks independently and self-feeds.

 To understand how movement develops, we have studied three action systems that represent a range of functional tasks. These are posture, rhythmic interlimb coordination, and goal-directed reaching/drawing. Posture represents those actions that keep us in a positional equilibrium (e.g., quiet standing) and in a desired orientation (e.g., leaning over to pick up a toy off the floor). Rhythmic interlimb coordination is reflected in actions where repetitive movements of one limb are co-ordered with the actions of other limbs (e.g., walking and drumming). A reach is comprised of those actions where we act on and with objects and people in our environment (e.g., to draw, or pick up a spoon). While these three action groups represent separate functions and an array of specific tasks, they all result from perception and action working together. Clearly, they bring their own unique challenges to the developing infant and child, but together they cover a wide range of functions in which to investigate developing perception-action systems.

 In addition to understanding how motor development is achieved in typically developing (TD) children, we have also investigated children who have Developmental Coordination Disorder (DCD). This term first appeared in the American Psychiatric Association’s *Diagnostic and Statistical Manual* (DSM Version IIIR) in 1987. Simply put, it refers to a condition where children are both late in developing motor skills and exhibit movements of poor quality that interfere with daily life and that cannot be explained by other factors. DSM-V (American Psychiatric Association, 2013) states the following four diagnostic criteria: A) Learning and execution of coordinated motor skills is below age level given the child’s opportunity for skill learning. B) Motor difficulties significantly interfere with activities of daily living, academic productivity, prevocational and vocational activities, leisure and play. C) Onset is in the early developmental period. D) Motor coordination difficulties are not better explained by intellectual delay, visual impairment, or other neurological conditions that affect movement. From a research perspective (Geuze et al., 2001), children with DCD are objectively enrolled in a study primarily by satisfying criterion A and through scoring either below the 16th percentile (possible DCD) or below the 6th percentile (probable DCD) on a standardized test for motor impairment such as the Movement Assessment Battery for Children (Henderson et al., 2007). Other criteria are typically assessed by more subjective measures such as parent/teacher questionnaires and interviews. Since these children have no specific etiology (APA, 2013), are very heterogenous (Dewey, 2002), and are noted to have sensorimotor integration problems (Wilson et al., 2017), they provide a window into atypical motor development that is not caused by a specific insult or disease, but may be enlightened by probing perception-action functioning.

Perception-Action: A Framework

 As we study human motor development, our focus is, of course, first on the changes that occur across the lifespan and on the processes that underlie these changes (Clark & Whitall, 1987). Whilst we seek to understand how perception-action systems develop, we need to situate our discussion in a defined framework that makes explicit our terms and the relevant observations and data. Our goal is to determine the relationship between the dynamics of the sensory-perceptual system and that of the musculoskeletal system so as to provide a framework for understanding the development of stable, adaptive action patterns that result in the control and coordination of our multi-segmented body in an ever-changing environment. As in all science, our conceptual or theoretical framework shapes the changes described, how those changes are characterized, and finally, how the changes are explained.

 Extant frameworks for the study of perception-action systems include the dynamical systems approach (Thelen, 1990; Turvey & Fitzpatrick, 1993) and control systems approaches (Wolpert et al., 1995; Wolpert & Kawato, 1998). A dynamical systems approach to the development of perception-action systems seeks to describe the formation and differentiation of dynamic action patterns based on biological and physical principles. Perception and action are viewed as a mutually coupled dynamical systems (Warren, 2006). On the other hand, the control systems approach assumes that there are two internal processes – the forward and inverse models – that produce, guide, and control action (Kawato, 1999). Today, these two approaches are moving closer together (Sternard, 2000) and in our work, the two together form a basis for our framework and conceptualization.

 From the dynamical systems perspective, we embrace the importance of self-organizing, dynamic relationships that are constrained by the environment, the organism, and the task at hand (Kelso, 1997; Kugler, Kelso, & Turvey, 1982; Newell, 1986; Thelen & Smith, 1996). Where appropriate, we also use some of the methodological techniques of modeling limb coordination or sensorimotor coupling using concepts from oscillatory dynamics such as phasing, stability, and entrainment (Kelso, 1997). From this perspective also, sensory input is viewed as information to the motor system and thus provides one set of “constraints” that shape the action.

 The control-theoretic approach provides a framework for relating the input and output features of behavior in a dynamic “internal model” (Kawato, 1999; Wolpert & Flanagan, 2009; Wolpert & Kawato, 1998). First deployed in engineering to control machines, these models and concepts have been used in human behavioral modeling to capture the dynamic and causal relationship between sensory information and action and between the action and its sensory consequences (e.g., Kawato, 1999; Wolpert & Ghahramani, 2000). One internal model, referred to as the *inverse* model, uses the initial sensory information to derive the desired action command. A second model, the *forward* model uses a “copy” of the motor command and predicts the sensory consequences of this action (Wolpert & Ghahramani, 2000). Like all models, these are representations and in our case, representations of how the neuromusculoskeletal system achieves goal-directed actions through dynamic relationships between the sensory and motor systems. And as with all models, we are not attempting to “prove” them right or wrong, but rather to use these models to better understand the perception-action system and its development.

Our Experimental Approach

 To understand any system, a scientist finds ways to ‘poke’ or perturb the system so that the system may reveal better how it works. Indeed, this has been our experimental approach to understanding the perception-action system and its development. For our work, we have used the strategy of perturbing the perceptual system and measuring the effect on the motor system. We recognize, however, that one could also perturb the motor system and study the effect on the perception of sensory information.

 Together, we have perturbed four sources of sensory system information - vision, proprioception, cutaneous, and audition (both spatial and timing) across the three different action systems mentioned earlier. We employed two principal strategies across the systems: 1) removing or adding a static source of sensory information believed to be salient to the task at hand; and, 2) enhancing a dynamic source of sensory information either implicitly or explicitly. Within each strategy, the role of intersensory integration also was investigated. Below, we describe each strategy, separately, for the appropriate task systems and summarize what we have learned. Finally, we return to our questions of whether studying perception-action systems have informed our understanding of typical and atypical motor development.

 As we probe the perception-action systems, we are interested in the developmental changes that happen both within a single sense (intra-modal) and across senses (inter-modal). When sensory inputs are eliminated, added, enhanced, or diminished, how does the developing perception-action system respond? One characterization of how individuals respond to changes in the sensory input is the notion that these inputs are dynamically re-weighted within the perception-action mapping so as to adapt the actions to the changing sensory conditions (Nashner et al., 1982). This adaptation results in a new “mapping” of the sensory input to the action (Shadmehr & Wise, 2005).

**Strategy 1: Removing or adding a static source of perceptual information**

 Our first perturbation to the perception-action relationship was to remove or add one of the senses that we assumed formed the basis of the perception-action relationship of a particular task. We hypothesized that motor performance would deteriorate or improve in the short-term if a salient source of perceptual information were abruptly eliminated or added. Owing to their more stable and multi-dimensional perception-action systems, we expected that adults would have little disruption to their actions compared to children as they could adapt their relationships to the changes. Furthermore, we reasoned that children with DCD would show a greater performance deterioration compared to age-matched TD children, since the perception-action systems of those with DCD were assumed to be delayed or different. Finally, we also hypothesized the removal of a salient sensory source for a perception-action system might result in the re-weighting of an alternative source of information such that the motor performance under investigation would not necessarily be affected. This re-weighting mechanism is much like what might happen when you get up in the middle of the night and it is pitch black. If you have a mature, well-functioning perception-action system, the loss of reliable visual information would immediately result in downweighting vision and upweighting the cutaneous information from your feet or perhaps your finger tips to maintain your postural stability. One might also upweight another source of information such as sound if you lived with numerous pets and wanted to avoid tripping over their moving bodies.

**1.1 Development of posture**

 Infants. Human infants take about five months before they sit upright without support and about 10-11 months before they stand “hands free” (i.e., not touching any surface) (Piper & Darrah, 1994). Postural control for maintaining these upright positions requires a fine-tuned relationship between the visual, vestibular, and somatosensory systems and the muscles that control the top-heavy, multi-segmented body in the upright position. To probe the perception-action relationship in the developing infant’s postural control, we first focused on the somatosensory input that infants employ naturalistically, namely, touching a stable surface. Pulling themselves to the upright, the infant’s first upright bipedal postures rely on the coffee table, the couch, or perhaps a parent’s hand to provide biomechanical support. But as we demonstrated in infants from the onset of pulling to stand, to standing alone, to walking onset, and to 1.5 months post-walking, there is a systematic developmental course in the perception-action relationship between touch and posture (Barela et al., 1999).

 Using an instrumented (with force transducers) bar that was placed at hip level and to the infant’s side, infants touched (but could not hold) the surface of the rounded instrumented bar. At the onset of pull to stand, infants used the bar for support as evidenced by high vertical forces applied to the touch bar. By the time they could stand alone, the infants had already reduced their vertical forces on the bar and were using the sensory input from touch to modulate their standing sway. By the time they had been walking for 1.5 months, the touch information from the bar was being used ‘prospectively’ or in a feedforward manner to regulate postural sway. Indeed, in another study (Metcalfe et al., 2000), we found that the infants with varying degrees of walking experience were using touch information provided by the instrumented bar to explore their sway parameters and subsequently, we hypothesized were developing an accurate ‘internal’ model that would eventually be used for walking. This internal model provided a consistent, prospective relationship between perception and action.

 But what happens when there is a transition from one motor skill to another such as from sitting to walking? Is the perception-action relationship disrupted or does it easily transition to the perceptual and motor demands of the new skill? Again, we used “touch” as our window into this relationship (Chen et al., 2008). Nine infants were followed longitudinally (every month) from the onset of independent sitting to the time when they had been walking for nine months. Our findings revealed that with the onset of walking, sitting (which the infants had been doing for months) was disrupted such that the infants’ postural sway during sitting was greater than it had been at any other age (before and after the transition). Clearly, the infants were re-calibrating the perception-action system as the new behavior was brought on line. It was not a long disruption, but it was clearly evident. Again, we argued that the internal model was expanding to include postural control for upright bipedal locomotion. In a re-analysis of the same data, we used a stabilogram-diffusion technique to measure the time-evolving properties of the effect of touch over the 9 months of walking after its onset (Metcalfe et al., 2005). The main finding was that the effect of touch in reducing sway was constant for the magnitude of the sway variability, while the rate of variability reduction decreased over time and walking experience. This differentiation between rate and magnitude, we argued, could reflect a dual role for the sensory system in both mapping with the motor commands (a basic internal model) and in adjusting to experience and growth, i.e., fine-tuning the model over time.

 As we have described, this work used static and single sensory sources with infants limited to the “touch or no touch” paradigm. While this work revealed new insights into the emerging perception-action relationships and the task was highly naturalistic for infants, it was limited to the “touch” sense, salient as it may be. In a later section, we will discuss our work with dynamic and multiple senses during infancy. Next, we continue with a similar paradigm with children, where we had more opportunity to explore the richness of other sensorimotor relationships.

 Children. If a particular perception-action coupling is not strong and multi-dimensional, then withdrawing a source of information would presumably result in motor difficulties. Indeed, that is exactly what happens. When children (6-9 years of age) were asked to close their eyes while standing on one foot for as long as possible, not surprisingly, they struggled to maintain a steady one-foot stand (Clark & Watkins, 1984); this was made more difficult by constraint changes in the support surface they stood on (standing crosswise or lengthwise on a stick) or the body position they assumed (hands hanging free, hands on hips, arms folded on chest or trunk bent over). In a later study of 4-, 6-, and 8-year-old children and adults, we combined our touch paradigm with a vision condition (eyes open, eyes closed) (Bair et al., 2011). As with the infants, lightly touching a stationary bar had a positive effect on the postural sway of all the children and adults with or without vision. Taking away vision did not have a deleterious effect on the children’s postural control regardless of whether they touched the bar or not. The latter finding for vision may be due to the postural task employed( i.e., parallel foot position) which differed from the earlier work by Clark and Watkins (1984) where there were more challenging postures and foot positions (one-footed and on a narrow support surface) required.

 Taken together, however, these two studies would suggest that by the time children are school age or a little younger, they have a functioning perception-action system that is stable if “perturbed” by taking away a sensory input (i.e., vision) or adding one that is not usually involved in the task (i.e., touch). But what of the children who are having movement difficulties, is their perception-action system stable in the face of a sensory perturbation?

 Children with DCD. In the same paper, Bair and colleagues (2011) reported a second study in which children with DCD were tested in the touch (present or absent) and vision (present or absent) conditions, although this time the participants were in a semi-tandem stance (one foot ahead of the other and slightly apart). Another sample of typically developing children was also included. The condition with vision and without light touch are the “normal” conditions the children encounter every day. But adding the conditions in which the children were to touch lightly a stationary bar and/or to close their eyes are not typical. It was hypothesized, therefore, that the effect of light touch would improve sway in both groups as it had done previously for typically developing children and adults and that taking away vision would challenge the perception-action system, particularly in the children with DCD. Our findings reveal that the children with DCD have more postural sway than TD children when they are in the “typical” situation of vision and no touch, and when they are in the atypical situation of no vision. However, when touch and vision are present, their sway is better than if they just had vision though their performance is still below that of typically developing children. Indeed, having more sensory information than normally available helped the children with DCD more than it did for the TD children and adults, suggesting their internal model was deficient compared to their typically developing cohorts.

**1.2 Development of rhythmic interlimb coordination**

 Infants. When infants have developed enough trunk postural control to stand, their next motor milestone is independent walking. This is a motor skill requiring rhythmic interlimb coordination; namely, the coordination of the two walking legs in a 180-degree phasing relationship. In an early study of newly walking babies (Clark et al., 1988), we found that, on average, the infants were able to accomplish the same phasing pattern as adults, but with a much larger within-individual variability. However, the addition of *light* touch from a parent or experimenter’s hand had a stabilizing effect on the variability of the infant’s interlimb leg coordination such that new walkers appeared as stable with touch as they were four weeks later without touch. This illustration of light touch modulating action in a positive manner, although not experimentally planned at the time, was the first example of a perception-action coupling with touch in walking and provides an analog to our work on the effect of touch on standing posture described above.

 Children. Later, in children 7-8 years of age compared to adults, we employed two experimental rhythmic coordination tasks to examine perception-action coupling. One gross-motor multilimb task was for participants to clap two cymbals together at the same time that they stepped in place, with the goal of timing the claps to each foot step at their own comfortable speed (McKenzie et al., 2008). The second fine-motor task was to produce bilateral antiphase finger tapping at their own comfortable speed (Roche et al., 2011). For both experiments, we systematically manipulated vision and hearing in four conditions: normal (with vision and hearing), without vision, without hearing, and without either vision or hearing. We expected to see a deterioration of performance when sensory information was removed, with greater deterioration in the children. In both experiments, adults performed better than children, but the coordination between the clap and steps or the two fingers (relative phasing) and the consistency of each limb movement (coefficient of variation) were not affected by the differing sensory information (vision and audition) in either children or adults, thus not supporting our hypothesis. This indicates that either these two sensory sources of information were not salient for these tasks or that both groups were able to equally upweight their somatosensory information to maintain the level of performance in the normal condition. The latter would indicate a well-tuned adaptive mechanism of re-weighting to maintain perception-action coupling for both children and adults.

 Children with DCD. In the same two papers (McKenzie et al., 2008; Roche et al., 2011), we also tested aged-matched children with DCD to assess whether their perception-action coupling was further impaired under the reduced sensory information conditions. To our surprise, we had the same non-effect on movement performance under the different sensory conditions despite absolute differences in motor performance between the typically developing children and those with DCD. In the tapping experiment (Roche et al., 2011), when we analyzed each child with DCD individually, we found that 40% performed similarly to those without DCD and that there was a subset who actually performed with less variability without vision, possibly because they could tune their internal model better without visual distraction.

 That seeing one’s fingers or hands/feet did not influence movement accuracy or variability is less surprising than the lack of an effect from hearing self-produced sounds. We had ensured that the fingers produced an audible click when tapping and the hands used loud cymbals when clapping so that these audible sounds could potentially be used as feedback in the conditions with hearing present. This is also surprising in that the ‘enhancement’ of sensory information (in this case, sound or vision) did not help the children with DCD as it had done in the postural task. However, we cannot rule out that these self-produced noises might have influenced performance if we had asked the participants to pay attention to their feedback in order to accomplish the task. In addition, we cannot rule out that if we had specifically asked the participants to pay visual attention to their finger movements in relation to the sounds made that we might have seen an effect. Taken together with the developmental findings, we concluded that neither vision nor hearing were salient sources of perceptual information for producing these two rhythmic self-constrained coordination tasks. We doubted that any re-weighting occurred because we found the same results for both sensory sources in all three groups.

**1.3 Development of goal-directed reaching and drawing**

 Children. Producing accurate sensorimotor behavior depends on precise localization of the body in space that can be estimated by multiple sensory sources, especially vision and proprioception. This multisensory integration is known to change across age but it was not known whether the development of visuomotor or proprioceptive intra-sensory modulation would differentially affect the intersensory modulation. In an experiment using a two-tier apparatus with a digitizing tablet on the lower tray and a flat screen monitor on the upper tray, we tested 7- to 13-year-old children in a positional hand-matching experiment (King et al., 2010). The participants used a digitizer pen with the dominant pronated hand on the tablet of the lower tray whose position was displayed on the upper tray monitor. The participants were asked to match the position of the pen seen on the monitor with their nondominant, supinated hand underneath the digitizing tablet. By manipulating information on the top tray monitor, we were able to test the motor performance from visual, proprioceptive, and concurrent visual and proprioceptive stimuli. We then placed the concurrent visual and proprioceptive stimuli in conflicting locations to determine the relative contributions of vision and proprioception to the multisensory estimate of target positions. Results clearly revealed that the visual estimate of target position contributed more to the multisensory estimate in the younger children, whereas the proprioceptive estimate was up-weighted in the older children. Additionally, regardless of age, improvement in proprioceptive, but not visual, functioning was correlated with an up-weighting of proprioception in the incongruent trials suggesting that children’s improvements in a unimodal sensory system may influence multisensory integration.

 A subsequent study investigated the relationship between seeing a target and moving the digitizer pen to one of multiple targets “as fast and as straight as possible” in a task known as the center-out paradigm in 5- to 12-year-old children and adults (Kagerer & Clark, 2015). The control condition, which was always first, allowed online visual feedback of the movement. In Experiment 1, the perceptual perturbation was to occlude vision of the pen and target during the movement, thus forcing individuals to rely on proprioceptive feedback. In the control condition, the usual developmental trends of increasing speed, accuracy, and consistency were observed. Similarly, the proprioceptive-motor condition showed that older children and adults were much more accurate in their movement trajectory, indicating less reliance on visual feedback. Two findings were unexpected. The 7- to 12-year-olds were more variable to the ipsilateral target without vision, in contrast, to being more variable to the contralateral target with vision; and accuracy to the endpoint target showed a reverse developmental trend such that adults and older children were more variable than younger children. These findings were interpreted as being consistent with the dynamic dominance hypothesis (Mutha et al., 2013) whereby non-dominant hands are specialized for impedance control that is needed for better endpoint accuracy. Thus, the ability to form finely tuned internal models is influenced by the development of lateralization over time.

 In Experiment 2, the perceptual perturbation was to substitute the visual cue for an auditory cue that required spatial localization of auditory targets. Since there was no visual information available for the participant, the amplitude of the movement was not specified and only initial directional error was recorded. All groups performed relatively accurately. The lack of a developmental trend suggests that it is task experience of this specific perception-action relationship rather than other age-related factors that influence performance since auditory-motor internal models appear to be functional by 5-6 years. The two experiments together provide novel insights into both proprioceptive-motor and auditory-motor development of spatial localization. Both highlight the influence of experience in different ways.

**Strategy 1: Summary of main findings**

 The development of perception-action systems needs to be considered across varied sensory manipulations and action systems since results are both general and, in some cases, specific to tasks. Looking across the findings above, we would suggest the following summary:

 1.Developmentally, adding touch (cutaneous) input stabilizes posture (and locomotion for infants) equally across all ages measured. Children with DCD are also able to use touch input.

 2. Developmentally, vision is also salient for maintaining posture in infants and young adults, but less so in older children unless their stance (i.e., their base of support) is challenged. Children with DCD are affected more by loss of vision than all other groups.

 3. Developmentally, vision and hearing are apparently not salient informational sources for self-produced rhythmic interlimb coordination. The same is true for children with DCD.

 4. Developmentally, young children rely more on vision than proprioception in a reaching task while older children are easily able to up-weight proprioceptive information, supporting the finding of less deterioration of performance with older children when vision is removed. In addition, some aspects of reaching performance without vision are affected by the development of lateralized specialization formed by experience.

**Strategy 2: Enhancing a dynamic source of perceptual information**

 In addition to removing or adding static sensory information, we also perturbed the sensory information by enhancing its salience in a variety of situations. Removing or adding sensory information offers insights into what sources of information are well-integrated and salient for the perception-action mapping, but how the information “tunes” the relationship temporally requires that we examine the dynamics of the sensory information. In these experiments, we distinguish between *implicit* sources of information where the mover is unaware that the sensory information has been changed and *explicit* sources of perceptual information where the goal is to match sensory cues that are brought to the attention of the mover. For the former, across all tasks, we hypothesized that typically developing infants and children would be less responsive to the dynamically enhanced cues than would adults; and that children with DCD would likely be less responsive than those without DCD. For explicit cues, and specifically for auditory timing information, we hypothesized that typically developing children would be less able than adults to use the cues to synchronize their movements, and that children with DCD would be the least able to use the explicit information.

**2.1 Development of posture**

Infants. To examine the sensory dynamics in the perception-action relationship of postural control, we employed a “moving” rather than a stationary sensory input. In one set of experiments, we used a gently moving touch bar and in the other a moving visual display (i.e., a moving room). In both cases, we assumed that these dynamic oscillations were implicit and we did not draw attention to either set of stimuli. In our first experiment, we had infants lightly touch (but not hold) a hip-level moving bar gently oscillating medial-laterally in one of three dynamic conditions (using touch bar oscillations at frequencies of 0.1, 0.3, and 0.5 Hz and amplitudes of 1.6, 0.59, and 0.36 cm, respectively) (Metcalfe et al., 2005). Tested longitudinally from one month prior to independent walking onset until they had been walking 9 months, infants demonstrated increasing temporal stability between the oscillating touch bar and their postural sway. That is, they increased the synchronization between the bar and their sway. Walking experience appeared to provide an opportunity for the active tuning of the perception-action relationship so as to facilitate a refinement of the temporal dynamics of this relationship.

 As walking develops, sensitivity to visual surround is critical to the development of self-motion. So, would we see improved visual-postural sway coupling as infants gained more experience in walking? To test the dynamics of the visuomotor relationship, infants sat in a 3-walled room with an anterior-posterior (AP) moving visual display with five varying frequency and amplitude combinations (Chen et al., 2016). Four groups of infants were tested based on the time they achieved certain postural milestones: 1) onset of independent sitting; 2) onset of independent standing; 3) onset of independent walking; and, 4) 1-year-post-walking onset. Not surprisingly, the new sitters had a highly variable relationship between the moving visual stimuli and their postural sway. Indeed, it appeared that they were not responding to the dynamic visual signal. However, after a few months of sitting exposure and from the onset of independent standing, infants were able to couple their sitting postural sway to the moving visual stimulus. And as we had observed previously with static touch (Chen et al., 2007), we now observed the same with vision; namely, at the onset of walking, infants showed a transient disruption in their postural sway, suggesting a re-calibration of the perception-action relationship as a new action (i.e., walking) emerged.

 In addition, by varying the visual signal’s amplitude, we were able to push the infants to ‘re-weight’ when the amplitude of the visual signal was so large as to be unreliable. Indeed, we found that except for new sitters, all the infants showed evidence of re-weighting. This adaptive mechanism is much like what might happen visually when a train goes by very fast as you are standing on the station platform. The visual flow from the train is ‘down-weighted’ as it is perceived as too large to be meaningful to your postural stability. The ability to re-weight the sensory inputs within the perception-action map is an important adaptive ability, both in real-time, but also across developmental time where the ‘re-weighting’ might become a permanent change in the perception-action relationship.

 Children. As we examine the developmental landscape for dynamic perception-action relationships in young children, the importance of how the multiple senses are related to each other and to the emerging action becomes increasingly more important. In posture, three sensory systems – vestibular, visual, and somatosensation – play critical roles in controlling and coordinating the orientation and equilibrium of the multi-segmented body. Input from these three systems must be integrated and when needed, adapted to changes within and across modalities by re-weighting the sensory information. As discussed earlier, in infants we had observed within modality (vision) re-weighting (Chen et al., 2016). But what happens when two modalities are presented and one is unreliable? Will the child re-weight to the other sense? To answer this question, we presented children, ages 4 to 10 years, with simultaneously moving small-amplitude visual stimuli on a screen and an oscillating touch bar (Bair et al., 2007). Is the young child’s perception-action mapping sufficiently robust to accommodate changes in two different sensory systems whilst maintaining a stable posture? Our findings suggest that the children’s mapping is robust, but only first within a modality (i.e., intra-modal) (present at age 4). It is not until the children are older (~10 years) that they demonstrated inter-modal integration where the senses act more like a single modality rather than as separate modalities. Responses to changes in one modality (i.e., vision) are adjusted both within and across modalities. Thus, for the mature perception-action system, unreliable sensory information in one sense can be down-weighted, while up-weighting another more reliable sense.

 Children with DCD. Children with DCD are often thought to have “sensory integration” problems (Dewey, 2002). So would we find that the perception-action system of children with DCD is able to accommodate multi-sensory changes in a similar fashion to their typically developing peers? Based on their motor performance and motor learning difficulties, we hypothesized that they would not adapt well to the changing sensory stimuli nor show multi-sensory re-weighting. Secondly, if they under-perform compared to their typically developing peers, are they merely delayed in their development or is their development qualitatively different?

 To answer these questions, a sample of children with DCD, who matched the age of our typically developing sample described above, were tested on the same experimental protocol in which visual and touch stimuli oscillated as children were to maintain a quiet upright posture (Bair et al. 2012). Our findings reveal a developmental pattern that is different from their typically developing peers. First, the 6-year-old children with DCD were only able to reweight to touch but not to vision. It was not until they were 10 years old that they could reweight to changes in visual motion. However, even the oldest children with DCD (10-year-olds) did not demonstrate multisensory re-weighting. In addition, the children with DCD had a phase lag in their response to changes in the visual and touch bar motions. Thus, the children with DCD have a different developmental trajectory for their perception-action trajectory.

**2.2 Development of rhythmic interlimb coordination**

 In examining the development of rhythmic interlimb coordination and enhanced sensory information, we have divided the work into two sections. First (section 2.1), we report on the work we have done on providing explicit sensory cues to interlimb coordinative patterns that are familiar to participants. Then, in the second section (2.2) we describe studies on how participants respond to sensory information in novel patterns of rhythmic interlimb coordination.

**2.2.1 Development of rhythmic interlimb coordination using explicit cues**

 In contrast to the implicit dynamic sensory information we manipulated in the postural experiments, our first investigation of dynamic sensory information for rhythmic interlimb coordination utilized explicit auditory cues. Recall that when auditory information was self-produced in a non-cue condition (section 1.2) the information was not used by any group of participants.

 Children. How adept at matching their actions to explicit auditory cues are children compared to young adults? In both the multi-limb gross-motor clapping and stepping task and the bilateral anti-phase fine-motor task described earlier, we employed auditory cueing at four frequencies with instructions to time clapping and steps (or fingers) to the beat. In the multi-limb task, adults were more closely coupled to the beat than the children although even the adults were up to 15% either side of the beat (Whitall et al., 2006). Adults also demonstrated synchronized coordination between their arms and legs at all frequencies, whereas children were more likely to do so as the auditory cue frequency increased. It is not clear why children have problems with precise coordination at lower frequencies except that it may be influenced by the intersegmental joint interactions that become entrained at higher frequencies for this multi-limb task.

 In another study, we found that both children and adults adjusted their movements equally well to the set frequencies when tapping bilaterally (Whitall et al., 2008). Analysis of the synchronization to the beat revealed, however, that children were more variable than adults and that they tended to tap behind the beat rather than in front of the beat which adults do, particularly at the slower frequencies. This finding suggests that children may not have yet fine-tuned their inverse internal model to produce consistent motor commands and, also, that they are not able to use information from a forward model to anticipate the beat, but rely on slower feedback processing (Desmurget & Grafton, 2000).

 Children with DCD. And how would children with DCD handle the coordination between limbs and auditory signal? For the multi-limb clapping and stepping task, children with DCD were similar to their age-matched controls regarding matching the beat across all frequencies (Whitall et al., 2006). However, they differed considerably in their ability to demonstrate absolute coordination between their arms and legs because, as the frequency increased, children with DCD became less coordinated between limbs rather than more coordinated. There are several related explanations for these findings. One possibility is that children with DCD are unable to access their inverse internal model quickly enough when the frequency is increased. A second explanation is that their access is quick enough, but they cannot use feedback quickly to adjust their forward model. A third is that they have not been able to build or fine-tune their inverse model to control the inertial properties of large segmental interactions of the four limbs. The last explanation would seem to have some support given our results from the study on bilateral anti-phase tapping where the inertial properties (of the fingers) were minimal (Whitall, 2008). In the tapping study, children with DCD were equally adept as TD children at matching the frequency except for the very slowest frequency when about half the children with DCD had trouble slowing down (inhibiting their response). Being able to match the auditory cue with a tap on average, however, did not mean that children with DCD were equally as accurate and consistent. Individual tap analysis showed neither a tendency to be ahead (adult-like) or behind (children-like) the beat but rather an inability to synchronize consistently at all (i.e., they were extremely variable in their tap responses to the stimuli).

 We interpret the findings from these two studies as suggesting that the auditory-motor coupling from explicit auditory cues is indeed impaired in children with DCD and contributes to their motor performance deficits. To examine more closely whether the children seem delayed or atypical in development, we undertook an individual analysis of their performance. We found that 20% of the children with DCD were similar to TD children, 50% were deficient in all areas (potentially developing atypically) and 30% were deficient in some areas (potentially delayed). Nevertheless, the fact that, as a group, the children with DCD were able to generally match the beat also suggests that there may be some implicit coupling with the beat, as we will see in the next section.

**2.2.2 Development of novel rhythmic interlimb coordination using either explicit or implicit cues**

 Children: It is well known that there are only two “stable” tapping patterns, or indeed typical forms of interlimb coordination: in-phase (0%; 0/360°) and antiphase (50%; 180°) (Tuller & Kelso, 1989). Can children demonstrate these tapping patterns by the age of 7 years? We designed a novel perturbation paradigm for auditory-motor coupling by asking children (7-11 years) and adults to explicitly and implicitly learn a different (new) phasing relationship between the fingers, one that was neither in-phase nor antiphase, but off-phase at 12.5% (225°) (Roche et al., 2016). From preliminary work, we had established that this off-phase relationship was above the perceptual threshold of children (i.e., perceivable). That is, we knew that our participants could perceive the difference between an anti-phase beat and this off-phase beat. Participants first practiced the anti-phase pattern to a set audio-cued frequency that was known to be attainable from a previous experiment (Whitall et al., 2008). The new 12.5% phasing relationship was then introduced making this an explicit perturbation. An implicit perturbation was tested by gradually increasing the phasing offset from baseline antiphase by 3.05% or 11°. These changes in phasing were under the measured perceptual threshold of the children and not perceivable until 12.5% for most children. Surprisingly, children performed the new off-phase relationship in both the explicit or the implicit conditions as quickly as adults tested in a separate experiment (Kagerer et al., 2014). All groups reacted to the very first change in phasing relationship of 3.05% (and subsequent changes) even though this was below their own established perceptual threshold. This finding might suggest some form of implicit learning. Comparing across the studies, the adults did have a lower perceptual threshold, as well as lower levels of variability of phasing. We concluded that this “new” phasing relationship was adapted to equally by both groups, meaning that the perception-action coupling for this perturbation was not different across age groups and was in place by 7 years.

 Children with DCD. In the above experiment (Roche et al., 2016), children with DCD were no different than their age-matched peers in quickly responding to the explicit or implicit changes in phasing relationship provided by the auditory stimuli despite differences in performance for their phasing variability. To our knowledge, this specific auditory-motor paradigm was the first to demonstrate motor responses without perceptual awareness in either typical or atypically developing children. Taken together with the tapping studies in section 2.2, we suggest that children with or without DCD and adults are able to detect and act on both explicit and implicit auditory cues that change in frequency or phasing. What distinguishes the three groups is the ability to accurately reproduce the necessary motor adjustment to the perturbed perceptual cue on every movement. Put another way, the inverse internal model appears not as finely-tuned for children as adults or for children with DCD as compared to TD age-matched children.

**2.3** **Development of goal-directed reaching and drawing**

Children: Using the center-out paradigm where participants draw lines between a center target and one of four (randomized) peripheral targets “as fast and straight as possible), we set out to enhance perceptual information by increasing the amount of transformation needed from viewing the visual-spatial target to the movement commands required to reach the target (Bo et al., 2006). The “normal” transformation condition consisted of being able to view the participant’s hand, the pen path and the targets throughout the condition. In this case, no transformation was needed because visual and kinesthetic guidance of the hand was present. The “aligned” condition consisted of occluding view of the hand but seeing the pen path and targets reflected from a monitor suspended above the participant’s hand (thus occluding direct vision of the hand but not excluding visual feedback). The transformation to motor commands without vision of the hand was in the same plane as the spatial map of the targets. The “vertical” transformation condition was achieved by using a computer directly in front of the individual requiring the need to transfer the vertical coordinates of the target to a movement requiring a horizontal displacement. The need for these transformations was explicit to the individual although it is unclear that individuals would use conscious processing of this fact.

 In all age groups (4-, 6-, 8-year-olds and adults), movement speed, smoothness, and variability were negatively affected by the increase in the transformation; however, the rate of change among the tasks was similar in both children and adults. The young children (4 and 6 years), on the other hand, showed significantly more variability than the older children and adults. We concluded that the increased variability could be a result of imperfectly tuned parameters of the inverse kinematic model or an inability to switch between multiple models, particularly if each transformation required a different model.

 In the above experiment, the task required that the nervous system estimate motor commands after transforming the visual-spatial information to accomplish the movement, a process called state estimation. In a later experiment, we looked specifically at the development of dynamic state estimation using a center-out paradigm with feedback of the movement occluded after movement initiation. In 75% of the trials (single step) there was no additional perturbation but in 25% (double step) there was an unexpected brief (dynamic) displacement of the target (King et al., 2012). Two age groups (6-8 years and 10-12 years) and adults were tested. Results of the single step condition suggested no age-related changes in speed and initial directional error. However, in the double step condition, there were substantial age-related changes with the younger age group being more variable and consistently overshooting the displaced target. The pattern of errors suggested that they relied on delayed sensory feedback and less on feedforward processes.

**Strategy 2. Summary of key findings**

 As we saw earlier, the different task paradigms again provided both similar and unique findings. As we look across our studies, we would summarize our findings as such:

 1. Developmentally, all paradigms show that with increasing age and experience, there is a decrease in the variability of movement response within and/or across trials in response to the same enhanced, dynamic sensory perturbation. This is true for touch, vision, and auditory information (timing). Early longitudinal development of postural sway indicates that this variable response returns briefly as new skills are added. Children with DCD are also typically more variable than TD children in postural sway and rhythmic interlimb coordination.

 2. Developmentally, all paradigms have results that indicate a reliance on feedback processing in younger children, whereas adults and older children (10 and above) are able to use feedforward processing much more effectively.

 3. Developmentally, the ability to re-weight touch or visual information to maintain a stable posture occurs within either modality by or before 4 years but not between these modalities until about 10 years, at which point it is adult-like. Children with DCD, however, can re-weight touch by 6 years and vision by 10 years and are unable to re-weight between the modalities at ten years of age.

 4. Developmentally, by age 7, children are equally adept as adults at matching the frequency of a rhythmic auditory cue, but adults can synchronize with and anticipate the beat while children tend to be behind the beat. Surprisingly, children with DCD can also match the beat at most frequencies but are less able to actually synchronize.

 5. Developmentally, children and adults respond similarly when presented with “new” visual-spatial transformations for reaching or “novel” auditory phasing relationships in tapping (either explicitly or implicitly). Children with DCD also perform similarly to TD children and adults.

**Concluding Comments**

 We return to our original questions. How have our experiments on perception-action systems and their development contributed to our understanding of typical and atypical motor development? At one level, we can state that our summary sections list the key research findings that we consider to be relatively novel and therefore contribute to the knowledge base of motor development and that of the atypical development of children with DCD. However, we would like to make a broader comment about the usefulness of studying perception-action systems relative to motor development and human development in general.

 Fundamentally, we consider that perception-action coupling is an underlying mechanism/foundation/constraint of motor development in the sense that the ongoing processing of sensations and the planning and execution of movements are how the brain produces movement behavior. Therefore, we need a good understanding of how this coupling changes or adapts over time in order to better understand how motor behavior develops across the lifespan. For example, the ability to adapt (or re-weight) our sensory information is fundamental to actions in the real world where the sensory conditions are constantly changing induced by environmental and task constraints as well as the consequences of injury, disease, or aging processes. But as we have shown in our work, the perception-action systems of infants, children, and adults differ. Understanding these differences and how they change informs our efforts in scaffolding typically developing children as well as interventions for those who are developmentally delayed. As our work with children with DCD demonstrated, children who are not typically developing may not just be delayed, but may be developing differently. How then might our interventions differ across the spectrum of those not developing typically?

 Let us be clear, also, that our enthusiasm and efforts to understand developing perception-action systems does not mean that we believe this is the only contributing mechanism to motor development. Clearly, there are other developing systems, such as the musculo-skeletal or the cognitive system that are likely to affect how behaviors change. These and changes in other systems need to be investigated as constraints that affect the fine-tuning of “internal” models (using the control-theoretic conceptualization) or as behavioral attractor states (using a broad dynamical systems conceptualization). There is also the contribution of adaptation mechanisms on longer time scales such as consolidation which will potentially accelerate or deaccelerate the rate of change in developing movement behaviors and will result in “learning” new perception-action mappings.

 Regarding atypical development specifically, we would argue that our paradigms would be useful for other populations. They have detected differences in responding to sensory perturbations between children with and without DCD that correspond to other experiments and known characteristics of these children. In addition to our general remarks above, we have suggested that the heterogeneity of this population demands that individual analyses against a landscape of TD children are important for determining whether children are delayed or on a different trajectory (King et al., 2011).

**Future Directions**

 There are many potential avenues of future research including obvious ones such as extending the paradigms to older adults, carrying out further longitudinal work, or correlating each task paradigm with neurophysiological data. Here we highlight three we think are particularly important.

 1. Perturb the sensorimotor mapping rather than the sensory information alone which we chose to do in the above experiments. There is an existing visual-motor adaptation paradigm that alters the existing mapping relationship (by rotating visual feedback) between seeing the target and planning the movement. This paradigm allows one to investigate: (1) how quickly and completely an individual adapts to the new relationship, as well as (2) whether this relationship is learned as evidenced by after-effects when the rotation is removed.

 2. Investigate the role of cognition in conjunction with the perception-action paradigms we already use. For example, what role does attentional focus or intention play in whether the sensory information is salient or whether the individual is aware of the implicit enhancements of sensory information changes? In this regard, too, it would be useful to ensure that changes in sensory information are above or below a perceptual threshold for a particular sense.

 3. Investigate how to promote the learning of perception-action coupling. Given its importance, can we promote, for example, the ability to re-weight visual information in young children with DCD in order to potentially have them demonstrate motor behavior that is more like their peers? The suggestion here is that we already have discovered insights into the development of perception-action coupling and perhaps these insights can be utilized for interventions or methods of promoting motor development in children with and without DCD.

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