Reaching beyond limits: Motor development and adaptive strategies in children with congenital upper limb differences

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Laura-Ashleigh Bird

Abstract

Motor development can be defined as the process of learning to control the movements of the body (Haywood & Getchell, 2019). Emerging motor skills foster independence and support broader cognitive and social growth by creating new opportunities for exploration, interaction, and learning. Contemporary theories conceptualise motor development as flexible and experience-driven, shaped by dynamic interactions between the body, cognition, and environment. Children with congenital upper limb differences, born with a partial or missing hand, offer a powerful test case for exploring the limits of this theory. Specifically, how motor skills emerge when typical anatomical structures are altered or absent. This thesis employs a multi-method approach across four empirical studies to investigate (1) the emergence of early gross motor milestones, (2) the development of compensatory motor strategies in childhood, (3) the roles of imitation and self-guided exploration in innovative problem-solving, and (4) the flexibility of internal motor models in adapting to new sensorimotor mappings. We test the overarching hypothesis that motor development is shaped by the dynamic interplay between sensorimotor experience, cognition, and environmental interaction. By examining how children with anatomical constraints develop flexible and creative motor behaviours, this thesis reveals how alternative developmental pathways can support adaptation and demonstrate the fundamental flexibility of the developing motor system. Our findings show that children with upper limb differences follow distinct yet functional motor trajectories, characterised by adaptive use of alternative effectors and exploratory problem-solving. These adaptations go beyond compensation, to reflect creative and embodied learning shaped by individual anatomy and experience. Together, these findings support a dynamic, experience-driven model of motor development and offer novel insights into how structural variation influences both functional outcomes and cognitive processes. Beyond theoretical advances, this work offers practical implications for clinical assessment and parental reassurance, highlighting alternative developmental pathways as valid, adaptive routes to functional success.

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Thesis submitted for the degree of Doctor of Philosophy

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July 2025

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Declaration

The author confirms that none of the material presented in this thesis has been submitted elsewhere for any other qualification and is the author’s own work unless referenced otherwise.

Statement of copyright

Acknowledgements

First and foremost, I would like to thank my supervisors Dorothy Cowie and Ulrik Beierholm. Dorothy, thank you for your unwavering support, encouragement, and belief in me. Your guidance has not only shaped this project, but the researcher I am today. Ulrik, I'm incredibly grateful for all the hours we spent wrangling data. Thank you for your patience, and for teaching me everything I know in R. Your expertise and mentorship have been invaluable, and I've learned so much from you. Next, a thank you to Tamar Makin, for welcoming me into a new research community. Your insight, support, and generosity with your time and expertise have had a profound impact on this project and my development. To Bruce Rawlings and Jordan Taylor – thank you for your collaboration, ideas, and input throughout this project. It's been a pleasure working with you. To Reach and LimbBo, and to every child and family who took part in this research – thank you, this project would not have been possible without you. Your strength, enthusiasm, and fierce determination continue to inspire me. It's been an honour to be part of your stories. I'd also like to thank Emerald Grimshaw, Isabel Castelow, and Nefeli Strongylaki for the countless hours spent video coding. Your hard work and dedication to the project were crucial to bringing this data to life. To Mathew, Ali, and Maggie – thank you for your help with testing. Your support behind the scenes made a real difference. To lab members past and present – Hayley, Rachel, Sam, Oscar, Jamie, Louise, Emerald, Isabel, Nefeli – thank you for your friendship, support, and brilliant conversations along the way. A special thank you to Emerald, who not only worked tirelessly but also travelled up and down the country with me; I truly couldn't have done it without you. To Stuart, my partner, thank you for being my constant source of support, for reading draft after draft, and for always being by my side. And finally, to Isaac, your joy, laughter, and endless energy gave me the strength and motivation when I needed it most. You are my biggest inspiration.

Dedication

This thesis is dedicated to my dad David, my greatest champion who always encouraged me to reach for the stars.

Chapter 1: Introduction

Motor development is a cornerstone of human growth, underpinning how individuals interact with the world and facilitating independence. From grasping objects to walking independently, motor development encompasses both fine and gross motor skills, which in turn scaffold development across other domains, particularly social and cognitive, by providing new opportunities for exploration, interaction, and learning (Adolph & Hoch, 2019; Haywood & Getchell, 2024). While traditionally viewed as a linear, biologically-driven process, contemporary theorists conceptualise motor development as flexible, shaped by dynamic interactions between the body, cognition, and environment (Adolph & Hoch, 2019; Iverson, 2021). This shift toward a more experience-dependent view of motor development raises important questions about how motor skills emerge when key mechanisms are disrupted, for example, when typical anatomical structures are altered or absent. Children with congenital upper limb differences, who are born with a partial or missing hand, offer a compelling opportunity to investigate these questions. Despite significant biomechanical constraints, these children often demonstrate remarkably effective motor skills (Tucciarelli et al., 2024), yet little is known about how these abilities develop. If motor development was solely dictated by a fixed, biologically pre-determined trajectory, we would expect these children to show delayed or impaired motor outcomes due the absence of specific anatomical structures and neural circuits assumed to be necessary for typical development. In contrast, if development is guided by sensorimotor experience and adaptive interaction with the environment, then we might expect these children to discover alternative, compensatory strategies, following an individualised developmental trajectory to achieve functional motor success. Here adaptive interaction refers specifically to how children with congenital upper limb differences adjust their motor behaviour in response to a two-handed world. While these children are not adapting in the traditional sense of modifying an existing ability, they learn to navigate environments, tasks, and social expectations largely designed for two-handed individuals. Adaptability therefore captures how these children develop alternative, often innovative strategies to perform actions they predominantly see executed with two hands. This thesis aims to address this gap by investigating how and when children with atypical limb structures acquire, refine, and flexibly apply motor strategies across a range of contexts, from early gross motor milestone attainment to novel problem-solving tasks. In doing so, this work sheds light on the role of sensorimotor experience and biomechanical constraints in shaping motor development. More broadly, it contributes to theoretical debates about the flexibility of motor development, offering insights into the mechanisms that support adaptive behaviour in the developing motor system. particularly the dynamic interplay between imitation and self-guided exploration in learning.

Congenital upper limb differences encompass a wide range of anomalies affecting one or both arms, from fused digits to the complete absence of the hand and arm (Tonkin, 2017). These conditions are estimated to occur in approximately 19-27 out of every 10,000 live births, though prevalence rates vary across countries (Chan et al., 2022). At first glance, it may be assumed that the functional limitations associated with a partial or missing hand would negatively impact day-to-day activities, particularly those requiring fine motor manipulation or coordinated use of both hands. Consider a child unpacking her lunchbox; to do so she must unzip her bag, open a packet of crisps, and peel her banana, all of which involve distinct grips and coordinated two-handed actions. A child unable to perform a pincer grip in the affected limb(s) may therefore experience difficulties in completing such tasks. To overcome these challenges, children may turn to others for help or choose to avoid situations and activities that highlight their functional limitations (Franzblau et al., 2015; McDougall et al., 2021). However, growing evidence shows that these children adapt their motor behaviour to compensate for their reduced functionality, enabling them to complete bimanual tasks independently and without great difficulty. Consistent with the hypothesis that motor development is shaped by flexible adaptation to sensorimotor constraints, research shows that children with congenital upper limb differences develop remarkably functional motor skills (Ardon et al., 2014; Tucciarelli et al., 2024) and participate fully in society (Ardon et al., 2014; Bae et al., 2018; McDougall et al., 2021). For example, Ardon et al. (2014) found that children aged 10–14 with congenital upper limb differences actively incorporated their affected limb in bimanual tasks, demonstrating good coordination and functional use, as measured through both self-report and behavioural assessments. Similarly, Tucciarelli et al. (2024) found that children and adults with congenital upper limb differences frequently incorporated alternative body parts, such as the legs or feet, to achieve functional outcomes typically accomplished with the hands. These findings support the idea that adaptive motor strategies can emerge not only in the presence of typical structures, but also when those structures are absent, provided the system has opportunities for experience-driven learning.

Whilst some functional challenges may exist, the latter highlights the remarkable effectiveness of compensatory motor strategies. Almost all studies conclude that motor impairments associated with congenital upper limb differences are minor and do not affect day-to-day functioning. Relative to the general population, these children typically score within the normal range on functional (James et al., 2006), and social and emotional domains (Bae et al., 2018). However, existing evidence almost exclusively comes from self-report measures and fails to explore how these functional capabilities are achieved day-to-day. This thesis aims to experimentally assess the development of adaptive motor behaviours in children with upper limb differences to better understand how and when these compensatory strategies develop. Furthermore, as congenital upper limb differences have no known co- occurring cognitive impairments (Allen et al., 2024), they offer a unique opportunity to test foundational theories of motor development. Specifically, it allows us to test the idea that motor skill acquisition is not strictly biologically-driven, but rather shaped by sensorimotor experience (Adolph & Hoch, 2019). In line with this theory, functional outcomes can be achieved through multiple developmental pathways. That is, while children with upper limb differences may achieve similar motor outcomes as their two-handed peers, the developmental trajectory and strategies they use to reach those outcomes may be markedly different.

Based on this framework, we propose the following hypotheses, each addressed by one of four studies in this thesis. First, we hypothesise that children with upper limb differences will follow an altered path of early motor development, reaching gross motor milestones but later than their two-handed peers due to differences in motor exploration and complex balance constraints associated with asymmetrical limb lengths. Second, we hypothesise that these children will develop alternative motor strategies to complete everyday tasks by engaging a broader range of body parts to compensate for their missing functionality, while achieving comparable efficiency to their two-handed peers. Third, we hypothesise that children with upper limb differences will demonstrate a superior ability to solve novel problems. Given the rarity of their condition, they are less likely to encounter peers with similar functional differences to imitate and are therefore more likely to rely on self-guided exploration, an approach that may foster greater innovation and flexible problem-solving. Finally, we hypothesise that this reliance on self-guided exploration supports the development of more flexible internal models of how motor actions interact with the environment, enabling more efficient learning of novel motor mappings compared to their two-handed peers. Together, these studies aim to advance our understanding of how children with upper limb differences develop functional motor skills. By taking a multidimensional approach, this thesis contributes new empirical evidence to debates on motor learning and embodied cognition.

From biological maturation to dynamic systems: theoretical shifts in motor development

Motor control changes most rapidly during infancy. A newborn infant struggles to support their head, yet by 12 months most can crawl or walk independently, demonstrating a substantial increase in control over their body. Given these rapid and visible changes, it is unsurprising that early developmental researchers focused their attention on this period. The field was initially dominated by maturational theories, which framed motor development as a biologically predetermined process unfolding in universal, age-related stages (Gesell, 1928, 1946; McGraw, 1935, 1943). According to this theory, motor behaviours such as sitting or crawling are governed by maturation of the central nervous system, such that milestones emerge once the neuromuscular system has reached the appropriate developmental stage. For example, before a child can learn to crawl, they must first develop strength in their leg muscles and learn to coordinate antagonistic muscle pairs. Although early theorists did acknowledge individual variability in development, including different rates of milestone attainment, temporary regressions, and the use of alternative strategies, their framework largely obscured these differences, emphasising that all children progress through the same stages in the same sequence, largely independent of external influence.

First proposed nearly a century ago, this framework continues to influence clinical practice today, forming the foundation of motor milestones charts and standardised developmental assessments (Bayley, 2006; Squires & Bricker, 2009). Building on these foundations, the World Health Organisation (WHO) sought to standardise developmental norms further, facilitating early identification of developmental delays by defining standard windows of achievement for gross motor milestones. For example, healthy infants are expected to walk independently between 8.2 and 17.6 months (Who Multicentre Growth Reference Study & de Onis, 2006a). Children who fall outside of these windows flagged as atypical, reinforcing assumptions about a standard trajectory of development.

These assumptions are further supported by developmental neuroscience. Before an infant can control their movements, it is thought that they must first develop an internal sense of their own body. In adults, internal body representations are well documented through somatotopic mapping of the sensorimotor cortex, in which different body parts are represented to distinct, spatially organised areas of the brain (Penfield & Boldrey, 1937). Remarkably, similar somatotopic maps have been observed in infants (Cusack et al., 2024; Dall'Orso et al., 2018; Meltzoff et al., 2019). Meltzoff and colleagues (2019), found that two-month-old infants displayed distinct lateralised EEG responses to tactile stimulation of the hands, feet, and lips, despite having limited motor experience. Furthermore, fMRI studies revealed adult-like somatotopy in pre-term infants in response to stimulation of the wrists, ankles, and mouth (Dall'Orso et al., 2018). These findings reinforce the view that motor development has a strong biological basis.

In the first few weeks of life newborn infants elicit alternating leg movements reminiscent of walking if held in an upright standing position. Maturational theories call this a 'stepping reflex', claiming these movements are involuntary precursors to locomotion. In line with this theory, this reflex is repressed in early infancy to allow for neuromuscular maturation, supporting the later emergence of independent walking (McGraw, 1932). Electromyographic

(EMG) recordings of the leg muscles during newborn stepping revealed two patterns of neuromuscular control (Dominici et al., 2011). These same two patterns were identified in adult walking alongside two additional patterns thought to be acquired in the toddler phase. Despite the stepping reflex being repressed around 6 weeks after birth, these primitive patterns of neuromuscular control appear to be inbuilt and retained throughout development, providing further support for the idea that foundational motor patterns are biologically ingrained.

While maturational theories have provided key insights into the biological scaffolding of motor development, they also impose a rigid structure that cannot account for the variability observed in real-world settings. Over time, it became increasingly clear that biological maturation alone could not account for the complexity of motor development. In practice, children do not acquire motor skills in a uniform sequence, nor do they reach milestones at identical ages (Who Multicentre Growth Reference Study & de Onis, 2006a, 2006b). Variability in the environment, body type, and caregiving practices all impact how and when motor behaviours emerge. These observations prompted a theoretical shift away from biologically deterministic models toward frameworks that emphasise experience. The dynamic systems theory for example, proposes that motor behaviours arise from the interaction of multiple subsystems, including the central nervous system, biomechanics, cognition, and environmental context (Thelen, 1995; Thelen & Smith, 1994). In this view, motor development is not a fixed sequence, but a process shaped by the opportunities for action available to the child. This framework offers a more flexible account of development, arguably one that is well suited to explaining individual differences and alternative developmental pathways. Yet, while this flexibility has been demonstrated in response to cultural or environmental variability, it remains less clear how motor development adapts to more extreme biomechanical constraints, such as missing limbs. The following section explores the role of experience in shaping motor outcomes and sets the stage for investigating how children with upper limb differences learn to act in a world designed for two-hands,

The role of experience in shaping early motor development

The shift toward dynamic systems theories marked a renewed interest in how motor development unfolds in childhood. In this view, experience, whether derived from individual exploration, social scaffolding, or cultural caregiving practices, can shape both the timing and form of emerging motor skills. While infants may be born with a basic neural representation of the body (Cusack et al., 2024; Dall'Orso et al., 2018; Meltzoff et al., 2019), there is growing evidence to suggest that early mappings are actively shaped and refined by sensorimotor experience after birth (Marshall & Meltzoff, 2020; Rigato et al., 2014). For instance, biologically, infants are born with primitive patterns of neuromuscular control that underpin walking (Dominici et al., 2011). However, newly walking infants adopt immature gait patterns, take small unsteady steps, stand with wide stance, and fall frequently – their walking is far from adultlike (Adolph et al., 2018). So how do these early uncoordinated movements mature into smooth adult-like walking? Crucially, it is not age, but walking experience, measured in days, that best predicts walking skill in infancy (Adolph et al., 2003). These findings illustrate the pivotal role of experience in shaping motor control. Since the everyday experiences of infants vary widely, an experience-driven approach to motor development may offer a more compelling explanation for the unexplained variability in how and when children acquire their early motor milestones.

In the first year of life, infants lack independence and rely on their caregiver to meet their basic needs. As a result, childrearing practices can have a profound effect on early experience, impacting the frequency and type of opportunities to develop. Caregiving practices vary widely across cultures, and therefore typical developmental trajectories are likely to deviate from the 'one size fits all' approach. That being said, the developmental standards established by the WHO attempted to account for cross-cultural variability by recruiting families from six geographically diverse areas (Who Multicentre Growth Reference Study & de Onis, 2006a, 2006b). Despite finding moderate variability in the onset of key milestones between countries, data was pooled under the assumption that differences were a result of typical variation expected in healthy infants. However, the study omitted families in Central Asia and those using culturally specific childrearing practices. Therefore, it is unlikely the concluding windows of achievement represent the developmental trajectories of all children.

In rural China for example, infants are often placed in sandbags for toileting, restricting movement and delaying sitting (Mei, 1994). Similarly, in Tajikistan, infants' arms and legs are bound in a traditional gahvora cradle for up to 17 hours a day, delaying the onset of independent walking (Karasik et al., 2018, 2023). Even in Westernised societies, increased time spent in the supine position, stemming from safe sleep guidelines that recommend placing infants on their backs, has been associated with delays in gross motor milestones such as rolling, sitting, and crawling (Carson et al., 2022; Majnemer & Barr, 2006). However, in contrast, caregivers in Jamaica often engage in a formal handling routine from birth, comprising of passive stretching, massage, and active stepping interventions. These practices have been linked to earlier attainment of sitting and walking milestones compared to infants who are not exposed to this practice (Hopkins & Westra, 1990). Furthermore, the majority of Jamaican infants in the study skipped crawling altogether, potentially reflecting a cultural view that crawling is hazardous and thus discouraged. Whilst these studies are relatively small in comparison to the large cross-cultural study run by the WHO, they provide compelling evidence that early motor development is profoundly shaped by experience.

Crucially, these alternative trajectories are not necessarily atypical – just different, reflecting the child's unique interaction with their environment rather than a deviation from a fixed biological timeline. For example, even when motor experience is radically constrained, infants still achieve functional outcomes, albeit on a delayed timeline (Karasik et al., 2023). This suggests that development can emerge through different paths depending on available opportunities for movement and interaction. Children with congenital upper limb differences may represent an especially striking example of this principle. In their case it is not caregiving practices or cultural norms, but their own anatomy that shapes their sensorimotor experience. This raises critical questions about how they develop goal-directed adaptive motor behaviours despite missing key anatomical structures.

Experience-driven frameworks offer a more flexible account of motor development, one that accommodates the wide variation seen in how and when children achieve their motor milestones. Motor skills emerge through practice, adaptation, and feedback from the environment, rather than unfolding strictly according to biological maturation (Adolph & Hoch, 2019). This perspective is particularly important for understanding children whose biomechanical structures differ from the norm. For instance, crawling and walking have been shown to emerge significantly earlier in leaner, well-proportioned infants compared to those with higher body weight and muscle mass, suggesting that even subtle biomechanical differences can influence early motor development (Payne & Isaacs, 2024).

Children with congenital upper limb differences present a more pronounced case of biomechanical asymmetry. Their sensorimotor experiences are not only shaped by environmental factors but also by the altered affordances and constraints of their own bodies. This raises questions about how major structural differences affect opportunities for movement, balance, and exploration in early development, and how such children learn to navigate the world despite these constraints.

Goal-directed action and adaptive motor strategies

The emergence of motor control extends beyond achieving foundational motor skills such as sitting and walking. These foundational skills provide a platform for increasingly purposeful, goal-directed behaviours. Once infants can sit, reach, or walk, they begin to use these abilities in flexible and adaptive ways to explore, solve problems, and interact with their surroundings. Understanding how motor actions are planned and adjusted across development offers insights into the mechanisms that support motor flexibility and adaptation. These themes are especially relevant for children with congenital upper limb differences whose interactions are shaped by structural constraints that demand alternative yet functionally effective strategies for interacting with the world.

According to dynamic systems frameworks, goal-directed actions are driven by continuous interactions between the motor, visual, and cognitive systems (Fooken et al., 2023; Thelen & Smith, 1994). The visual system supports object identification and provides real-time feedback, while the cognitive system supports prospective planning, and the integration of sensory input. Through repeated interactions with their surroundings, infants gain critical experience that helps them to discover object properties and affordances, and adapt their movements based on feedback and error. Reaching is one of the earliest observable examples of such behaviour. By 18 weeks of age, infants begin to demonstrate predictive planning, successfully intercepting moving objects during their trajectory, rather than reacting to or chasing them (von Hofsten, 1980). This suggests that even in early infancy, motor actions are not random but are guided by perceptual and cognitive systems working together to achieve a goal. As motor control improves, infants begin to exhibit increasingly sophisticated motor planning tailored towards task demands. Between 5 and 7 months, they adjust their grasp based on the orientation of objects, reaching differently for vertical versus horizontal rods, even when visual input is occluded (McCarty et al., 2001). Similarly, by 10 months, infants modulate the speed of their actions based on task demands, slowing their movements when a task requires greater precision, such as pushing a ball into a narrow tube, versus throwing it into open space (Claxton et al., 2003). These examples highlight how sensorimotor experience leads to increasingly refined motor planning, such that even very young infants show evidence of flexible motor adaptation. However, these forms of online adjustment are distinct from the more advanced skill of end-state comfort, broadly defined as adopting an initially awkward grip to ensure a comfortable or useable end position (Rosenbaum et al., 1990). This phenomenon is considered a hallmark of prospective planning as it requires anticipating several steps ahead. Such planning contrasts with the habitual motor responses seen in younger children who often prioritise initial comfort over final efficacy (Comalli et al., 2016; Keen, 2011; Ossmy et al., 2022).

Interestingly, periods of developmental transition, such as the onset of walking, can temporarily disrupt previously established motor abilities. Around this time, infants often revert from unimanual reaching strategies back to bimanual (Corbetta & and Bojczyk, 2002), a behaviour that may reflect an adaptative response to immature postural constraints by stabilising the body while the new skill is perfected. Once balance improves, typically a few weeks after the onset of walking, adaptive reaching behaviours re-emerge. There are two interesting conclusions we can draw here. Firstly, the dynamic theory of motor development offers a compelling explanation for the non-linearity and variability observed in motor development; and secondly, motor flexibility is surprisingly present in early infancy, enabling infants to adjust their strategies in response to changing bodily or task demands. This early flexibility may be foundational for later motor adaption and is particularly relevant for children with upper limb differences, who must develop alternative strategies to achieve functional outcomes. For example, unequal limb lengths may impair balance or prevent the use of traditional hands-and-knees crawling. Understanding how and when these compensatory strategies emerge lies at the heart of this thesis.

Motor flexibility in typical development: Foundations for adaptation

This early flexibility lays the foundation for understanding how children refine their motor strategies throughout development. In line with the dynamic systems theory of motor development, motor behaviours are shaped by an end goal, however there is rarely a single path to achieving it. Instead, children explore multiple solutions in parallel, adapting to the constraints of their bodies, the task, and the environment (Adolph & Hoch, 2019). For example, when learning to crawl, infants often display wide variation in strategy. Rather than adopting traditional hands-and-knees crawling as described in the universal stages models, some infants 'army crawl' by pulling themselves along with their arms, others 'bear crawl' on hands and feet, and some remain seated, locomoting by 'bum- shuffling' (Franchak & Adolph, 2024). These strategies are not indicative of motor delay but reflect diverse solutions to a shared motor goal. Similarly, the emergence of independent walking is equally variable across children. To successfully maintain balance while functionally coordinating their limbs to produce forward motion, infants use different strategies shaped by their physical characteristics and energy levels (Snapp-Childs & Corbetta, 2009). Some infants 'twist' or rotate their torso to propel their leg forward, others take cautious 'stepping' movements using knee flexion, while those who are most unstable 'fall' forward, using momentum to initiate locomotion. Despite these differences in form, all strategies help to achieve independent locomotion.

Crucially, when infants acquire a new skill, they do not abandon old ones. Instead, they build a repertoire of motor strategies, that allow them to flexibly adapt to meet the demands of the everchanging environment. For example, a child who can walk might still choose to crawl when navigating a narrow tunnel, not because they can't walk, but because crawling is more efficient in that context. When faced with steep or slippery slopes, infants have been observed spontaneously exploring a range of solutions for getting down, including walking, crawling, and sliding down backwards, often replicating these strategies across multiple sessions (Adolph et al., 2010). These findings show that children are not rigidly bound to their most recently acquired skill but rather draw flexibly from earlier-learned strategies to adapt to any given situation. This idea is central to our hypothesis, which examines how children with upper limb differences acquire a unique repertoire of compensatory strategies and flexibly apply them across a range of contexts.

Together, these findings demonstrate that motor development in typically developing two-handed children is shaped by flexibility, adaptation, and the active selection of strategies based on task demands and environmental constraints. Rather than discarding older skills, children build a diverse motor repertoire that allows them to respond adaptively across contexts. These principles provide a critical foundation for the current work. We hypothesise that children with congenital upper limb differences will show this same adaptive flexibility, and perhaps even amplify it, as they must discover alternative solutions to everyday motor tasks from the outset of development. Their biomechanical variation may prompt earlier and more creative exploration of compensatory strategies, revealing how motor skills can emerge through novel developmental pathways shaped by experience, rather than constrained by biology.

Adaptive strategies in congenital upper limb differences

Children with congenital upper limb differences offer a powerful test case for experience-driven accounts of motor development. From birth, they must navigate goal-directed actions with unique biomechanical constraints, often without the typical anatomical structures presumed necessary for bimanual coordination. If motor skills emerge through practice, feedback, and adaptation, then we should see these principles at work, perhaps even more clearly, in children whose motor systems must compensate from the outset. Examining how these children develop effective, and often highly creative, strategies to achieve functional goals offers a valuable lens into how motor behaviours emerge, adapt, and generalise in the context of structural variation.

Every day we perform hundreds of tasks requiring bimanual coordination. For instance, to open a water bottle, an individual with two hands typically uses one hand to hold the bottle while using the other to turn the lid. Despite the absence or partial formation of one or both upper limbs, individuals with congenital upper limb differences often develop remarkably effective motor skills, achieving comparable functional outcomes through compensatory strategies (Hahamy et al., 2017; Tucciarelli et al., 2024). In studies simulating real-life tasks, such as removing a note from a wallet or wrapping a present, adults with a limb difference employed a broader range of effectors (e.g., lower limbs and mouth) compared to two-handed controls (Hahamy et al., 2017). These behaviours, known as compensatory strategies, involve adapting existing motor plans to incorporate available body parts or environmental supports in place of missing hand function. Returning to the bottle example, an individual with an upper limb difference may stabilise the bottle between their residual limb and torso or use their teeth to turn the lid.

While adults with upper limb differences often function with impressive ease, less is known about how and when these compensatory motor behaviours develop in childhood. The developmental literature in this area is limited and at times, contradictory. Some studies highlight difficulties with fine-motor skills: for example, over 50% of children in an interview-based study reported difficulties personal care such as dressing (Kelley et al., 2016), while other studies report an inverse pattern, identifying weaknesses in gross but not fine motor skills. Mano and colleagues (2018) found that while fine motor abilities appeared largely intact, children with upper limb differences exhibited weaknesses in gross motor tasks, particularly those requiring bilateral coordination. These difficulties presented after infancy and became more pronounced with age. The authors proposed that this could be due to later gross motor skills, such as riding a bike, requiring equal use of both hands/arms making adaptation more challenging than fine motor tasks, such as using scissors, which can be more easily adapted to one-handed strategies. A follow-up intervention study found that these weaknesses in gross motor skill significantly improved after 18 months of prosthetic and occupational therapy (Mano et al., 2020). Therapy sessions comprised of prosthesis training and practicing compensatory movements without the prosthesis. However, interpretation of these findings is limited by key methodological concerns. First, both the original and follow-up studies were based on small samples (9 and 10 children respectively), spanning a broad developmental window during which motor skills undergo significant change (0-6 years). Second, the absence of a control group in the intervention study makes it difficult to conclude whether improvements were due to therapy or general developmental progression. Third, improvements were seen regardless of prosthesis use, raising questions about whether the gains stemmed from prosthetic practice or from engagement with therapeutic motor challenges.

Contrasting these findings, a large-scale study assessing 489 children with unilateral upper limb differences found that children with and without prostheses scored within the normal or near-normal range across a series of validated self-report measures, targeting function, physical health, and socioemotional well-being (James et al., 2006). These findings suggest that prosthesis use may not be necessary for achieving good functional outcomes. While prosthesis use is minimal in this group, children with congenital upper limb differences adapt well and participate fully in society (Ardon et al., 2014; Bae et al., 2018; McDougall et al., 2021). We hypothesise that children with congenital upper limb differences will acquire functional motor strategies by adapting typical movement patterns to incorporate alternative effectors, such as the legs and feet. We further predict that these strategies will vary with age and task complexity, and that while they will differ from those used by their two-handed peers, they will be equally efficient.

Answering these questions is not only important for theoretical models of motor development but also has clear practical implications. Early identification of motor delays can be highly beneficial in driving early intervention, helping to optimise long-term functioning. Analogous research in Cerebral Palsy (CP), which is associated with severely impaired motor functioning in one or both arms, provides compelling evidence that targeted early intervention can substantially improve motor outcomes. During a 5-week intervention study, children with aged 6-11 years learned to use a series of new motor patterns, demonstrating motor quality improvements through faster, more direct movements, and increased elbow extension and shoulder flexion (Robert et al., 2013). Crucially, these motor improvements were retained at a 3-month follow-up and generalised to similar tasks. Despite children with CP often experiencing co-occurring cognitive impairments (Stadskleiv, 2020), their progress illustrates the plasticity of the motor systems and the substantial benefits of early intervention. However, direct comparisons between children with congenital upper limb differences and children with CP should be made with caution. The former group typically exhibit intact cognitive functioning (Allen et al., 2024), making them a particularly good test case for studying how sensorimotor experience and biomechanical constraints interact to shape motor development. Studying this population allows us to ask fundamental questions about the role of experience versus biology in motor development.

Neural bases of compensatory motor behaviour

These observable behavioural differences are supported by a growing body of research highlighting neural reorganisation. Congenital limb differences offer a unique opportunity to study the mechanisms of cortical plasticity, driven primarily by two factors: sensory deprivation and compensatory motor behaviour (Tucciarelli et al., 2024). In cases of complete congenital hand absence, the brain regions typically dedicated to hand function are deprived of sensory input and motor output. This raises the question: what becomes of these cortical areas which as in essence ‘freed up’?

Evidence is currently mixed. Some studies suggest that plasticity is primarily driven by neuroanatomical topography (Muret & Makin, 2021; Striem-Amit et al., 2018). For instance, five adults with a bilateral limb difference self-reported that they largely relied on their feet in everyday life, using them for up to 92% of tool use activities such as using kitchen utensils. Despite this, during an fMRI scan, movements of various body parts (hands, feet, shoulder, lips, abdomen)), the deprived area of the sensorimotor cortex was more strongly activated by body parts such as the lips and shoulder located topographically close to the hand region than by the feet - the effector which was used dexterously in everyday life to compensate for the missing hand (Striem-Amit et al., 2018). This finding suggests that, even when a more distant body part like the foot is used dexterously, the cortical reorganisation may still follow anatomical rather than compensatory use.

However, contrasting evidence supports the role of behavioural experience in shaping cortical reorganisation (Hahamy et al., 2017; Hahamy & Makin, 2019; Makin et al., 2013; Root et al., 2022; Stoeckel et al., 2009). For example, Makin et al., (2013) highlighted differences in compensatory strategies between adults with congenital and acquired upper limb differences. Congenital one-handers relied significantly more on their residual limb, whereas acquired amputees compensated primarily with their intact hand. Correspondingly, fMRI results showed that the deprived hand area was preferentially activated by the limb used most for compensation: the residual arm in congenital one-handers, and the intact hand in acquired amputees. These results provide evidence for experience-driven plasticity rather than topographical proximity. Two groups of individuals with different experiences of hand loss demonstrated different patterns of reorganisation in the deprived brain region dependent on the limb they are using to compensate for their missing hand. Compensatory behaviours however do not solely rely on the use of the upper limbs (Dempsey-Jones et al., 2019; Hahamy et al., 2017; Striem-Amit et al., 2018; Tucciarelli et al., 2024). Hahamy and colleagues (2017) further supported the notion of experience-driven plasticity finding that compared to two-handed controls, adults with congenital hand differences showed increased activation in the missing hand territory during movement of the residual arm (non-dominant arm for controls), lips, and feet. This suggests that cortical plasticity may reflect the functional repertoire of effectors engaged in compensatory motor strategies.

More recent findings complicate this picture, suggesting that topography is largely pre-determined, with early life experience subtly refining, rather than fundamentally reshaping neural structures (Tucciarelli et al., 2024). According to this view, the scope for reorganisation may be more constrained than previously thought, especially later in development. While experience plays a role, it may do so within the bounds of an already established network. These findings highlight the complexity of cortical plasticity in the face of deprivation. Crucially, understanding the interplay between plasticity and sensorimotor experience requires tracking how compensatory strategies evolve over time. By studying children with congenital upper limb differences across a broad developmental period, we can begin to evaluate how strategies are selected, refined, and consolidated into more stable motor patterns.

Mechanisms of learning: from imitation to self-guided exploration

A key factor shaping this developmental process is the learning mechanism through which children acquire new motor strategies. For most children, imitation plays a central role in learning(Tomasello, 1999). However, due to their unique biomechanical constraints and the rarity of their condition, children with upper limb differences have fewer opportunities to directly imitate the motor behaviours they observe in others. As a result, they are likely to depend on alternative learning mechanisms, particularly self-guided exploration, to discover effective solutions to everyday motor problems.

Humans are inherently social learners, acquiring knowledge through both direct instruction and passive observation of others (Csibra & Gergely, 2009; Tomasello, 1999; Tomasello et al., 2005). Unsurprisingly, when faced with a novel task, both adults and children prefer to observe a demonstration over trying to solve the task independently (Flynn et al., 2016; Rawlings, 2022), reflecting a general bias towards social learning. From an early age, imitation plays a fundamental role in development, functioning not only as a tool for instrumental learning, but also a powerful means of signalling social affiliation and conformity to group norms (Legare & Nielsen, 2015). However, when imitation is rigid or indiscriminate, it may constrain behavioural flexibility, limiting children's abilities to innovate novel solutions. For example, 3-5-year-old children switched to a less efficient method of solving a puzzle box after observing an adult using it, even though they had previously discovered a more efficient solution themselves (Davis et al., 2022). This illustrates the potential costs of over- imitation, particularly when the drive to affiliate overrides behavioural efficiency. For children with upper limb differences, who are often unable to directly replicate the motor actions of others, these constraints may be even more pronounced. They face a unique developmental challenge: do they imitate less because of their unique motor constraints, or do they persist in imitation at a cost to efficiency in order to maintain social alignment? We hypothesise that children with congenital upper limb differences will be less reliant on imitation when the observed motor solution is biomechanically unfeasible. However, we also expect that social pressure may lead some children to persist in ineffective imitation in tasks involving adult observation.

With age, two-handed children become increasingly selective imitators. By around 3 years, they prefer to copy familiar adults (Corriveau & Harris, 2009), and begin adapting their behaviour based on others' failures (Want & Harris, 2001). By age 4-5, children increasingly evaluate the reliability of models, favouring those who have provided an accurate source of information in the past (Corriveau & Harris, 2009), and rejecting demonstrated strategies when they are likely to fail (DiYanni & Kelemen, 2008). Yet, even when children can identify irrelevant or inefficient actions, many continue to reproduce them. Lyons and colleagues (2007) found that 2-4 year-old children imitated both relevant and irrelevant steps to retrieve an object, despite previously labelling some actions as 'silly'. These findings suggest that imitation may be used as a default, or safe, strategy in contexts of uncertainty. As children mature, they are increasingly likely to trust their own judgement, moving away from direct replication, instead adopting more flexible, innovative approaches to problem-solving. This developmental shift is further illustrated by Carr et al (2015), who examined children's responses to an adult model attempting to open a puzzle box with varying levels of success. In this study, children aged 4-9 were presented with a novel puzzle box containing a reward that could be accessed by using multiple strategies, entry points, and tools. Before attempting the task themselves, children observed an adult model attempt to retrieve the reward eight time systematically manipulated levels of success (0%, 25%, 50%, 100%). Despite allowing for creative problem-solving, 90% of children imitated the model on at least one of their attempts to retrieve the reward. However, from 6 years, children were increasingly likely to abandon the observed strategy in favour of more innovative, self-guided strategies, particularly as effectiveness decreased. Notably, children in the control condition, who received no demonstration, produced the greatest variety of solutions, highlighting how imitation of an inefficient model can constrain problem-solving abilities by anchoring children to an inefficient approach. These findings support the idea that while imitation is a powerful mechanism for learning, it can also limit the discovery of novel or efficient approaches.

While imitation provides a powerful means of acquiring knowledge from others, in situations where copying is unfeasible or ineffective, such as for children with congenital upper limb differences, exploration becomes a vital alternative for discovering successful motor solutions. From an early age, infants are intrinsically motivated to explore, and the dynamic nature of everyday environments provide rich opportunities for learning (Adolph & Hoch, 2019). While object manipulation in infants and toddler may appear aimless with no specific goal (Karasik et al., 2011), engaging in a variety of motor actions such as mouthing, squeezing, and rotating allows infants to gather information about the properties and possible functions of objects (Adolph et al., 2018; Bourgeois et al., 2005; Palmer, 1989; Rochat, 1989). Though seemingly unstructured, these interactions often lead to the accidental discoveries: that toys with wheels can be pushed, or that rattling sounds indicate something is inside. These early interactions are not only informative but also lay the groundwork for later, more purposeful goal-directed action.

Crucially, exploration is often guided by curiosity, structured by uncertainty, and shaped by feedback. Humans often seek to explore unfamiliar or novel options as these are the most advantageous for gathering information (Kidd & Hayden, 2015; Sutton & Barto, 2018). The benefit of exploration goes beyond what is discovered, to include how it is discovered. Unlike imitation, which provides a known solution, exploration encourages children to generate their own strategies by trying, failing, and refining. This process provides rich sensorimotor experiences that promote cognitive flexibility, motor creativity, and resilience. As Piaget (1945) emphasised, curiosity and play are crucial for actively gathering information through interactions with the environment. From this perspective, learning is not simply the internalisation of observed actions but the result of embodied experimentation, where the child's own activity drives discovery. Empirical work supports these ideas, showing that children who explored a novel toy without first observing a demonstration engaged in broader exploration, more varied play, and ultimately discovered more of the toy's functions (Bonawitz et al., 2011). In contrast, children who were shown how the toy worked tended to fixate on the demonstrated function, constraining their exploration. This suggests that while instruction can provide clarity, it may also constrain children's exploratory and innovative behaviours, particularly when the demonstrated solution is not optimal. Through self-guided exploration, children are more likely to engage in iterative, trial-and-error learning to optimise their behaviour (Adolph & Hoch, 2019; Sutton & Barto, 2018).

The capacity to flexibly toggle between imitation and innovation may be especially important for children with congenital upper limb differences, who are often physically unable to directly replicate many observed actions. Exploration is therefore essential for discovering effective ways to interact with the environment. The process of trying, failing, adjusting, and trying again provides rich sensorimotor feedback and fosters both problem- solving ability and creative adaptation. Rather than following a conventional process of motor skill acquisition, these children may instead discover 'what works' by experimenting with their own body and environment, using available limbs, postures, or external supports in novel and adaptive ways. By engaging in uncertainty and discovering solutions through self-guided exploration, these children may also have stronger internal models of motor control and become better equipped to adapt to new motor challenges. This process may not only support functional independence, but also a cognitive advantage in flexibility and adaptive motor learning. This raises two empirical questions: first, does every day, self-guided exploration enhance children's abilities to solve novel motor problems? Second, does it facilitate faster acquisition of alternative motor mappings compared to two-handed children? These questions speak to broader theories of learning, embodiment, and plasticity, and underscore the potential of exploration as a powerful driver of development. We hypothesise that children with upper limb differences will show a greater reliance on self-guided exploration to discover effective motor strategies, and that this reliance may support more flexible adaptation in novel problem-solving tasks compared to children with two hands.

Clinical relevance of tracking compensatory behaviours

Theoretical perspectives and experimental findings clearly demonstrate the value of exploration in fostering flexible and innovative motor behaviours. This may be especially relevant for children with congenital upper limb differences who must learn to navigate a world designed for two-handed people. In clinical contexts, the primary aim in supporting children with congenital upper limb differences is to maximise limb function. This may involve a combination of surgery, prosthetics, occupational therapy, and physiotherapy (Watson, 2000). Function is typically assessed using the International Classification of Functioning, Disability, and Health (World Health Organisation, 2001), which conceptualises functioning at three levels (1) body functions and structures, (2) activities, and (3) participation. Under this framework, a child with a limb difference has impaired body functions and structures. Consequently, impairments may arise in activities and participation. However, there is currently no universal assessment standardised for children with upper limb differences.

In practice, clinicians use a combination of self-report questionnaires and functional assessments to evaluate upper limb function. These typically focus on range of motion, dexterity, and grip and pinch strength (Buffart et al., 2006; Ho & Clarke, 2005; Kelley et al., 2016; Waljee et al., 2015), as weaknesses in these areas may impact a child's ability to perform everyday tasks. Among the most widely used self-report tools is the Pediatric Outcomes Data Collection Instrument (PODCI), administered to adolescent patients (11-21 years) and parents/caregivers of patients aged 2-21 years (Lerman et al., 2005). This questionnaire evaluates a broad range of domains including physical functioning, comfort and pain, happiness, and sports. It also takes into account the level of limb difference (e.g., above or below elbow), and prosthesis use. The PODCI, amongst others, is highly correlated with the Patient-Reported Outcome Measurement Information System (PROMIS; Waljee et al., 2015). The PROMIS is an alternative questionnaire similarly measuring the physical, mental, and social health, and correlates well with functional assessments of grip strength, key pinch strength, and dexterity.

Buffart and colleagues (2006) reviewed commonly used functional and self-report assessments of motor function to determine which were most suitable for children with congenital upper limb differences. They identified the Assisting Hand Assessment (AHA) and Unilateral Below Elbow Test (UBET) as the most appropriate functional tests, and the Prosthetic Upper limb Functional Index (PUFI) and the ABILHAND-Kids as the most appropriate self- report measures. These assessments were selected based on clinical 'usefulness' defined as a) representative of bimanual daily activities to ensure the assessment captures what the child can do with their affected limb, b) quality of movement and difficulty with performance, and c) attractive to children. However, Buffart et al (2006) acknowledged that for any assessment to become a 'gold standard', further validation is needed, particularly regarding reliability, sensitivity to change, and validity for both children and congenital conditions.

The AHA uses bimanual play to functionally assess how children with a unilateral upper limb difference collaboratively use their affected and unaffected arms (Cordray et al., 2025;

Krumlinde-Sundholm et al., 2007). For younger children (18 months-5 years), the assessment centres around free play, while for older children (6-12) years, the same toys are used to play an adventure-themed board game. The UBET evaluates limb function in a slightly more nuanced way, using two scales: 'Completion of Task' and 'Method of Use' across 9 bimanual activities, adapted for age (2-21 years) and prosthetic use (Bagley et al., 2006; Bagley & James, 2004). However, while both the AHA and UBET functionally assess bimanual play, their primary focus lies in evaluating whether children can complete typically bimanual tasks and the extent to which they incorporate their affected limb. These assessments, however, do not capture how children adapt their motor strategies through the use of other body parts or indeed how efficient these motor behaviours are compared to their two-handed peers. This leaves a gap in understanding the qualitative nature of task performance and the broader compensatory mechanisms children employ to achieve functional goals.

In parallel, self-report measures present their own challenges. There is often a notable discrepancy between child and parent reports, with children typically reporting better functional outcomes, increased happiness, and better quality of life (Ardon et al., 2012, 2014; Sheffler et al., 2009). Perceived functional difficulties and quality of life are ground in lived experience, therefore the child's own perspective may be of greater clinical relevance. The PUFI assesses prosthesis use in daily life, comparing performance on a series of activities with and without a prosthesis (Wright et al., 2001; Wright et al., 2003), while the ABILHANDS-Kids questionnaire assesses manual ability across 21 everyday activities, scored as easy, difficult, or impossible based on the parent's assessment (Arnould et al., 2004). However, these self-report tools typically assess what children can and cannot do, rather than how they complete tasks.

The present research seeks to address the gaps in this literature, investigating *how* children learn to adapt to their limb difference in real time. Crucially, patient- and parent-reported outcomes such as the PUFI have not been validated for use in children with a congenital upper limb difference, and do not assess all domains outlined in the International Classification of Functioning, Disability, and Health (Adkinson et al., 2015; World Health Organisation, 2001).

Motor learning and adaptation in children with congenital upper limb differences: A multi-method approach

To address these gaps, the current research project adopts a multi-method developmental approach to investigate how children with congenital upper limb differences acquire, refine, and adapt motor strategies across different contexts. First, we examine retrospective motor milestone data to assess whether early motor development follows a typical or delayed trajectory in this population. Second, we observe how children aged 3–9 perform semi-ecological bimanual tasks, allowing us to identify specific compensatory strategies (e.g., use of legs, feet, mouth) and track changes in efficiency and strategy use with age. Third, we use problem-solving and overimitation paradigms to assess whether children with limb differences are more likely to innovate due to biomechanical constraints, or whether imitation is retained as a strategy for social affiliation. Finally, we use a visuomotor adaptation task to determine whether children with upper limb differences exhibit greater flexibility in updating motor plans in response to unexpected outcomes. Together, these studies aim to reveal the developmental mechanisms underlying functional adaptation and the potential cognitive advantages that may arise from sensorimotor constraint.

Across these studies, we test the overarching hypothesis that motor development is not solely biologically determined, but shaped through the dynamic interplay of sensorimotor experience, environmental feedback, and social learning. By examining how children with anatomical constraints develop functional, flexible, and creative motor behaviours, we aim to reveal how alternative developmental pathways can support and even enhance adaptation. The central theme of this research is that biomechanical constraints do not limit motor potential, but instead foster the emergence of novel, experience-driven strategies that illuminate the fundamental flexibility of the developing motor system.

Chapter 2: Developmental trajectories of gross motor milestones in children with congenital upper limb differences

Abstract

Aim: To examine whether gross motor milestone attainment in children with congenital upper limb differences diverges from the typical developmental trajectory observed in two-handed children. *Method:* Parents and caregivers of 84 children with unilateral congenital upper limb differences (*M* = 4.01 years) and 154 two-handed controls (*M* = 3.49 years), completed a retrospective survey reporting the age their child achieved six key gross motor milestones: sitting, crawling, standing with support, standing independently, walking with support, and walking independently. *Results*: Children with upper limb differences showed modest delays of 2-4 weeks in sitting independently (p = .005), standing with support (p = .001), and standing independently (p = .005), and 5-6 weeks in walking with support (p < .001) and walking independently (p = .002), relative to two-handed controls. No significant delay was observed in traditional hands-and-knees crawling (p = .875, BF_{10} = .20), though only 51% used this method, compared to 84% of two-handed children. Use of alternative crawling strategies, such as commando crawling or bum-shuffling, did not influence the age of walking onset (p = .285, BF_{10} = .41). *Interpretation:* Despite modest delays in gross motor milestones, children with a unilateral congenital upper limb difference followed a broadly typical developmental trajectory. While body form influences *how* milestones are achieved, the sequence and timing remain relatively consistent, highlighting the adaptability of early motor development.

Introduction

Congenital limb differences affect approximately 1,800 babies in the UK each year, with presentations ranging from minor abnormalities to the complete absence of a limb (*NCARDRS Congenital Anomaly Statistics*, 2021). While some differences are identified prenatally, around 63% are first diagnosed at birth, often prompting significant concerns among parents and caregivers, particularly regarding their child's future independence and physical development (Mason, 1991; *NCARDRS Congenital Anomaly Statistics*, 2021). A limited understanding of how limb differences impact development, results in insufficient guidance and support for parents, leaving many questions unanswered (Clelland et al., 2024). This study aims to address some of these uncertainties by retrospectively investigating the attainment of early gross motor milestones in children with congenital upper limb differences, providing valuable insights for both healthcare professionals and affected families.

Traditional theories of infant motor development have long attributed the acquisition of gross motor milestones to a process of biological maturation. These theories suggest that infants progress through a series of universal, age-related stages determined by neuromuscular development, beginning with symmetrical flexing of the arms and legs at one week old and culminating with independent walking at approximately 60 weeks (Gesell, 1946). While this approach acknowledges that children develop at different rates and may adopt alternative strategies, it largely obscures the variability in development. Contemporary theorists challenge this view by emphasising the flexibility of motor development. They argue that motor behaviour is not solely the result of biological maturation, but also shaped by body morphology and everyday experiences (Adolph & Hoch, 2019). With no known associated cognitive impairments (Allen et al., 2024), congenital limb differences offer a unique opportunity to explore how body form influences motor development. This will expand our understanding of the flexibility of motor development and provide valuable practical insight into the typical developmental trajectories of children with upper limb differences. In this study, we focus on gross motor milestones as they are foundational for independent daily living and play a critical role in cognitive development by facilitating exploration and interaction with the environment, thereby creating new opportunities for learning (Kretch et al., 2014).

Children with congenital upper limb differences are typically offered a combination of surgery, prosthetics, and physical therapy to help maximise upper limb functioning and equalise limb length (Watson, 2000). However, prosthetics are frequently rejected due to discomfort and the inhibition of sensory feedback (Biddiss & Chau, 2007). Therefore, in practice, differences in limb length remain during infancy and the early years. Given this context, there are several reasons to believe that gross motor milestones may be delayed in this population. Firstly, we note that these individuals tend to develop alternative motor strategies, using other body parts to compensate for their limb difference – for example using the legs or feet to stabilise or manipulate objects (Hahamy et al., 2017; Stoeckel et al., 2009; Tucciarelli et al., 2024). This alternative use of the lower limbs may delay walking in favour of crawling, allowing the child to flexibly switch between using the leg for stabilising objects and for transport. Secondly, the unilateral absence of a limb can impact posture and balance, potentially hindering the child's ability to maintain a steady posture during sitting, standing, or walking.

We therefore hypothesise that sitting, standing, and walking milestones will emerge later in children with upper limb differences, with progressively longer delays as balance requirements increase, resulting in the greatest delay in walking independently. This aligns with the pattern of milestone attainment in neurodevelopmental conditions such as autism and developmental coordination disorder, where early motor delays tend to increase in magnitude with age (Bowler et al., 2024). Furthermore, given the wide variation in the type of limb difference, we hypothesise that the age of attainment will be more variable in children with a limb difference compared to two-handed controls. Finally, the absence of a limb can have direct physical consequences for crawling, in terms of removing the ability to spread pressure across the two hands and creates unequal lengths of the front two limbs. Due to these physical differences, we hypothesise that children with upper limb differences will primarily employ alternative crawling strategies, and those who do achieve traditional hands-and-knees crawling will do so later than their two-handed peers.

The present study investigates whether the attainment of gross motor milestones in children with upper limb differences diverges from the developmental trajectory of two-handed children, using the World Health Organization's (WHO) standards of typical motor development for reference (Who Multicentre Growth Reference Study & de Onis, 2006b). To do this, we collected retrospective reports of milestone attainment – a method that has been widely used in developmental research (Karasik & Robinson, 2022; Matsubara et al., 2022). We focus on six key gross motor milestones: sitting independently, crawling, standing with support, standing independently, walking with support, and walking independently. These milestones play a crucial role in broader developmental cascades, having been linked to perceptual, cognitive, and social development (Adolph & Hoch, 2019).

Although these standards provide a useful framework for understanding typical developmental progress, it is important to acknowledge that they may not fully capture the diversity of milestone attainment (Karasik & Robinson, 2022; Keller, 2017; Matsubara et al., 2022). Even within the WHO's own internationally sampled cohort, notable site-specific variability was observed in attainment (Who Multicentre Growth Reference Study & de Onis, 2006a). As such, while these standards offer a valuable global benchmark, they are best interpreted as a guide rather than a strict developmental progression. For this reason, and due to methodological differences, the WHO data was not used as a direct comparison group in this study. The WHO data was collected prospectively under highly standardised conditions, with stringent inclusion criteria related to nutrition, health, and caregiving practices that differ markedly from those in our sample. Moreover, the WHO data does not include a UK cohort. To ensure consistency within our retrospective approach, children with upper limb differences were therefore compared to a group of two-handed children whose data were collected using the same methods.

Method

Participants

We recruited parents and caregivers of 245 children to complete a retrospective milestones questionnaire. Inclusion criteria specified that all children were born at or after 35 weeks gestation and were 8 years old or younger at the time of participation. To ensure a focused analysis of the effects of upper limb differences, five children were excluded due to lower limb differences or neurodevelopmental conditions such as autism and global developmental delay. The final sample consisted of 86 children with a congenital upper limb difference (M = 4.01 years, SD = 2.26) and 154 age-matched two-handed controls (M = 3.49 years, SD = 2.18; BF_{10}.21). Subsequent analyses confirmed that children born between 35- and 36-weeks gestation did not affect the age of milestone attainment (Appendix A).

Parents and caregivers of children with congenital upper limb differences were recruited through two UK-based charities and one US-based charity that support children with limb differences and their families. All children in this sample had one unaffected hand with no visible limb difference. Among them, 81 lacked a pincer grip on the affected side, 37 had a difference affecting the right arm, and 70 had a below-elbow difference. The specific details of limb differences were self-reported by parents and caregivers, with 36% of reports validated by the researcher during in-person meetings. While not all children had received definitive clinical diagnoses, 40% had been formally diagnosed by multidisciplinary hand and upper limb services. Reported diagnoses included symbrachydactyly, radial dysplasia, ulna aplasia, complex congenital hand anomaly, amniotic band syndrome, transverse arrest, radial hypoplasia, congenital amelia, and oligodactyly. Regarding prosthesis use, 73 children had never been fitted with or did not wear a prosthesis, 8 used a prosthesis monthly, and 5 used it weekly. Among those who used a prosthesis, 5 reported using it only for specific tasks, such as riding a bike.

Two-handed control children were recruited through an existing university database of volunteer families and an affiliated Facebook page. Of the 154 children, 79 were right-handed, 12 were left-handed, and 63 showed no clear hand dominance. This distribution is consistent with the expected pattern of handedness development observed in infancy and early childhood (Michel et al., 2013).

This study was approved by the ethics committee at Durham University (PSYCH-2019-08- 30T10_08_45-mnvj24).

Survey Instrument

Parents and caregivers completed a survey retrospectively detailing the age, in months, at which their child first achieved six gross motor milestones: sitting independently, crawling, standing with support, standing independently, walking with support, and walking independently. To enhance accuracy in recalling the age of milestone attainment, parents and caregivers were encouraged to consult baby books, photos, videos, and notable events such as seasonal holidays and birthdays (Adolph et al., 2011). Data collection primarily occurred online, supplemented by approximately 30 participants from each group who completed the surveys in person. Data from milestones that had not yet been attained, or for which the age of attainment could not be confirmed, were excluded from the analysis.

Statistical analysis

Milestone attainment in two-handed children compared to WHO standards

To evaluate whether our sample of two-handed children aligned with internationally accepted benchmarks of development, we conducted a comparative analysis against the WHO's standard windows of achievement (Who Multicentre Growth Reference Study & de Onis, 2006b). The WHO provides globally recognized standards that reflect the expected developmental progression for gross motor milestones, thereby serving as a reference for our retrospective approach, although there is also significant national variation (Who Multicentre Growth Reference Study & de Onis, 2006a).

For each milestone, we first calculated the percentage of children in our sample who attained the milestones by the 99^{th} percentile of the WHO standard window of achievement. By comparing milestone attainment in our sample to the upper limit of the WHO-defined achievement window, we were able to assess the typicality of our sample, which was crucial for validating subsequent analyses measuring motor delays in children with upper limb differences. To assess with more granularity how well the distribution of milestone attainment in our two-handed sample aligned with the WHO standards, we conducted chi-square goodness of fit tests for each milestone. Specifically, we compared the number of children in our sample who achieved the milestone by the 50th percentile of the WHO standard to the expected number based on the WHO distribution.

Milestone attainment in children with upper limb differences

To evaluate whether children with upper limb differences experience significant delays in developmental milestone progression, we performed Mann-Whitney U tests comparing the age at which they attained key gross motor milestones with that of children in our two-handed sample. This non-parametric test was chosen because the data did not follow a normal distribution.

We then compared the variability of milestone attainment between the groups. To assess whether there were significant differences in variability, we used Levene's test for equality of variances. This test allowed us to determine whether the dispersion of milestone attainment was significantly different between children with upper limb differences and their two-handed peers.

As milestone attainment ages being were reported in months, there was substantial overlap in age ranges across milestones, limiting the precision of longitudinal comparisons. However, to explore differences in the sequencing of milestone attainment between groups, we first inspected the mean age of attainment for each milestone. Based on these observations, we conducted Wilcoxon signed-rank tests to examine whether children with upper limb difference and their two-handed peers differed in the order of achieving two closely related milestones – stand independently and walk with support.

Finally, chi-square analyses were conducted to identify whether there were significant differences in the types of crawling strategies employed by children with upper limb differences compared to two-handed children, and whether these strategies impacted the attainment of independent walking. Parents reported that one child with a limb difference had not yet achieved crawling at the time of participation, and 15 children (3 one-handers, 12 two-handers) skipped crawling entirely, with no differences in this non-crawling proportion between the groups (χ^2 (1, N = 240) = 1.74, p=.187). These 'non-crawlers' were not included in these analyses. Importantly, skipping crawling is not uncommon in typical development: crawling was in fact recently removed from the Centre for Disease Control's developmental milestones checklist in part due to a inconsistencies in what constitutes crawling, high variability in attainment, and evidence suggesting that not all typically developing children crawl (Kretch et al., 2022).

Results

Milestone attainment in two-handed children compared to WHO standards

The majority of children in our two-handed sample achieved their milestones by the 99th percentile of the standard windows of achievement outlined by the WHO (Figure 2.1). Specifically, the percentage of children who met their milestones within the expected timeframe were as follows: sit independently (99%), stand with support (95%), crawl on hands and knees (100%), walk with support (96%), stand independently (99%), and walk independently (97%). This close alignment with the WHO's globally recognised benchmarks for typical milestone attainment (Who Multicentre Growth Reference Study & de Onis, 2006b) suggests that milestone attainment in our two-handed sample is largely typical, and supports the validity of our retrospective approach to measuring motor milestones.

Comparing milestone attainment at the 50th percentile of the WHO's expected distribution (Figure 2.1) revealed that around this midpoint, the distribution of our sample was similar to the WHO sample for two milestones: sit independently ($\chi^2(1, N = 153) = 2.36$, $p = .125$, $BF_{10} = 0.33$) and stand independently ($\chi^2(1, N = 154) = 1.27$, $p = .259$, $BF_{10} = 0.19$). However, around this age, compared with WHO significantly more children in our sample could crawl on hands and knees ($\chi^2(1, N = 118) = 5.73$, $p = .017$, $BF_{10} = 2.01$) and walk independently ($\chi^2(1, N = 147) = 4.25$, $p = .039$, $BF_{10} = 0.86$); while fewer children could stand with support ($\chi^2(1, N = 154) = 14.96$, $p < .001$, $BF_{10} = 192.14$) and walk with support ($\chi^2(1, N = 154) = 5.84$, $p = .016$, $BF_{10} = 1.87$).

Our two-handed sample, therefore, largely achieved their milestones within the WHO's benchmark of typical development. The two later-reported milestones in our sample were those where a skill is performed with support — stand with support and walk with support. These may be particularly prone to subjective interpretation by parents or caregivers, and are known to be prone to most national variation (Who Multicentre Growth Reference Study & de Onis, 2006a). In contrast, the accelerated distribution of crawling and independent walking in our two-handed sample compared to the WHO norms may be attributed to the recent emphasis on tummy time and the growing focus on limiting use of baby containers such as bouncers and walkers, which have been shown to negatively impact developmental milestones (Alghamdi et al., 2024; Hewitt et al., 2020; Kretch et al., 2022). These minor discrepancies, while similar to previous measured variations from the globally-sampled WHO norms (Who Multicentre Growth Reference Study & de Onis, 2006a), underline the importance of comparing our one-handed sample to a two-handed sample measured within the same cultural, national population and the same retrospective approach, rather than directly to WHO norms.

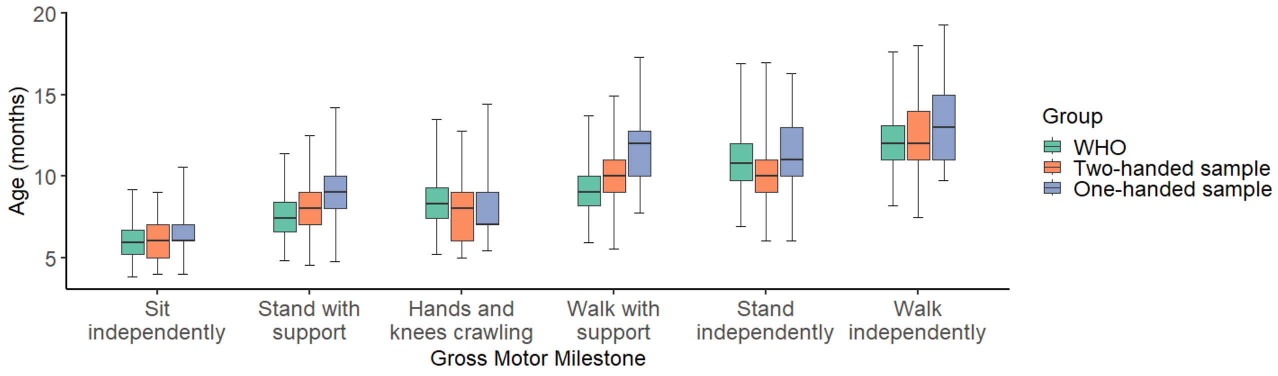


Figure 2.1. Windows of milestone achievement expressed in months bounded by 1st and 99th percentiles for WHO normative data, our sample of two-handed children, and our sample of children with congenital upper limb differences. Box plots also display the 50th percentile for each group.

Milestone attainment in children with upper limb differences

In line with our hypotheses, motor milestones emerged significantly later in children with limb differences. Except for hands-and-knees crawling (W = 2379.00, p =.875, BF_{10} = .20), the results revealed significant delays in the age of attainment for all milestones: sit independently (W = 7635.50, p = .005), stand with support (W = 7632.00, p = .001), walk with support (W = 7828.00, p < .001), stand independently (W = 6903.00, p = .005), and walk independently (W = 6899.00, p = .002). The magnitude of delay was <1 month for all sitting and standing milestones, and >1 month for walking milestones (Table 2.1).

Table 2.1. Average age of attainment for six gross motor milestones in our sample of two-handed children and children with upper limb differences

	Two-handed sample		**One-handed sample**		**Difference score (months)**
	N	**Mean (SD)**	**N**	**Mean (SD)**	
Sit independently	153	5.83 (1.18)	82	6.37 (1.40)	0.54
Stand with support	154	8.26 (1.74)	79	9.16 (2.08)	0.90
Hands-and-knees crawling	118	7.94 (1.84)	41	8.05 (2.17)	0.11
Walk with support	154	10.09 (1.92)	74	11.57 (2.29)	1.48
Stand independently	154	10.52 (2.04)	73	11.32 (2.40)	0.80
Walk independently	147	12.30 (2.14)	75	13.49 (2.62)	1.19

Variability in milestone attainment

The windows of achievement for six gross motor milestones for both participant groups are depicted in Figure 1. Contrary to our hypothesis, Levene's tests showed that, for most milestones, the age of attainment for children with an upper limb difference was not significantly more variable than for two-handed children: sit independently (F(1, 233) = .46, p = .498), stand with support (F(1, 231) = 3.30, p = .071), traditional crawling (F(1, 157) = 0.36, p = .549), walk with support (F(1, 226) = 3.04, p = .082), and stand independently (F(1, 225) = 3.05, p = .082). Children with upper limb differences did, however, exhibit significantly higher variability in the age at which they learned to walk independently (F(1, 220) = 4.17, p = .042), with a variance of 6.84 (SD = 2.62), compared to a variance of 4.57 (SD = 2.14) in their two-handed peers.

For both groups of participants, the narrowest window was observed for sitting independently (one-handed children: 9 months, two-handed children: 6 months). Wider windows were observed for all other milestones, with attainment varying between 9 and 13 months.

Sequence of attainment

A detailed longitudinal analysis was difficult because milestones were reported in months, not days, meaning some milestones overlapped (e.g., standing with support and crawling). However, the average ages of attainment indicated a difference in the sequence of milestones for children with upper limb differences and their two-handed peers, particularly for walking with support and standing independently (Table 2.1). To examine this specific difference, two Wilcoxon signed-rank tests were conducted on the respective milestones. The results revealed that children with upper limb differences tend to stand independently before walking with support (W = 655.00, p = .025), while two-handed children typically walk with support before standing independently (W = 1516.00, p = .001), Figure 2.2. However, given the later age of attainment for milestones 'with support' identified between the WHO standards and our two-handed sample, this finding must be interpreted with some caution.

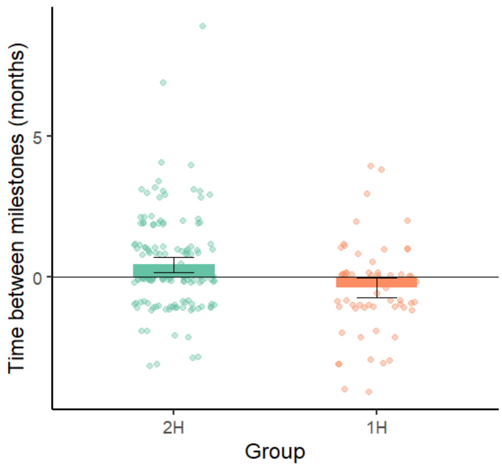


Figure 2.2. Mean difference in months between standing independently and walking with support milestones for children with two hands and children with upper limb differences. Error bars represent 95% confidence intervals.

Crawling strategies

While traditional hands-and-knees crawling emerged around the same time in children with upper limb differences and two-handed controls, a notable difference in crawling strategies was observed between the two groups. Only 51% of children with an upper limb difference employed hands-and-knees crawling, compared to 84% of two-handers (Figure 2.3). Chi-square analyses confirmed that significantly fewer children with an upper limb difference crawled on their hands and knees compared to two-handed controls ($\chi^2(1, N = 224) = 27.30$, $p < .001$). Instead, children with upper limb differences exhibited more varied crawling strategies. The two most common strategies were commando crawling and bum shuffling, both of which had a higher prevalence in children with an upper limb difference (26% and 22%, respectively) than in two-handers (10% and 4%, respectively). Chi-square analyses further confirmed that children with upper limb differences were significantly more likely to employ these alternative strategies compared to two-handed controls (commando crawl: $\chi^2(1, N = 224) = 9.78$, $p = .002$; bum shuffle: $\chi^2(1, N = 224) = 17.07$, $p < .001$). Parents reported that five children (1 one-hander, 4 two-handers) crawled in an alternative way not listed (e.g., bear crawl).

A Chi-square analysis was conducted to assess whether crawling strategies were associated with the type of limb difference in children born with one hand. Results indicated that 81% of children with an above-elbow limb difference (13/16) used alternative crawling strategies (any method other than hand-and-knees crawling), compared with 41% of the subsample of 66 children with a below elbow difference. This difference was statistically significant (χ^2 (1) = 8.39, p = .004).

Further analyses confirmed no significant difference in the age of attainment of crawling based on strategy (W = 765.00, p = .467, BF_{10} = .27), indicating that alternative crawling methods such as commando crawling and bum-shuffling (M = 8.37, SD = .35) emerged around the same time as traditional hands-and-knees crawling (M = 8.05, SD = .34) in children with an upper limb difference. Further, alternative crawling methods did not affect the age at which children born with an upper limb difference walked independently: a Mann-Whitney U test revealed no significant difference in walking age across crawling methods (W = 553.00, p = .285, BF_{10} = .41).

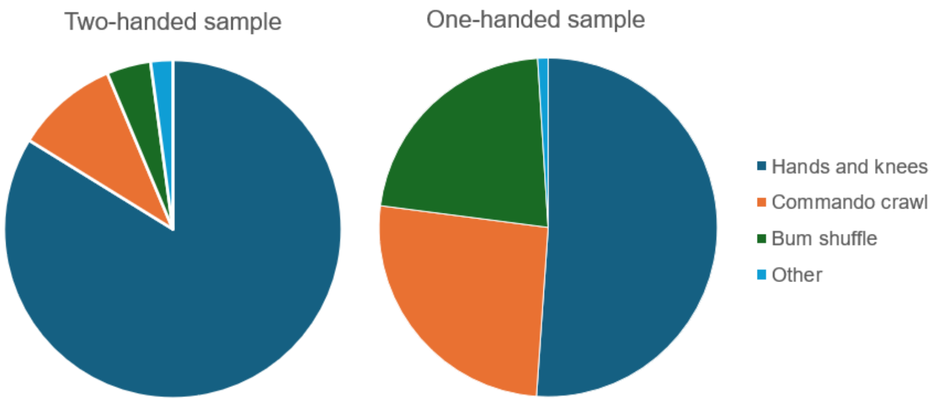


Figure 2.3. Proportion of crawling strategies in our sample of two-handed children and children with upper limb differences

Discussion

This study investigated the attainment of early gross motor milestones in children with congenital upper limb differences, with the aim of addressing common concerns among parents and caregivers regarding their child's physical development and exploring the broader influence of body form on early motor skill acquisition. As hypothesised, children with upper limb differences experienced delays in milestones such as independent sitting, standing, and walking compared to their two-handed peers. However, contrary to our expectations, the magnitude of these delays was relatively modest, and, except for independent walking, variability in milestone attainment was largely comparable across groups.

Children with upper limb differences experienced delays of 2-4 weeks for sitting and standing milestones, and 5-6 weeks for walking milestones. These differential delays likely reflect the increasing postural and balance demands of later-developing skills. Sitting and standing primarily rely on core stability and the capacity to shift weight while maintaining a stable base, whereas walking requires a more complex interplay of bilateral coordination, dynamic balance, and the ability to maintain an upright posture with a single point of contact with the floor during alternating leg movements (Adolph et al., 2011). From a systems perspective, this increasing complexity of skill integration arguably makes these milestones more vulnerable to disruption by structural variation. Crucially, however, these delays are relatively short, which may offer reassurance to caregivers, who often expect more pronounced delays due to the visible nature of their child's limb difference.

Interestingly, upper limb differences indirectly affected milestones traditionally associated with the lower limbs, such as standing and walking. A limited capacity to grasp objects for support combined with unequal limb lengths which introduces asymmetries in body weight distribution, may potentially reduce stability during transitional movements such as pulling to stand or cruising. Consequently, these children may need more time to develop the sufficient balance and postural control necessary for upright movement.

This pattern of milestone attainment, characterised by delays of increasing magnitude, mirrors that seen in children with neurodevelopmental conditions, in which later milestones, such as walking, often show more pronounced delays relative to typical motor trajectories (Bowler et al., 2024). However, the delays observed in children with upper limb differences were considerably shorter than those typically observed in motor disorders such as developmental coordination disorder, in which walking may not be achieved until approximately 16 months—2 to 3 months later than the average child with an upper limb difference. These findings suggest that milestone attainment in children with upper limb differences more closely resembles typical developmental trajectories than the more pronounced delays characteristic of neurodevelopmental conditions.

One of the most striking findings was that crawling was less impacted by upper limb differences than any other milestone. Despite its reliance on all four limbs for balance and propulsion (Adolph et al., 1998), children with upper limb differences did not show significant delays in the onset of traditional hands-and-knees crawling. This may be due to the inherent stability provided by four points of contact with the floor, enabling children with upper limb differences to maintain a stable base despite unequal limb lengths. Nevertheless, nearly half of the children with upper limb differences adopted alternative movement strategies, such as commando crawling or bum shuffling. These adaptations, particularly common in those with above-elbow differences, highlight the flexibility of motor planning in response to structural constraints.

Rather than fundamentally altering developmental pathways, upper limb differences appear to influence *how*, rather than *when*, milestones are reached. Children in our sample employed a range of strategies to navigate their environment, yet all ultimately reached independent walking within a similar timeframe. These findings align with the dynamic systems theory, which posits that multiple pathways, driven by the interactions between the individual, task, and environment, can lead to the same functional outcomes (Cole & Adolph, 2023; Thelen, 1995).

We also observed a slight variation in the sequence of milestone attainment. While two-handed children typically walked with support before standing independently, children with upper limb differences more commonly achieved these in reverse. This further points to difficulties balancing on one leg and using the arms for support, making unsupported standing more accessible than supported walking. Importantly, such variations in sequence did not disrupt developmental progression; instead, they demonstrate how motor development is constrained in its endpoints but allows for flexible strategies and sequences along the way.

This view of constrained yet adaptable development is supported by findings from research on children raised in constrained environments, such as those bound in the gahvora cradle for up to 20 hours a day. Though these children show delays in early milestones, they attain comparable motor skills to their peers by 4-5 years (Karasik et al., 2023). This demonstrates how extreme early experiences can affect the timing of milestone attainment but do not hinder long-term development. In comparison, upper limb differences—though impactful—are less extreme. In these children, delays in milestone attainment often reflect the need for adaptive strategies or additional time to build foundational skills, rather than disruptions in developmental progression.

Our findings should be interpreted in light of several limitations. The reversal in milestone order whereby standing independently emerged before walking with support in children with upper limb differences may reflect true variation, but also the limitations of retrospective reporting and milestone criteria. Our two-handed sample, while within WHO windows, showed different distributions in attainment from the WHO windows of achievement, potentially due to measurement criteria. Furthermore, the retrospective reporting of milestones may be prone to parental bias and recall error. Longitudinal studies with fine-grained tracking of milestone in days rather than weeks would offer clearer insights into the nuances of individual developmental trajectories. Further work is also needed to explore how specific characteristics of limb differences, specifically the presence of bilateral limb malformations influence both the timing of milestone attainment and the selection of motor strategies. Such work would enhance our understanding of the mechanisms through which structural differences shape developmental pathways and provide guidance for families that reflects the range of adaptive pathways children may follow.

In summary, while children with upper limb differences show modest delays in the attainment of key motor milestones, their overall developmental trajectory remains broadly intact. These findings underscore the adaptability of the developing motor system: individual factors such as body form shape *how* milestones are achieved, but the sequence and endpoints of development remain remarkably consistent (Adolph & Robinson, 2015). Children with upper limb differences may require more time to develop specific skills, such as balancing on one leg or maintaining an upright posture without using their arms for support, but they ultimately reach the same developmental endpoints as their two-handed peers. By better understanding both the nature of these delays and the strategies used to overcome them, we can offer more accurate and reassuring guidance to families, while contributing to theoretical models of motor development as constrained but adaptable.

References

Adolph, K., Berger, S. E., & Leo, A. J. (2011). Developmental continuity? Crawling, cruising, and walking. *Developmental Science*, *14*(2), 306–318. https://doi.org/10.1111/j.1467-7687.2010.00981.x

Adolph, K., & Hoch, J. (2019). Motor Development: Embodied, Embedded, Enculturated, and Enabling. *Annual Review of Psychology*, *70*(1), 141–164. https://doi.org/10.1146/annurev-psych-010418-102836

Adolph, K., & Robinson, S. (2015). Motor Development. In *Cognitive processes* (Vol. 2, pp. 113–157). https://doi.org/10.1002/9781118963418.childpsy204

Adolph, K., Vereijken, B., & Denny, M. A. (1998). Learning to Crawl. *Child Development*, *69*(5), 1299–1312. https://doi.org/10.1111/j.1467-8624.1998.tb06213.x

Alghamdi, Z. S., Orlando, J. M., & Lobo, M. A. (2024). Evaluation of the Movement and Play Opportunities and Constraints Associated With Containers for Infants. *Pediatric Physical Therapy: The Official Publication of the Section on Pediatrics of the American Physical Therapy Association*, *36*(4), 458–466. https://doi.org/10.1097/PEP.0000000000001125

Allen, K. R., Smith, K. A., Bird, L.-A., Tenenbaum, J. B., Makin, T. R., & Cowie, D. (2024). Lifelong learning of cognitive styles for physical problem-solving: The effect of embodied experience. *Psychonomic Bulletin & Review*, *31*(3), 1364–1375. https://doi.org/10.3758/s13423-023-02400-4

Biddiss, E., & Chau, T. (2007). Upper-Limb Prosthetics: Critical Factors in Device Abandonment. *American Journal of Physical Medicine & Rehabilitation*, *86*(12), 977–987. https://doi.org/10.1097/PHM.0b013e3181587f6c

Bowler, A., Arichi, T., Austerberry, C., Fearon, P., & Ronald, A. (2024). A systematic review and meta-analysis of the associations between motor milestone timing and motor development in neurodevelopmental conditions. *Neuroscience & Biobehavioral Reviews*, *167*, 105825. https://doi.org/10.1016/j.neubiorev.2024.105825

Clelland, A. D., Lester, R., Duncan, Ó., & Lam, W. L. (2024). Parental experience after diagnosis of a congenital upper limb difference: A national survey. *Journal of Hand Surgery (European Volume)*, *49*(11), 1327–1333. https://doi.org/10.1177/17531934241249014

Cole, W. G., & Adolph, K. E. (2023). Learning to Move in a Changing Body in a Changing World. *Integrative and Comparative Biology*, *63*(3), 653–663. https://doi.org/10.1093/icb/icad083

Gesell, A. (1946). The ontogenesis of infant behavior. In L. Carmichael (Ed.), *Manual of child psychology.* (pp. 295–331). John Wiley & Sons Inc. https://doi.org/10.1037/10756-006

Hahamy, A., Macdonald, S. N., van den Heiligenberg, F., Kieliba, P., Emir, U., Malach, R., Johansen-Berg, H., Brugger, P., Culham, J. C., & Makin, T. R. (2017). Representation of Multiple Body Parts in the Missing-Hand Territory of Congenital One-Handers. *Current Biology*, *27*(9), 1350–1355. https://doi.org/10.1016/j.cub.2017.03.053

Hewitt, L., Kerr, E., Stanley, R. M., & Okely, A. D. (2020). Tummy Time and Infant Health Outcomes: A Systematic Review. *Pediatrics*, *145*(6), e20192168. https://doi.org/10.1542/peds.2019-2168

Karasik, L. B., Adolph, K. E., Fernandes, S. N., Robinson, S. R., & Tamis-LeMonda, C. S. (2023). Gahvora cradling in Tajikistan: Cultural practices and associations with motor development. *Child Development*, *94*(4), 1049–1067. https://doi.org/10.1111/cdev.13919

Karasik, L. B., & Robinson, S. R. (2022). Milestones or Millstones: How Standard Assessments Mask Cultural Variation and Misinform Policies Aimed at Early Childhood Development. *Policy Insights from the Behavioral and Brain Sciences*, *9*(1), 57–64. https://doi.org/10.1177/23727322211068546

Keller, H. (2017). Culture and Development: A Systematic Relationship. *Perspectives on Psychological Science*, *12*(5), 833–840. https://doi.org/10.1177/1745691617704097

Kretch, K. S., Franchak, J. M., & Adolph, K. E. (2014). Crawling and Walking Infants See the World Differently. *Child Development*, *85*(4), 1503–1518. https://doi.org/10.1111/cdev.12206

Kretch, K. S., Willett, S. L., Hsu, L.-Y., Sargent, B. A., Harbourne, R. T., & Dusing, S. C. (2022). “Learn the Signs. Act Early.”: Updates and Implications for Physical Therapists. *Pediatric Physical Therapy : The Official Publication of the Section on Pediatrics of the American Physical Therapy Association*, *34*(4), 440–448. https://doi.org/10.1097/PEP.0000000000000937

Mason, K. J. (1991). Congenital Orthopedic Anomalies and Their Impact on the Family. *Nursing Clinics of North America*, *26*(1), 1–16. https://doi.org/10.1016/S0029-6465(22)03001-8

Matsubara, K., Hattori, T., & Narumi, S. (2022). Achievement of Developmental Milestones Recorded in Real Time: A Mobile App-Based Study. *The Journal of Pediatrics*, *245*, 201-207.e9. https://doi.org/10.1016/j.jpeds.2022.02.018

Michel, G. F., Nelson, E. L., Babik, I., Campbell, J. M., & Marcinowski, E. C. (2013). Multiple Trajectories in the Developmental Psychobiology of Human Handedness. In *Advances in Child Development and Behavior* (Vol. 45, pp. 227–260). Elsevier. https://doi.org/10.1016/B978-0-12-397946-9.00009-9

NCARDRS congenital anomaly statistics: Annual data. (2021, September 29). GOV.UK. https://www.gov.uk/government/publications/ncardrs-congenital-anomaly-annual-data

Stoeckel, M. C., Seitz, R. J., & Buetefisch, C. M. (2009). Congenitally altered motor experience alters somatotopic organization of human primary motor cortex. *Proceedings of the National Academy of Sciences*, *106*(7), 2395–2400. https://doi.org/10.1073/pnas.0803733106

Thelen, E. (1995). Motor development: A new synthesis. *American Psychologist*, *50*(2), 79–95. https://doi.org/10.1037/0003-066X.50.2.79

Tucciarelli, R., Bird, L., Straka, Z., Szymanska, M., Kollamkulam, M., Sonar, H., Paik, J., Clode, D., Hoffmann, M., Cowie, D., & Makin, T. R. (2024). *Shaping the developing homunculus: The roles of deprivation and compensatory behaviour in sensory remapping* (p. 2024.11.26.624817). bioRxiv. https://doi.org/10.1101/2024.11.26.624817

Watson, S. (2000). The principles of management of congenital anomalies of the upper limb. *Archives of Disease in Childhood*, *83*(1), 10–17. https://doi.org/10.1136/adc.83.1.10

Who Multicentre Growth Reference Study, & de Onis, M. (2006a). Assessment of sex differences and heterogeneity in motor milestone attainment among populations in the WHO Multicentre Growth Reference Study. *Acta Paediatrica*, *95*(S450), 66–75. https://doi.org/10.1111/j.1651-2227.2006.tb02377.x

Who Multicentre Growth Reference Study, & de Onis, M. (2006b). WHO Motor Development Study: Windows of achievement for six gross motor development milestones. *Acta Paediatrica*, *95*(S450), 86–95. https://doi.org/10.1111/j.1651-2227.2006.tb02379.x

Appendix A: Supplementary materials for chapter 2

Milestone attainment in two-handed children born full term (≥37 weeks gestation) compared to WHO standards

To ensure that the inclusion of near-term infants did not bias our findings, we repeated the milestone analysis after excluding children born at 35- and 36-weeks gestation. The pattern of milestone attainment remained virtually unchanged. The majority of children in our two-handed sample continued to achieve their milestones by the 99th percentile of the standard windows of achievement outlined by the WHO. Specifically, the percentage of children who met their milestones within the expected timeframe were as follows: sit independently (99%), stand with support (95%), crawl on hands and knees (100%), walk with support (96%), stand independently (99%), and walk independently (97%).

We also repeated our comparisons to the 50th percentile of the WHO's expected distribution after excluding near-term infants (born at 35-36 weeks gestation). Around this midpoint, the distribution of our sample was similar to the WHO sample for three milestones: sit independently ($\chi^2(1, N = 146) = 0.99$, $p = .321$, $BF_{10} = 0.17$) and stand independently (χ^2 $(1, N = 147) = 3.00$, $p = .083$, $BF_{10} = 0.46$), and walk with support (χ^2 $(1, N = 147) = 3.60$, $p = .058$, $BF_{10} = 0.619$). However, compared with WHO standards, significantly more children in our sample could crawl on hands and knees ($\chi^2(1, N = 111) = 9.81$, $p = .002$, $BF_{10} = 16.42$) and walk independently (χ^2 $(1, N = 141) = 6.82$, $p = .009$, $BF_{10} = 3.18$); while fewer children could stand with support (χ^2 $(1, N = 147) = 11.44$, $p < .001$, $BF_{10} = 32.44$). These findings are consistent with out primary analysis and suggest that the inclusion of near-term infants did not meaningfully influence the observed patterns of milestone attainment.

Comparisons of milestone attainment in children with upper limb differences and two-handed children born full term (≥37 weeks gestation)

To assess whether the inclusion of near-term infants influenced our findings, we repeated the milestones comparisons including only children born at or after 37 weeks gestation. In line with our main analysis, motor milestones emerged significantly later in children with limb differences. Except for hands-and-knees crawling ($W = 1886.50$, $p = .797$, $BF_{10} = .21$), the results revealed significant delays in the age of attainment for all milestones: sit independently ($W = 6086.50$, $p = .019$), stand with support ($W = 6149.00$, $p = .003$), walk with support ($W = 6376.00$, $p < .001$), stand independently ($W = 5699.00$, $p = .023$), and walk independently ($W = 5616.50$, $p = .015$). These findings mirror those of the main analysis, supporting the robustness of our findings.

Chapter 3: Compensatory motor behaviour in children with congenital upper limb differences

Abstract

Aim. Every day we perform hundreds of bimanual motor actions – simply opening a water bottle requires one hand to hold the bottle and one hand to turn the lid. Each year, approximately 500 babies in the UK are born with an upper limb difference, ranging from fused digits to total absence of the hand and arm. This study investigates how children with upper limb differences develop alternative motor strategies through exploration and how these strategies change with age. *Method.* Sixty-seven children with a congenital upper limb difference and 44 two-handed children (2-9 years) completed a series of tasks, including threading beads and separating Lego bricks, designed to elicit bimanual coordination. *Results.* While two-handed children predominantly completed these tasks bimanually, children with limb differences engaged a broader range of body parts, using their torso, legs, and feet significantly more than their two-handed peers ($p < .05$). On average, children with upper limb differences utilised three effectors to complete bimanual tasks. Younger children exhibited a broad exploratory phase, experimenting with multiple strategies, while older children converged on fewer, more consistent approaches. The choice of alternative effectors was driven by task mechanics, age, limb anatomy, and functional success. C*onclusion.* Children with congenital upper limb differences demonstrate remarkable adaptability by exploring and refining a diverse range of motor strategies involving multiple body parts beyond the hands. Through an extended period of sensorimotor exploration, these children experiment with multiple body parts before converging on task-specific solutions tailored to their anatomy, environment, and functional needs. This adaptive process reflects a parallel developmental trajectory grounded in the same exploratory and feedback-driven mechanisms that guide typical motor development, highlighting the flexibility of the developing motor system relative to morphological variability.

Introduction

Humans possess an extraordinary ability to adapt to everyday physical challenges, a trait that is especially evident in individuals born with limb differences. Here, adaptability refers to the ways in which individuals with limb differences learn to navigate environments, tasks, and social expectations largely designed for two-handed individuals. For instance, a woman born without arms may learn to use cutlery with her feet, while a man born without legs may 'walk' on his hands (Blumberg, 2009). These remarkable adaptations reflect a fundamental flexibility in the human motor system, enabling individuals to discover alternative strategies when conventional ones are not possible. Children with congenital upper limb differences often develop such solutions through direct interaction with their environment, engaging in exploratory, trial-and-error based learning to optimise their behaviour (Adolph & Hoch, 2019; Sutton & Barto, 2018). This model-free learning process, driven by feedback rather than explicit instruction, may be particularly critical when typical motor strategies are not feasible. Recent work shows that 5-7 year old children with upper limb difference display striking behavioural diversity, using their feet, legs, and torso, to perform everyday tasks, whereas adults with similar differences tend to rely on their upper limbs, showing less variation in their adaptive behaviours (Hahamy et al., 2017; Tucciarelli et al., 2024). This contrast highlights the early developmental period as a critical window for studying motor flexibility and adaptive motor processes. The present study investigates how adaptive behaviours unfold in children with congenital upper limb differences, using a model-free learning approach to explore the inherent flexibility and adaptability of human motor development, particularly in response to physical constraints (Adolph et al., 2018; Adolph & Hoch, 2019).

Congenital upper limb differences can vary considerably in form, ranging from fused or missing digits to the complete absence of one or both arms. Because these conditions are rare, children with upper limb differences have limited opportunities to learn through imitation, a key mechanism readily available to two-handed children. As a result, they must rely on self-guided sensorimotor exploration to discover effective motor strategies for completing everyday tasks. From an early age, all children are naturally driven to explore, engaging in a variety of motor actions such as mouthing, squeezing, and rotating to learn about the properties and functions of objects (Adolph et al., 2018; Bourgeois et al., 2005; Palmer, 1989; Rochat, 1989). This active exploration supports the development of action-perception, guiding how children interact with different objects, for example, by choosing to push toys with wheels and shake objects that make noise. However, for children with upper limb differences, this exploration extends beyond learning how to interact with an object to discovering which alternative effectors – such as their residual arm, legs, or feet – can be used to execute actions typically performed with the hands.

In daily life, such actions are performed in the service of specific goals and contexts, such as flicking a switch to turn on a light or twisting a key to unlock a door. While these tasks may seem trivial to adults, young children must actively discover the appropriate actions for each. But with multiple solutions to everyday motor tasks (Pacheco & Newell, 2018), exploring all possible actions through trial-and-error is time-consuming and highly inefficient. To streamline this process, children narrow their search space by identifying target features, such as locating the opening of a box. Once identified, they can refine their exploration by systematically testing potential solutions, such as twisting, pulling, or pressing down on the lid (Ossmy, Han, et al., 2022). For children with upper limb differences, this process often includes coordinating multiple body parts, as it is unlikely a single effector can fully replace hand functionality (Tucciarelli et al., 2024). This might involve for example stabilising an object between the residual arm and torso or gripping it between the feet, while using the intact hand to twist, pull, or press the lid. This larger pool of solutions compared to two-handed children may result in a longer exploratory process, particularly in younger children who have yet to discover a repertoire of habitual motor strategies.

In response to these unique sensorimotor experiences, the brain undergoes a process of neuroplasticity (Markham & Greenough, 2004). Specifically, the deprived sensorimotor hand cortex, which would normally represent the missing hand, may be repurposed to support the motor control of alternative effectors such as the residual limb or feet (Amoruso et al., 2021; Hahamy et al., 2015; Root et al., 2022; Stoeckel et al., 2009). This cortical remapping is thought to enhance the functional capacity of these effectors, facilitating the development of efficient compensatory strategies (Hahamy et al., 2017; Hahamy & Makin, 2019). Such plasticity is not apparent when limb differences are acquired through amputation or accident in adult life (Amoruso et al., 2023; Muret & Makin, 2021). In a recent study, we found that remapping of the sensorimotor cortex (S1) largely occurred in early childhood, and that there is a correlation between the degree of neural remapping and compensatory motor behaviour (Tucciarelli et al., 2024). Notably, the dataset reported in Tucciarelli et al. represents a subset of the broader sample used in the current study, which enables further investigation into how alternative effectors support compensatory behaviours across development.

In the current study, 67 children aged 2 to 9 years with a congenital upper limb difference, and 44 age-matched two-handed controls completed a series of semi-ecological motor tasks designed to elicit bimanual coordination. In order to assess efficiency, we measured these during free-choice behaviour and also in more structured task conditions where a child was asked to use one specific effector. This age range was selected to capture a critical period of motor skill acquisition in children, encompassing early sensorimotor exploration through to more refined, feedback-driven motor coordination and strategy development. This study aimed to examine: (1) the use of alternative effectors during everyday motor tasks, (2) the efficiency of adaptive behaviours, (3) the development of task-specific strategies, (4) coordination of effectors, and (5) the key factors guiding adaptive behavioural choices. To enable an in-depth exploration of these factors, we recruited a functionally homogenous sample of children with limb differences — specifically, those who were born with one hand that, although possibly present and with digits, is unable to perform a functional pincer grip.

In line with previous findings, we first hypothesised that younger children would exhibit less efficient and more exploratory behaviour, characterised by the use of a broader range of effectors, greater variety of effector combinations within each task (Tucciarelli et al., 2024), and longer task completion times. In contrast, older children were expected to demonstrate more refined strategies, utilising fewer, more consistent, and faster effector combinations. Layered on top of a general shift towards efficiency, we also predicted that for the upper limbs specifically there would be increased use with age, even when this may not be the most efficient strategy, reflecting a growing awareness of social norms and expectations around typical motor behaviour. Finally, we predicted that the selection of effectors would be influenced by both physiological characteristics, such as limb anatomy, and the demands of the task. Specifically, we expected that children with below-elbow differences, (i.e. those with an elbow joint on their residual limb), would show greater reliance on their residual limb compared to those with an above-elbow difference, who may turn to other effectors, such as their legs or feet. We also expected that tasks requiring stabilisation would prompt the use of larger, more powerful body parts, like the legs or torso, providing a solid base for support; while tasks that demand fine motor manipulation, such as threading, would encourage the use of smaller, more precise effectors, such as the residual limb or mouth.

Methods

Participants

We recruited a total of 111 children aged between 23 months and 9 years, consisting of 67 children with congenital upper limb differences (*M* = 6.16 years, *SD* = 1.87; 34 female) and 44 two-handed controls (*M* = 6.73 years, *SD* = 1.70; 23 female). Children with neurodevelopmental conditions or global developmental delay were excluded in order to focus the analyses on the effects of limb differences.

Children with upper limb differences were recruited through two UK-based limb difference support charities. Within this group, 64 children had one unaffected hand. Though there was morphological variability within the group – ranging from complete absence of the forearm to a partial palm with non-functional residual fingers – all 67 children had one hand capable of performing a pincer grip between the thumb and any finger, and a residual limb with no functional gripping capability. Of the 67 children, 39 had an intact right hand (*M* = 6.38 years, *SD* = 1.93), while 28 had an intact left hand (*M* = 5.86 years, *SD* = 1.77). Three children with an intact right hand had a bilateral limb difference, but their right hand remained functional and capable of performing a pincer grip. The length of the residual arm was categorised into four distinct categories (Table 3.1). Regarding prosthesis use, 53 children had never been fitted with or did not wear a prosthesis, 9 used a prosthesis on a monthly basis, and 5 used a prosthesis weekly. Among those who used a prosthesis, 5 children reported using it only for specific tasks, such as riding a bike.

Two-handed control participants were recruited through an existing university database of volunteer families and an affiliated Facebook page. Of the 44 children, 30 were right-hand dominant. Children in the control group had no visible limb differences or known motor conditions.

This study was approved by the ethics committee at Durham University (PSYCH-2019-08- 30T10_08_45-mnvj24).

Table 3.1. Demographic breakdown of residual limb length in children with congenital upper limb differences by affected side.

	Affected side	
Length of residual arm	Left	Right
Above elbow	3	7
Below elbow, less than ½ forearm	12	4
Below elbow, more than ½ forearm	6	3
Wrist/partial non-functional hand	18	14

Task and procedure

To assess adaptive motor behaviours, participants completed the *Surprise Suitcase*, a series of 15 semi-ecological tasks designed to elicit bimanual coordination. This was designed after piloting with children with upper limb differences. Results from a smaller sample with this task are presented in Tucciarelli et al (2024). The tasks were categorised into three distinct groups based on the mechanics typically used by two-handed children: fine motor manipulation; stabilise-and-manipulate by twisting or pulling; and bilateral grasp-and-pull (see Table 3.2 for task list).

At the start of the session participants were instructed to remove their shoes and socks and sit on a soft play mat on the floor, allowing them to complete the tasks comfortably and without restriction to the legs and feet. Tasks were presented in a fixed order, beginning with unlocking and removing a padlock from a lightweight suitcase. Participants were asked to complete each task as they naturally would, using their typical behavioural strategies. Although they were given the option of wearing a prosthetic, all chose to perform the tasks without one, reflecting the limited day to day use. Participants were encouraged to keep trying each task until completion. If they showed signs of discouragement, the experimenter offered a brief, standardised prompt (e.g., you're doing great, keep trying you're almost there). If the participant could not complete the task or explicitly asked for help, the experimenter used a standardised intervention to reduce the difficulty of the task (e.g., loosening a jar lid or separating plaster tabs), then encouraged the participant to try again. This approach helped maintain participant motivation and preserved a sense of achievement throughout the session.

After completing the initial set of tasks, participants were asked to repeat a subset using a specified effector (either the torso, lower face, or legs and feet) to assist in task completion. This manipulation allowed us to examine how the usefulness of different effectors influences spontaneous motor choices. Although participants were instructed to use a particular effector in these runs, in practice this instruction was followed to varying degrees. This variability was accounted for in our subsequent analyses. Some participants completed only the free-choice condition, while others also participated in one or more of the 'specified effector' runs. Sessions lasted between 15 and 30 minutes and took place either at home, in a local community hall (used when home visits were not possible during the COVID19 pandemic) or in the lab. In all settings, a soft play mat was used to create a comfortable and naturalistic environment. Each session was video recorded to enable detailed offline analysis of adaptive motor behaviour.

Table 3.2. List of tasks included in the Surprise Suitcase, organised by typical solution mechanics. The stars indicate the tasks repeated in the additional specified effector runs.

Fine motor manipulation	Stabilise and manipulate	Bilateral grasp and pull
Open a padlock	Open a Velcro bookbag	Open a plaster packet*
Complete three buttons	Open a plastic envelope*	Remove the lid from a felt-tip pen*
Put a glove on the dominant hand*	Remove the lid from a large tin*	Separate two Lego bricks*
Thread three beads	Remove a jar lid	Open a plastic salad box*
	Unscrew a wooden nut and bolt	Unwrap a twisty sweet packet*
	Use a toy screwdriver to insert a screw into a small wooden block*	

Behavioural coding

Participants' motor behaviour during the *Surprise Suitcase* task was coded offline from video recordings by four independent raters – one primary rater and three secondary - using ELAN (Version 6.8). Each video was coded on a frame-by-frame basis (40ms per frame). Coding focused on the active use of specific body parts during task performance, including the intact or dominant limb, residual or non-dominant limb, torso, lower face, legs, and feet (Figure 3.1). Effector use was not coded as mutually exclusive, meaning that multiple body parts could be marked as active simultaneously when used in a coordinated strategy.

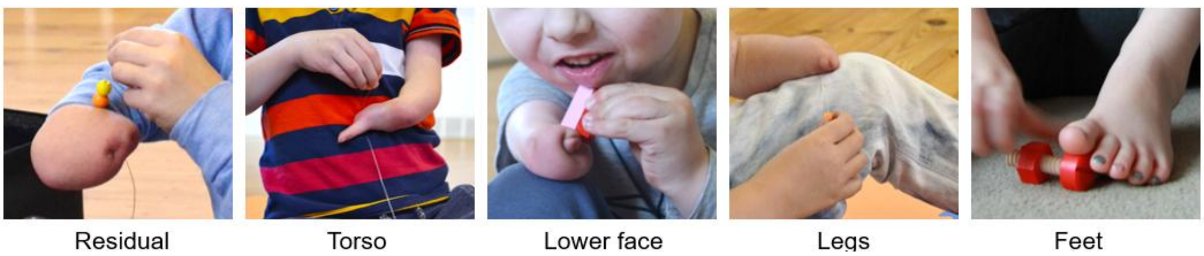


Figure 3.1. Examples of alternative effector use in children with upper limb differences

A detailed coding scheme was developed to ensure consistency across raters. This scheme outlined predefined start and stop criteria for each task. For example, in the separation of Lego bricks, coding began when the participant grasped the bricks and ended when the pieces were successfully separated. Active use was defined as purposeful, goal-directed movement of a body part that intended to contribute to task completion, regardless of whether the attempt was successful. For instance, using a foot to stabilise an object was coded as active use. Passive contact, such as resting limbs or incidental movements that did not contribute to the task were excluded.

The coding scheme also clearly defined rules for when coding should be paused. Pauses were implemented if the experimenter intervened, for example, by supporting objects or manipulating the task materials, or if the child disengaged from the task by stopping their attempt or pausing to talk to the researcher. Brief disengagements that were part of a continuous strategy, such as adjusting grip or repositioning a body part were not treated as interruptions, and in these cases coding continued uninterrupted.

All raters were trained using three sample videos, which were reviewed and discussed collaboratively. Following training, each rater independently coded their assigned videos. To assess inter-rater reliability, the primary rater double-coded approximately 15% of each rater's dataset. Inter-rater agreement was calculated based on the proportion of time each effector was actively engaged, corresponding to up to 90 coded items per video (6 effectors across 15 subtasks, depending on task completion). A two-way mixed-effects intraclass correlation coefficient (ICC[3,1]), was calculated separately for each rater. Agreement was consistently high: Rater 1, ICC = .996, 95% CI [.996, .996]; Rater 2, ICC = .988, 95% CI [.987, .989]; and Rater 3, ICC = .995, 95% CI [.995, .996]. Minor discrepancies typically reflected timing differences of a few seconds which did not meaningfully affect the data. Given this high reliability, the secondary raters' codes were retained for analysis.

Analysis

To investigate the development of adaptive behaviour in children with upper limb differences analyses were performed using R (version 3.6.1). These analyses were designed to explore: the use of alternative effectors during motor tasks; the efficiency of adaptive behaviours; the development of task-specific strategies; coordination of effectors; and the key drivers guiding adaptive behavioural choices.

Alternative effector use in children with upper limb differences

We first compared effector use during the free-choice condition between children with upper limb differences (N = 67) and two-handed controls (N = 44). For each subtask, the total duration of each effector's use was summed and expressed as a percentage of the subtask duration. Since effectors could be used simultaneously, their usage use was not mutually exclusive. As proportion data is bounded between 0 and 1, a logit transformation was applied prior to analysis to make the data suitable for regression. Subsequently, a mixed-effects linear regression model was fitted with fixed effects of group (children with upper limb difference vs. two-handed children), and effector (intact/dominant hand, residual/non-dominant hand, torso, lower face, legs, and feet), along with their interaction, given the expected group differences in effector use. Participant ID and task were included as random effects to account for within-subject and task-level variability.

Coordination of effectors in children with upper limb differences

To build on previous analyses by Tucciarelli et al. (2024), which quantified the number of effectors used in a task, we conducted a more granular analysis of strategy variation by examining the range of effector combinations used within each task during the free-choice condition. Specifically, we calculated how many combinations of effectors each participant employed over the course of a task—for example, using intact/residual/torso in one attempt, and intact/residual/legs in another, versus a participant who relied on a single combination (e.g., intact/residual/legs) throughout. To quantify this behavioural variability, we calculated Shannon entropy (Shannon, 1948), where higher values indicate greater diversity in effector combinations and lower values reflect more consistent patterns of behaviour. A mixed-effects linear regression was then used to examine the how entropy varied with age, including participant ID and task as random effects to account for variability within subjects and across tasks. We also extracted the most common combinations of effectors used across tasks in a data-driven manner.

Efficiency of adaptive motor behaviour in children with upper limb differences

To assess the efficiency of alternative motor behaviours in children with upper limb differences, we used task completion time as a primary indicator, with shorter durations reflecting greater efficiency. A mixed-effects linear regression was conducted with fixed effects of group and age, and random effects of participant ID and task as random effects to account for repeated measures and variability in task difficulty. This approach allowed for the inclusion of all available data without excluding participants who did not complete every task. A total of 111 participants were included in this analysis.

The development of task-specific strategies

To investigate whether children with upper limb differences develop context-dependent adaptive strategies, we analysed patterns of effector use across different subgroups of tasks in the free-choice condition. These subgroups were defined by the mechanical demands of the typical solution: fine motor manipulation, stabilise-and-manipulate, and bilateral grasp-and-pull.

A mixed-effects linear regression model was fitted with fixed effects of group, effector, and task mechanics subgroup, and random effects of participant ID and task to account for within-subject and within-task variability (*N* = 111). All two- and three-way interactions were included to capture potential differences in effector use across combinations of group and task mechanics. As in previous analyses, the intact or dominant hand was excluded from the model as it does not represent an alternative effector used for compensatory purposes.

To interpret three-way interactions (group x effector x task mechanics), we used estimated marginal means to compute model-adjusted means for each combination of predictors. Pairwise comparisons were conducted within each group-effector combination to determine whether effector use varied significantly across task mechanics. P-values were adjusted using the Tukey method to correct for multiple comparisons.

We also investigated the efficiency of these task-specific strategies by analysing task completion time in the free-choice condition using a separate mixed-effects linear regression, with fixed effects of group, task mechanics, and age, all two- and three-way interactions, and random effects of participant ID and task. Again, this analysis ensured that all available data were included without excluding participants due to missing task completions (*N* = 111). Estimated marginal means were then used to evaluate group differences in the efficiency of motor strategies across task types.

Key drivers of adaptive motor behaviour

To investigate the underlying factors driving the choice of alternative effectors in children with upper limb differences (*N* = 67), we conducted two mixed-effects linear regression models. The first model examined the influence of demographic and physiological factors on effector use in the free-choice condition. Fixed effects included age (in years), residual arm length (standardised), and effector, along with all relevant interactions. In line with previous analyses, the intact hand was excluded from the model as it does not represent an alternative effector used for compensatory purposes. Participant ID and task were included as random effects to account for within-subject and within-task variability.

The second model assessed whether the usefulness of a given body part predicted its use in the free-choice condition. Usefulness was coded from video recordings of the specified effector runs using a three-point scale: (i) the effector was not used, (ii) the child attempted to use the effector, but it did not contribute to task completion, and (iii) the effector was successfully used and contributed to task completion. Fixed effects included usefulness, effector, and their interaction, and random effects of participant and task. This analysis focused on the four most frequently used non-arm effectors, torso, lower face, legs, and feet. Data were available for 58 children with upper limb differences, although not all participants completed all tasks for every effector, resulting in slight variation in sample size across models.

Results

Alternative effector use in children with upper limb differences

During the free-choice condition, children with upper limb differences used a broader range of effectors compared to age-matched two-handed controls. The mixed-effects linear regression model explained a substantial proportion of variance in effector use (Conditional R^2 = .70), indicating a strong relationship between participant group and patterns of effector use. These group-level patterns are illustrated in Figure 3.2.

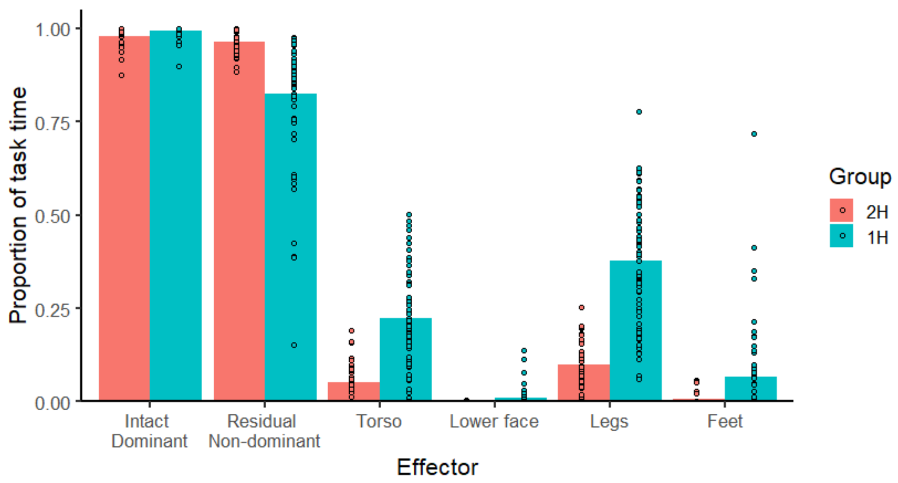


Figure 3.2. Average proportion of time each effector was used during task completion by children with upper limb differences (1H) and age-matched two-handed controls (2H).

As expected, both groups consistently engaged their intact or dominant hand throughout the tasks, with no significant group differences in use. Since this hand is not an alternative effector used for compensatory purposes, it was excluded from the model. The interaction terms between group and effector were statistically significant for all effectors (Table 3.3), indicating that the effect of group varied across body parts. Post hoc estimated marginal means revealed significant group differences for the residual/ non-dominant limb (β = -1.66, p < .001), torso (β = 1.56, p < .001), legs (β = 2.41, p < .001), and feet (β = 0.58, p < .001), though not for the lower face (β = 0.12, p = .97). Specifically, children with upper limb differences used their residual limb significantly less than two-handed controls used their non-dominant hand. In contrast, they relied more heavily on alternative effectors, using their torso and legs approximately four times more, and feet almost eleven times more, than two-handed children, based on raw proportional use.

Table 3.3. Interaction effects between participant group and effector type from the mixed-effects linear regression model. The residual limb was used as the reference category. Positive interaction terms reflect greater use of that effector in children with upper limb differences.

Predictor	B	CI	T value	*p* value
Group x residual	-1.66	-1.86 – -1.47	-16.83	*p*<.001*
Group x torso	3.23	2.96 – 3.49	23.82	*p*<.001*
Group x lower face	1.78	1.52 – 2.05	13.15	*p*<.001*
Group x legs	4.08	3.81 – 4.34	30.09	*p*<.001*
Group x feet	2.24	1.98 – 2.51	16.53	*p*<.001*

We note that the lower use of alternative effectors in two-handed controls is partly due to the number of participants in that group who did not use these effectors at all. When coding for use vs. non-use, there were significantly more instances of use in one-handed participants for torso (χ^2 (1, N = 111) = 13.41, p =.0003), lower face (χ^2 (1, N =111) = 12.23, p =.0005), legs (χ^2 (1, N = 111) = 4.70, p = .03), and feet (χ^2 (1, N = 111) = 15.87, p <.001). Consistent with previous research, these findings confirm that children with upper limb differences use a broader range of alternative effectors, including their lower face, more frequently than their two-handed peers.

Coordination of alternative effectors in children with limb differences

Two-handed children used their hands for 85.8% of the task time in the free-choice condition, comprising of using the dominant limb alone (3.6%), the non-dominant limb alone (1.9%), and both limbs simultaneously (80.3%). In contrast, children with upper limb differences used their hands for 39.4%, comprising of intact hand alone (11.0%), residual arm alone (0.5%), and both limbs simultaneously (27.8%). Instead, they frequently relied on coordinating multiple alternative effectors to compensate for their missing hand function during task completion. We hypothesised that younger children with upper limb differences would demonstrate a heightened exploratory phase, using many combinations of effectors, while older children would show convergence towards more consistent strategies. To test this, we examined whether the number of effector combinations used within a task decreased with age. Such a reduction would indicate that, motor strategies converge, becoming more stable and coordinated over time.

Across tasks, the simultaneous use of three effectors was the most common at 48.8%, followed by two effectors at 34%, a single effector at 11.6%, and four effectors at 5.5%. Notably, one participant was observed using five effectors simultaneously for a single task: intact, residual, torso, legs, and feet, highlighting the potential for complex multi-effector coordination in this population. On average, 2.89 effectors, inclusive of the intact hand, were used to substitute for typical hand function.

To characterise the typical coordination patterns, we identified all unique combinations of effectors used within each task, including cases where multiple combinations were used in sequence, and then calculated the most frequently occurring combinations of two, three, and four effectors across the dataset (Table 3.4).

Table 3.4. Most frequently observed effector combinations during task completion (≥3%). Full distribution available in Appendix B.

Effector combinations	Frequency (%)
Intact, residual, legs	29.84
Intact, residual	27.81
Intact, residual, torso	16.18
Intact, residual, torso, legs	5.02
Intact, feet	3.56

Notably, the most frequent combinations of effectors centred on the upper limbs, often supplemented by legs or torso, indicating that, in the absence of hand function, children draw on available body parts in a flexible manner, engaging multiple effectors to approximate bimanual capabilities.

To explore how the number of effector combinations changes with age, we assessed the variability using Shannon entropy (Shannon, 1948). Higher entropy reflects greater variability in effector combinations; that is, the use of a greater number of strategies within a task. A mixed-effects linear regression revealed a significant age-related reduction in entropy ($\beta = -0.05$, $t = -4.44$, $p < .001$), suggesting that younger children initially adopt a more exploratory approach, testing different combinations of effectors (Figure 3.3). Over time, these strategies appear to converge into more consistent and efficient motor solutions.

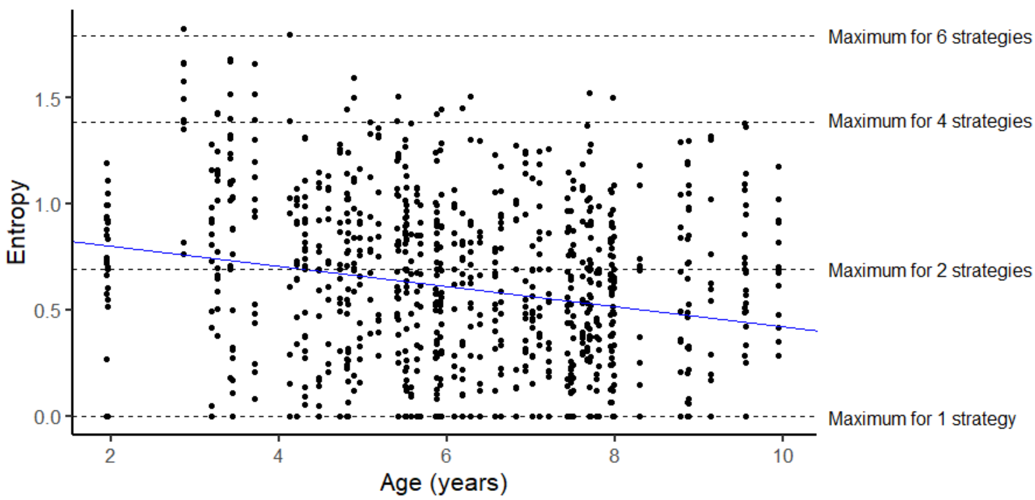


Figure 3.3. Relationship between age and entropy in free-choice behaviour of children with upper limb differences. Each point represents an individual task, and the blue diagonal line shows the fixed-effect regression line from the linear mixed-effects model, and the black dashed lines show the maximum entropy value for 1, 2, 4, and 6 strategies.

Efficiency of adaptive motor behaviour in children with upper limb differences

This analysis aimed to determine whether children with limb differences achieved comparable levels of efficiency, measured by task completion time, to their two-handed peers, and how this changed with age.

A mixed-effects linear regression revealed a significant effect of group, indicating children with upper limb differences completed tasks more slowly than their two-handed peers (β = 17.08, t = 2.92, p = .004). There was also a significant effect of age, indicating that older children completed tasks more quickly (β = -2.53, t = -3.65, p < .001). The interaction between group and age was not significant (β = -1.18, t = -1.36, p = .174), suggesting that both groups showed similar age-related improvements in efficiency. The model explained 74% of the variance in task completion time (Conditional R^2 = .74), indicating a strong overall fit. These findings suggest that although children become more efficient with age, those with upper limb differences consistently take longer to complete tasks than their two-handed peers (Figure 3.4).

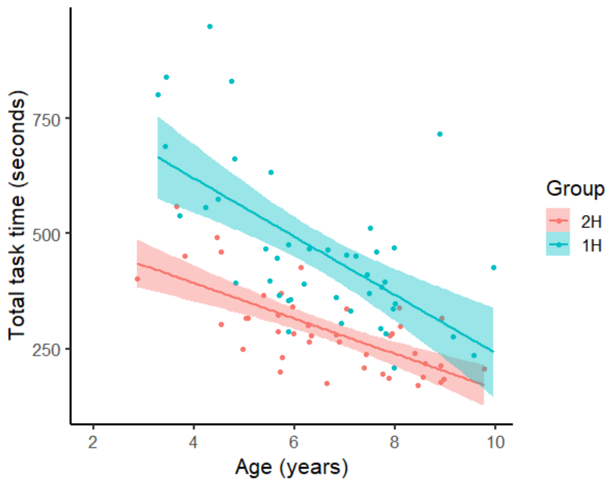


Figure 3.4. Overall task completion time as a function of age for children with upper limb differences (1H) and two-handed controls (2H) in the free-choice condition. Lines represent linear regression fits, and shaded areas indicate 95% confidence intervals.

The development of task-specific strategies

Effector use

To assess whether children with upper limb differences refine their adaptive motor strategies based on task demands, we analysed patterns of effector use across three different task mechanics groupings: fine motor manipulation, stabilise-and-manipulate, and bilateral grasp-and-pull. A linear mixed-effects model explained a substantial portion of the variance (Conditional $R^2 = 0.71$).

The model revealed a significant interaction between leg use and task type, with greater leg use during stabilisation tasks across groups ($\beta = 0.79$, $p = .002$; Figure 3.5). Post hoc pairwise comparisons of estimated marginal means confirmed that leg use was significantly higher during stabilisation tasks compared to fine motor manipulation ($\beta = -3.512$, $p = .001$). No significant difference was observed between stabilisation and bilateral grasp-and-pull tasks ($p = .13$). All other two-way interactions between effector and task type were not significant (*p*s >.051).

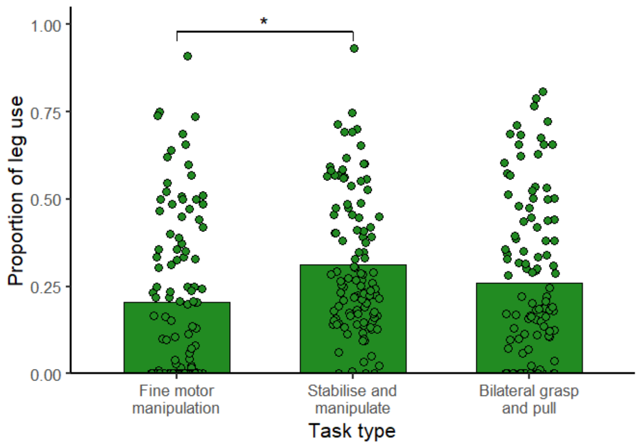


Figure 3.5. Interaction between leg use and task type, showing the average proportion of time children with upper limb differences used their legs in tasks requiring fine motor manipulation, bilateral grasp-and-pull, and stabilisation.

Significant three-way interactions emerged for torso use, indicating that children with upper limb differences showed different patterns of torso use compared to two-handed controls during tasks requiring bilateral grasp-and-pull (β = 1.19, p = .001) and stabilisation (β = 1.21, p < .001), relative to the reference category, fine motor manipulation. Fine motor manipulation was selected as the reference category as it typically represents the highest demand on precision and dexterity and is therefore more likely to elicit complex compensatory strategies in children with limited hand function. Post hoc pairwise comparisons of estimated marginal means revealed that children with upper limb differences used their torso significantly more during bilateral grasp-and-pull (β = –1.85, p < .0001) and stabilisation tasks (β = –1.76, p < .0001) compared to fine motor manipulation tasks (Figure 3.6). No such differences were observed in the two-handed group (all *ps* > .14). All other three-way interactions between group, effector, and task type were not significant (*ps* >.237). Together, these findings suggest that children with upper limb differences adapt their motor strategies based on task demands, particularly through strategic use of larger effectors like the torso and legs.

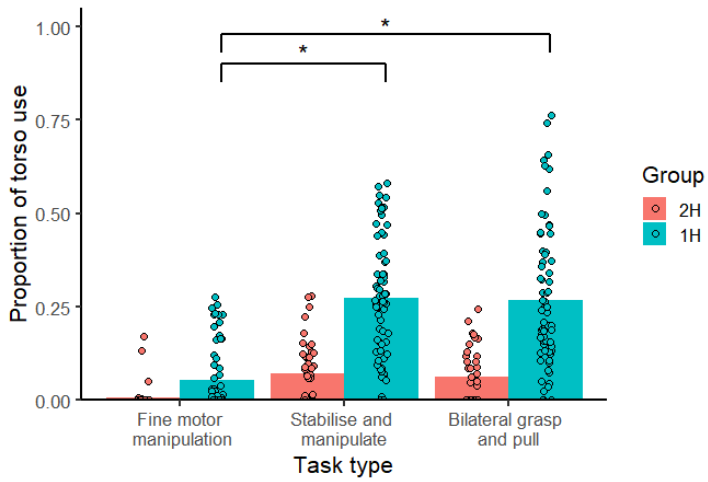


Figure 3.6. Average proportion of time the torso was used across different task types in the free-choice condition, shown separately for children with upper limb differences (1H) and age-matched two-handed controls (2H).

Efficiency

To assess the efficiency of these task-specific adaptive strategies, we analysed task completion time across the three task mechanics groupings: fine motor manipulation, stabilise-and-manipulate, and bilateral grasp-and-pull. A linear mixed-effects model was fitted with fixed effects of group, age, task type, and their interactions. The model explained a substantial proportion of the variance (Conditional $R^2 = 0.64$).

Task completion time decreased with age across all task types, indicating that children became more efficient over time. However, the rate of improvement differed by task. Specifically, the age-related reduction in time was steeper for fine motor tasks ($\beta = -4.15$, $p < .001$) compared to bilateral grasp-and-pull tasks, where the improvement was significantly less pronounced ($\beta = 3.04$, $p = .014$). No significant difference in age-related change was found between fine motor and stabilisation tasks ($p = .199$), suggesting a similar developmental trajectory, Figure 3.7.

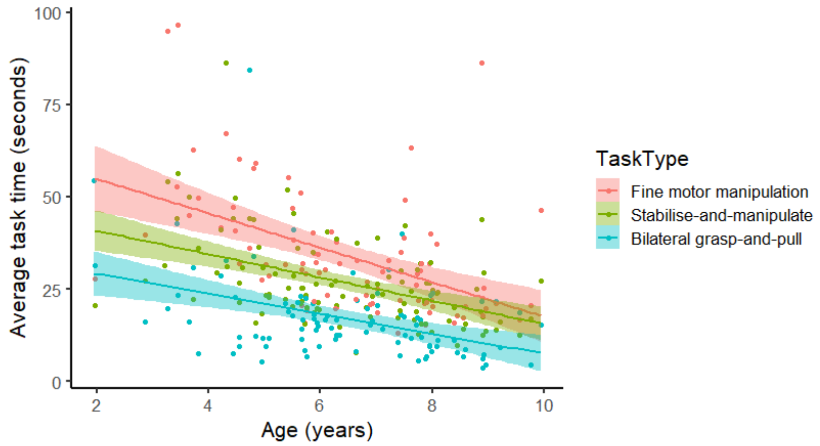


Figure 3.7. Average task time as a function of age for each task type in the free-choice condition. Lines represent linear regression fits, and shaded areas indicate 95% confidence intervals.

In addition to developmental trends, we examined group differences in task performance. Children with upper limb differences were significantly slower at completing fine motor tasks compared to two-handed controls (β = 21.16, *p* = .019), as confirmed by post hoc comparisons (β = -3.33, *p* <.001; Figure 3.8). No significant group differences were observed for the stabilisation or grasp-and-pull tasks (*ps* > .34).

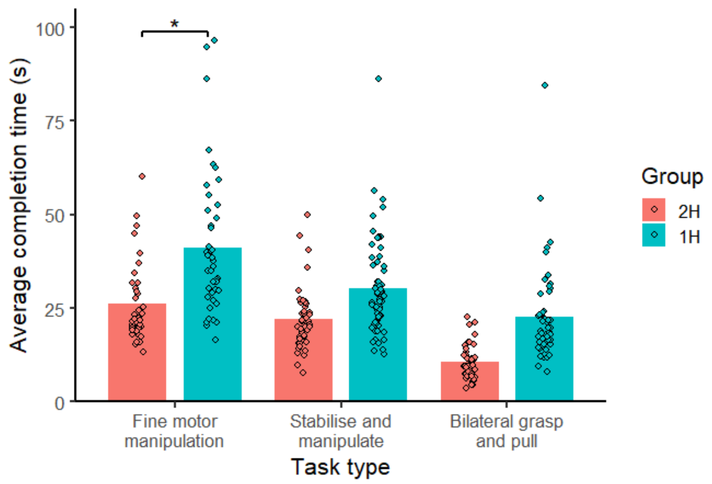


Figure 3.8. Average task completion time by task type for both children with upper limb differences (1H) and two-handed controls (2H).

Although fine motor tasks elicited slower performance in children with upper limb differences relative to controls, performance across the task types did not significantly differ within each group (*ps* > .47). This suggests that, within each group, children completed tasks with similar efficiency regardless of task demands.

Furthermore, no significant three-way interactions between group, task type, and age were found (*ps >.3*), indicating that age-related improvements in task efficiency were consistent across groups and task types.

Key drivers of adaptive motor behaviour

Having established that children with upper limb differences adopt a diverse array of compensatory behaviours, we sought to determine what factors drive these effector choices. We first examined how individual demographic and physiological differences—such as age and limb anatomy—predict effector use in the free-choice condition. The model explained a substantial proportion of the variance (Conditional $R^2 = 0.59$).

Age

Relative to the residual arm, the model revealed significant age x effector interactions for the torso ($\beta = -0.31$, $p < .001$), mouth ($\beta = -0.17$, $p = .001$), and feet ($\beta = -0.31$, $p < .001$), though not for legs ($p = .30$), indicating that age-related changes in leg use occurred at a similar rate to change in residual arm use. Post hoc estimated marginal means confirmed significant age-related changes in body part use: use of the residual limb ($\beta = 0.16$, $p < .001$) and legs ($\beta = 0.21$, $p < .001$) increased with age, while use of the torso ($\beta = –0.15$, $p < .001$) and feet ($\beta = –0.15$, $p < .001$) decreased (Figure 3.9). No significant age-related change was observed for lower face use ($p = .68$). These results suggest that younger children with upper limb differences rely on alternative effectors like the torso and feet, while older children increasingly rely on their residual limb and legs for everyday motor tasks. The observed increase in leg use may reflect a compensatory strategy to enhance stability, particularly given that testing was conducted with children seated on the floor, a posture which may have encouraged lower body use.

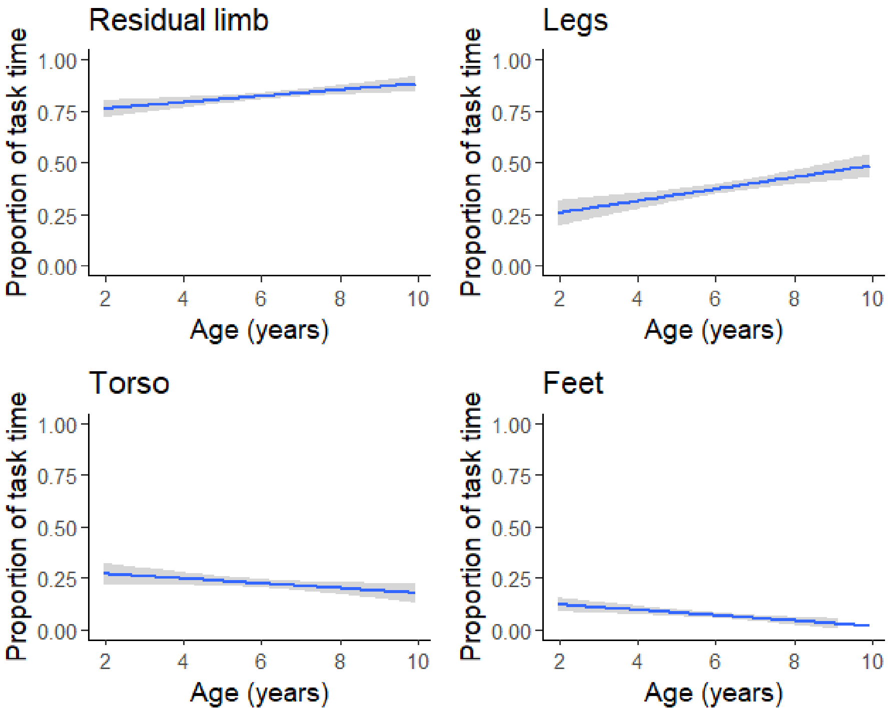


Figure 3.9. Age-related changes in effector use among children with upper limb differences. Each panel shows a linear regression line with 95% confidence intervals, showing the proportion of task time the residual limb, legs, torso, and feet were used as a function of age.

These age-related shifts may reflect trade-offs between effectors. Spearman correlations between residual limb use and other effectors showed a significant negative correlation between residual limb and foot use ($rs = –0.46$, $p < .001$), indicating that greater reliance on the residual limb was associated with reduced foot use. No significant correlations were found between residual limb use and torso ($rs = 0.18$, $p = .15$) or leg use ($rs = -0.07$, $p = .59$).

Limb anatomy

The model also revealed a significant main effect of limb anatomy ($\beta = 0.78$, $p < .001$) and significant interactions between residual limb length and effector use for the torso ($\beta = –0.53$, $p < .001$), mouth ($\beta = –0.87$, $p < .001$), legs ($\beta = –1.00$, $p < .001$), and feet ($\beta = –1.21$, $p < .001$) relative to the non-dominant hand. Post hoc pairwise comparisons of estimated marginal means showed that residual limb use was significantly lower in children with above-elbow differences compared to all other levels of below-elbow differences (*ps* < .001). Similarly, torso use was significantly lower in children with above-elbow differences compared to those with longer residual limbs (more than ½ forearm) or partial hands (*ps* < .001). Conversely, foot use was significantly higher in children in children with above-elbow differences relative to all other levels of below-elbow differences (*ps* < .001). A similar but less pronounced pattern was observed for leg use, with a significant decrease in those with a partial hand compared above-elbow differences (*p* = .06) and those with short residual arms below the elbow (less than half a forearm; *p* = .02). Mouth use remained stable across residual limb length (*p* > .30). These results are illustrated in Figure 3.10. Together, these findings indicate that residual limb and torso use increase with limb length, while leg and foot use decrease (Figure 3.10). Notably, this pattern ran counter to the age pattern described earlier: although children with longer residual limbs tended to be younger in our sample, they still showed increased residual limb use and reduced compensatory body use, suggesting that limb anatomy, rather than developmental maturity, is driving these effects.

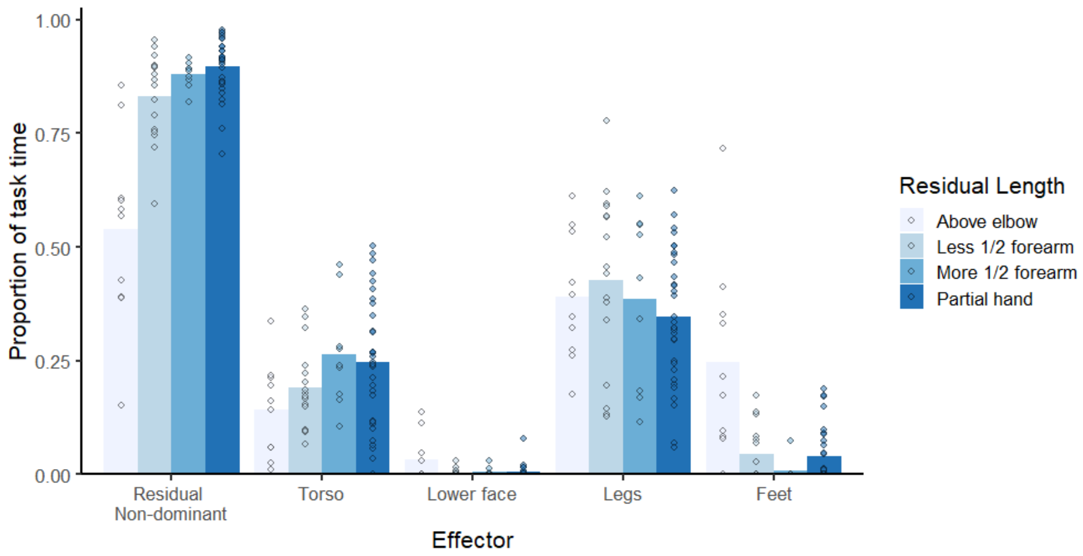


Figure 3.10. Relationship between residual limb length and free-choice use of alternative effectors in children with upper limb differences.

Functional success

We conducted a second mixed-effects linear regression to assess whether the functional success, or perceived usefulness, of a body part predicted its use as a compensatory effector in free-choice behaviour. This analysis focused on four frequently used non-arm effectors: torso, lower face, legs, and feet. The model accounted for a moderate proportion of the variance (Conditional R^2 = .34).

The model revealed significant usefulness x effector interactions between successful use of an effector in the specified effector run and free-choice behaviour for the torso (*β* = 1.33, *t* = 3.73, *p* <.001) and legs (*β* = 0.59, *t* = 2.27, *p* = .024), relative to those who did not attempt to use the effector in the specified effector run. Post hoc pairwise comparisons of estimated marginal means showed that for both torso and legs, children who had successfully used the effector during the specified effector run exhibited significantly higher free-choice use of that effector compared to those who had not attempted to use it when instructed ($p < .001$ and $p = .024$ respectively; Figure 3,11). Notably, no significant differences were observed between successful and unsuccessful users, nor between unsuccessful and non-users, suggesting that while effectors rated as more functionally successful were more likely to be used in free-choice behaviour, unsuccessful attempts do not predict free choice behaviour, nor do they reduce the likelihood compared to success. For feet and lower face, usefulness did not significantly predict free-choice behaviour (*ps* > .55). Collectively, these findings suggest that while functional feedback plays a role in compensatory effector selection, its influence varies by body part. For the torso and legs, successful use appears to reinforce free-choice selection, whereas for other effectors, factors beyond immediate effectiveness, such as age and limb anatomy, may exert a stronger influence.

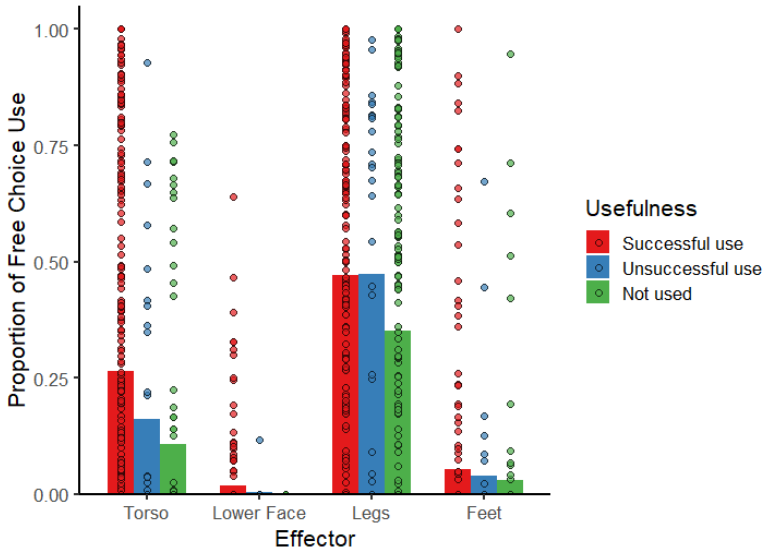


Figure 3.11. Proportion of time in the free-choice condition by usefulness for each effector (torso, lower face, legs, and feet). The usefulness rating indicates whether the effector was deemed successful, unsuccessful, or not used in task completion during the specified effector conditions.

Discussion

This study investigated how children with congenital upper limb differences acquire and refine adaptive motor strategies throughout development, with a specific focus on the role of sensorimotor exploration in shaping compensatory behaviour. We explored five key aspects of motor adaptation: (1) the use of alternative effectors, (2) the efficiency of adaptive behaviours, (3) the development of task-specific strategies, (4) the coordination of effectors, and (5) the key drivers guiding adaptive behavioural choices. Through this comprehensive analysis, we provide new insights into how children with upper limb differences navigate the challenges posed by missing hand functionality, and for the first time, how this adaptive process unfolds across development.

This study demonstrates that motor adaptation in childhood is not a uniform process but one influenced by the structure of the body. This highlights the importance of viewing motor development in the context of morphological variability. Children with upper limb differences relied on a wide range of alternative effectors much more frequently than their two-handed peers. Instead of using a single compensatory effector, on average they coordinated nearly three effectors to complete bimanual tasks, integrating the residual and intact limbs with additional body parts such as the torso, legs, and feet, to provide stability and control.

These findings extend embodied and dynamic systems theories of motor development which propose that motor behaviour emerges through exploratory action and feedback-driven adaptation, shaped by the constraints and affordances of the body, task, and environment (Adolph & Hoch, 2019; Franchak & Adolph, 2024). From early infancy, children must learn to control the growing bodies they inhabit, continually adjusting their motor strategies in response to an ever-changing environment (Cole & Adolph, 2023). While these frameworks are well established in typical infant development, our findings demonstrate how they are robust across morphological variability, not just in infancy but across childhood. Rather than viewing compensatory strategies as deviations from typical motor development, we propose that they represent a parallel pathway, guided by the same exploratory and feedback-driven processes. Our data show that motor adaption in children with upper limb differences is not a matter of simple substitution, but of creative, iterative problem-solving, grounded in sensorimotor experience and anatomical constraints.

This process of sensorimotor exploration reflects the emergence of goal-directed problem-solving. Young children tend to explore widely, testing multiple solutions to a problem, while older children engage in more targeted exploration, shifting from discovering which actions are possible to actively solving the problem (Meder et al., 2021; Ossmy, Han, et al., 2022). This developmental shift provides a useful framework for interpreting our own findings. Drawing on a larger and developmentally broader sample than in our previous work (Tucciarelli et al., 2024), we were able to track how this exploratory period unfolds in children with upper limb differences. Consistent with our hypothesis, children with upper limb differences initially explored a broad range of solutions, engaging different combinations of effectors to achieve their goals. With age, they converged on fewer, more refined strategies, although this occurs later than in their two-handed peers. This extended period of sensorimotor exploration likely reflects the need to develop novel motor strategies, due to the inability to directly replicate the typical motor patterns of others. Our findings align with theories which emphasise extensive exploration as a key mechanism for generating and refining motor strategies (Meder et al., 2021; Ossmy, Han, et al., 2022), reinforcing concept of a parallel developmental trajectory for children with upper limb differences.

We note that the simultaneous engagement of multiple effectors likely increases the cognitive and motor load of action planning. Unlike their two-handed peers, who typically rely on hand-based strategies, children with upper limb differences must coordinate multiple body parts to achieve similar goals. This added complexity places greater demands on planning, sequencing, and real-time sensory feedback, which may explain why these children engage in a prolonged period of sensorimotor exploration. Supporting this, Allen et al. (2024) found that both adults and children with upper limb differences spend more time thinking before acting compared to their two-handed peers. However, while this increased load may challenge the motor system, it may also drive the development of enhanced problem-solving abilities, fostering creativity and cognitive flexibility (Keen, 2011). Although they spend more time thinking, adults and children with upper limb differences take fewer attempts to reach a solution (Allen et al., 2024). In this sense, the motor challenges imposed by physical constraints may offer opportunities for broader developmental gains in cognitive flexibility and adaptive planning.

These increased demands were reflected in reduced task efficiency. Using task completion time as a proxy, we found that although both groups showed age-related improvements, children with upper limb differences completed tasks more slowly than their two-handed peers. Fine motor tasks posed particular challenges, likely since they place heightened demands on precision and dexterity – functions that are closely tied to typical hand function. While larger effectors, like the torso or legs, can compensate for gross motor actions, they lack the fine-grained control for precise delicate manipulation. The use of the residual limb, though increasing with age, may still fall short of replicating the nuanced motor capabilities of a typical hand. As a result, tasks requiring fine manipulation may remain persistently effortful, even as children develop more refined compensatory strategies.

By systematically analysing the mechanical requirements of each task, we found robust evidence that children with upper limb differences adapt their motor strategies in a context-sensitive manner. Fine motor tasks for example, elicited significantly less torso use in children with upper limb differences, likely because bracing against the torso can obscure the visibility required to guide fine motor movements. In stabilisation tasks, all children increased use of their legs, suggesting a strategic shift toward more stable effectors which place greater emphasis on power and stability. Taken together, these findings suggest that the choice and coordination of alternative effectors are guided not only by availability but also by context. This ability to adjust motor strategies based on context aligns with findings which show children can plan their actions by selecting an appropriate tool based on task constraints (Beck et al., 2011), or anticipating the final position needed for success, such as pre-shaping the hand to align with an object's orientation (Comalli et al., 2016; Ossmy, Kaplan, et al., 2022). Much like two-handed children, as seen in our findings, children with upper limb differences appear to select effectors based on the anticipated need of stability and visibility. Rather than applying a single compensatory strategy, children with upper limb differences prospectively tailor their adaptive behaviours in a flexible, task-specific manner, optimising for stability, force, visibility, or precision as needed. These results extend this body of work by demonstrating that such adaptive planning is not dependent on typical limb structure but emerges even under altered anatomical constraints.

This task-specific flexibility raises important questions about what other factors shape the development of compensatory adaptations. Our results show that individual characteristics—such as age, residual limb anatomy, and perceived functional success—also play a key role in guiding motor behaviour. Developmentally, we observed a trade-off between effectors. With age, children with upper limb differences shifted from early reliance on the feet towards increased use of the residual limb. Although this shift aligns with our expectations of a convergence towards upper limb strategies, contrary to our hypothesis, we found an unexpected decrease in torso use and corresponding increase in leg use. These developmental shifts may be partially explained by environmental context. All tasks were performed while seated on the floor – a position that naturally brings the legs into closer proximity to the hands and makes them readily accessible. The legs offer both stability and enhanced visibility, making them an attractive option for children attempting new tasks. However, in everyday contexts such accessibility is limited as children spend hours seated at school desks, or the legs are often otherwise engaged in standing or walking. These findings highlight how effector selection is strictly shaped by functional capacity, but also context and body positioning.

Beyond developmental trends, anatomical differences were found to influence adaptive behavioural choices. As expected, children with longer residual limbs (i.e., a below-elbow differences) used their residual limb and torso more frequently than children with above-elbow differences. This is likely due to the increased functionality of a longer residual limb, where the presence of an elbow joint provides an alternative means of grip, and more equal limb lengths allow for greater ability to stabilise larger objects. Conversely, children with shorted residual limbs tended to rely more heavily on the lower limbs, specifically the legs and feet. These patterns support the view that motor behaviours are constrained by the body and illustrates how children flexibly reconfigure their motor behaviours within these constraints. For example, while carrying an object two-handed infants take shorter, slower steps (Heiman et al., 2019).

Although we anticipated that the functional success of each effector would drive its spontaneous use, this pattern was only observed for the torso and legs. Children who used these effectors successfully when instructed were more likely to engage them in their free choice behaviour, suggesting that prior success may guide motor choices. However, this relationship did not reach significance for the lower face and feet despite visually similar patterns. This implies that factors beyond effectiveness, such as perceived comfort, control, or social appropriateness may also influence behavioural choices. These findings resonate with the concept of exploration and exploitation, which suggests that children have a propensity to explore, and that success-based decision-making only becomes dominant in late childhood (Blanco & Sloutsky, 2024; Kim & Carlson, 2024; Ossmy, Han, et al., 2022). For example, in a novel motor task children failed to generalise previously successful strategies to guide exploration in a near-identical task, even after achieving success, children continued to test alternative strategies rather than reliably repeating the effective action (Ossmy, Han, et al., 2022). Similarly, in our study, children with upper limb differences engaged in a process of trial and error, experimenting with different effectors to discover which strategies feel most comfortable. This pattern suggests that motor exploration in these children is not solely outcome-driven but instead reflects a broader developmental process of building a flexible movement repertoire where comfort, control, and adaptability may outweigh immediate efficiency.

Adaptive behaviours may be further constrained by parental attitudes and social norms (Derikx et al., 2021). For example, children are often taught to walk in public spaces rather than run. In our study, many parents expressed concerns about, and actively discouraged, their children using their mouths for manipulation, fearing potential risks such as choking or damaging teeth. This may explain the relatively low rates of face use, particularly post- COVID-19 during which there was heightened caution around cleanliness and hygiene. Similarly, the feet, though potentially effective, may be perceived as unconventional, especially as children grow older and become more self-conscious about appearing different. Together these findings paint a nuanced picture of how children with upper limb differences acquire and refine compensatory behaviours. Early childhood is marked by broad exploratory behaviour, where children experiment with many effectors and combinations, or strategies, to complete everyday motor tasks. Over time, these strategies become more refined, converging on stable and more efficient patterns that are tailored to the child's anatomy, preferences, and experiences. This flexibility showcases the remarkable adaptability of the developing motor system.

Importantly, our findings challenge the assumptions embedded in many standardised measures of upper limb function, which primarily focus on whether a child can complete a task and how much they use their residual limb (Bagley & James, 2004; Buffart et al., 2006; Krumlinde-Sundholm et al., 2007). For example, during nine bimanual tasks, including putting on a sock and threading beads, the unilateral below-elbow test scores children on two domains: task difficulty and majority use of the residual limb (Bagley & James, 2004). Neither measure accounts for how children compensate by engaging other body parts or how efficient these alternative motor strategies are. Our data show that two children may achieve the same goal with entirely different strategies and levels of effort. Rather than trying to mimic typical patterns of motor behaviour, we suggest that therapeutic approaches could focus on refining alternative motor strategies and supporting an individual's natural adaptations. Interventions grounded in this understanding may be more empowering, helping children develop efficient and self-directed ways of engaging with their world. While the current study offers valuable insight into the flexibility of motor behaviour and group-level patterns of behaviour, individual strategies were often highly idiosyncratic. Longitudinal research would be valuable to better track the progression of adaptive strategies over time, examining how behavioural strategies are refined, particularly as children begin to interact with their peers and adjust to changing environments like starting school.

In conclusion, children with congenital upper limb differences exhibit remarkable motor adaptability. Through sensorimotor exploration, they develop novel, self-guided strategies which allow them to achieve their goals using a wide range of effectors. These findings underscore the importance of supporting – not correcting – adaptive behaviours, and recognising the diverse paths that children can take toward functional independence. By understanding the factors that shape motor adaptation, we can design more inclusive assessments and interventions that celebrate flexibility and empower children to succeed on their own terms.

References

Adolph, K., & Hoch, J. (2019). Motor Development: Embodied, Embedded, Enculturated, and Enabling. *Annual Review of Psychology*, *70*(1), 141–164. https://doi.org/10.1146/annurev-psych-010418-102836

Adolph, K., Hoch, J., & Cole, W. (2018). Development (of Walking): 15 Suggestions. *Trends in Cognitive Sciences*, *22*(8), 699–711. https://doi.org/10.1016/j.tics.2018.05.010

Allen, K. R., Smith, K. A., Bird, L.-A., Tenenbaum, J. B., Makin, T. R., & Cowie, D. (2024). Lifelong learning of cognitive styles for physical problem-solving: The effect of embodied experience. *Psychonomic Bulletin & Review*, *31*(3), 1364–1375. https://doi.org/10.3758/s13423-023-02400-4

Amoruso, E., Kromm, M., Spampinato, D., Kop, B., Muret, D., Rothwell, J., Rocchi, L., & Makin, T. R. (2021). Stimulating the deprived motor 'hand' area causes facial muscle responses in one-handers. *Brain Stimulation*, *14*(2), 347–350. https://doi.org/10.1016/j.brs.2021.01.022

Amoruso, E., Terhune, D. B., Kromm, M., Kirker, S., Muret, D., & Makin, T. R. (2023). Reassessing referral of touch following peripheral deafferentation: The role of contextual bias. *Cortex*, *167*, 167–177. https://doi.org/10.1016/j.cortex.2023.04.019

Bagley, A. M., & James, M. (2004). The Unilateral Below Elbow Test. *Developmental Medicine and Child Neurology*, *46*, 33–34.

Beck, S. R., Apperly, I. A., Chappell, J., Guthrie, C., & Cutting, N. (2011). Making tools isn't child's play. *Cognition*, *119*(2), 301–306. https://doi.org/10.1016/j.cognition.2011.01.003

Blanco, N. J., & Sloutsky, V. M. (2024). Exploration, exploitation, and development: Developmental shifts in decision-making. *Child Development*, *95*(4), 1287–1298. https://doi.org/10.1111/cdev.14070

Blumberg, M. S. (2009). *Freaks of nature: What anomalies tell us about development and evolution* (1. issued as an Oxford Univ. Press paperback). Oxford Univ. Press.

Bourgeois, K. S., Khawar, A. W., Neal, S. A., & Lockman, J. J. (2005). Infant Manual Exploration of Objects, Surfaces, and Their Interrelations. *Infancy*, *8*(3), 233–252. https://doi.org/10.1207/s15327078in0803_3

Buffart, L. M., Roebroeck, M. E., Pesch-Batenburg, J. M. F. B., Janssen, W. G. M., & Stam, H. J. (2006). Assessment of arm/hand functioning in children with a congenital transverse or longitudinal reduction deficiency of the upper limb. *Disability and Rehabilitation*, *28*(2), 85–95. https://doi.org/10.1080/09638280500158406

Cole, W. G., & Adolph, K. (2023). Learning to Move in a Changing Body in a Changing World. *Integrative and Comparative Biology*, *63*(3), 653–663. https://doi.org/10.1093/icb/icad083

Comalli, D. M., Keen, R., Abraham, E. S., Foo, V. J., Lee, M.-H., & Adolph, K. (2016). The development of tool use: Planning for end-state comfort. *Developmental Psychology*, *52*(11), 1878–1892. https://doi.org/10.1037/dev0000207

Derikx, D. F. A. A., Houwen, S., Meijers, V., Schoemaker, M. M., & Hartman, E. (2021). The Relationship between Social Environmental Factors and Motor Performance in 3- to 12-Year-Old Typically Developing Children: A Systematic Review. *International Journal of Environmental Research and Public Health*, *18*(14), Article 14. https://doi.org/10.3390/ijerph18147516

Franchak, J. M., & Adolph, K. (2024). An update of the development of motor behavior. *WIREs Cognitive Science*, *15*(6), e1682. https://doi.org/10.1002/wcs.1682

Hahamy, A., Macdonald, S. N., van den Heiligenberg, F., Kieliba, P., Emir, U., Malach, R., Johansen-Berg, H., Brugger, P., Culham, J. C., & Makin, T. R. (2017). Representation of Multiple Body Parts in the Missing-Hand Territory of Congenital One-Handers. *Current Biology*, *27*(9), 1350–1355. https://doi.org/10.1016/j.cub.2017.03.053

Hahamy, A., & Makin, T. R. (2019). Remapping in Cerebral and Cerebellar Cortices Is Not Restricted by Somatotopy. *Journal of Neuroscience*, *39*(47), 9328–9342. https://doi.org/10.1523/JNEUROSCI.2599-18.2019

Hahamy, A., Sotiropoulos, S. N., Henderson Slater, D., Malach, R., Johansen-Berg, H., & Makin, T. R. (2015). Normalisation of brain connectivity through compensatory behaviour, despite congenital hand absence. *eLife*, *4*, e04605. https://doi.org/10.7554/eLife.04605

Heiman, C. M., Cole, W. G., Lee, D. K., & Adolph, K. (2019). Object Interaction and Walking: Integration of Old and New Skills in Infant Development. *Infancy*, *24*(4), 547–569. https://doi.org/10.1111/infa.12289

Keen, R. (2011). The Development of Problem Solving in Young Children: A Critical Cognitive Skill. *Annual Review of Psychology*, *62*(1), 1–21. https://doi.org/10.1146/annurev.psych.031809.130730

Kim, S., & Carlson, S. M. (2024). Understanding explore-exploit dynamics in child development: Current insights and future directions. *Frontiers in Developmental Psychology*, *2*. https://doi.org/10.3389/fdpys.2024.1467880

Krumlinde-Sundholm, L., Holmefur, M., Kottorp, A., & Eliasson, A.-C. (2007). The Assisting Hand Assessment: Current evidence of validity, reliability, and responsiveness to change. *Developmental Medicine & Child Neurology*, *49*(4), 259–264. https://doi.org/10.1111/j.1469-8749.2007.00259.x

Markham, J. A., & Greenough, W. T. (2004). Experience-driven brain plasticity: Beyond the synapse. *Neuron Glia Biology*, *1*(4), 351. https://doi.org/10.1017/s1740925x05000219

Meder, B., Wu, C. M., Schulz, E., & Ruggeri, A. (2021). Development of directed and random exploration in children. *Developmental Science*, *24*(4), e13095. https://doi.org/10.1111/desc.13095

Muret, D., & Makin, T. R. (2021). The homeostatic homunculus: Rethinking deprivation-triggered reorganisation. *Current Opinion in Neurobiology*, *67*, 115–122. https://doi.org/10.1016/j.conb.2020.08.008

Ossmy, O., Han, D., Cheng, M., Bianco, C., Kaplan, B., & Adolph, K. (2022). *First "Where" and then "How": Developmental Processes in Exploring Solutions to Problems with Hidden Demands*. OSF. https://doi.org/10.31234/osf.io/m7tcr

Ossmy, O., Kaplan, B. E., Han, D., Xu, M., Bianco, C., Mukamel, R., & Adolph, K. (2022). Real-time processes in the development of action planning. *Current Biology*, *32*(1), 190-199.e3. https://doi.org/10.1016/j.cub.2021.11.018

Pacheco, M. M., & Newell, K. M. (2018). Transfer of a learned coordination function: Specific, individual and generalizable. *Human Movement Science*, *59*, 66–80. https://doi.org/10.1016/j.humov.2018.03.019

Palmer, C. F. (1989). The discriminating nature of infants' exploratory actions. *Developmental Psychology*, *25*(6), 885–893. https://doi.org/10.1037/0012-1649.25.6.885

Rochat, P. (1989). Object manipulation and exploration in 2- to 5-month-old infants. *Developmental Psychology*, *25*(6), 871–884. https://doi.org/10.1037/0012-1649.25.6.871

Root, V., Muret, D., Arribas, M., Amoruso, E., Thornton, J., Tarall-Jozwiak, A., Tracey, I., & Makin, T. R. (2022). Complex pattern of facial remapping in somatosensory cortex following congenital but not acquired hand loss. *eLife*, *11*, e76158. https://doi.org/10.7554/eLife.76158

Shannon, C. E. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, *27*(3), 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Stoeckel, M. C., Seitz, R. J., & Buetefisch, C. M. (2009). Congenitally altered motor experience alters somatotopic organization of human primary motor cortex. *Proceedings of the National Academy of Sciences*, *106*(7), 2395–2400. https://doi.org/10.1073/pnas.0803733106

Sutton, R. S., & Barto, A. G. (2018). *Reinforcement Learning, second edition: An Introduction*. MIT Press.

Tucciarelli, R., Bird, L., Straka, Z., Szymanska, M., Kollamkulam, M., Sonar, H., Paik, J., Clode, D., Hoffmann, M., Cowie, D., & Makin, T. R. (2024). *Shaping the developing homunculus: The roles of deprivation and compensatory behaviour in sensory remapping* (p. 2024.11.26.624817). bioRxiv. https://doi.org/10.1101/2024.11.26.624817

Appendix B: Supplementary materials for chapter 3

Table B.1. Full distribution of effector combinations observed in children with upper limb differences during task completion.

Two		Three		Four	
Intact, residual	27.81%	Intact, residual, legs	29.84%	Intact, residual, torso, legs	5.02%
Intact, feet	3.56%	Intact, residual, torso	16.18%	Intact, residual, legs, feet	0.32%
Intact, legs	1.79%	Intact, residual, feet	1.73%	Intact, residual, torso, feet	0.03%
Intact, lower face	0.68%	Intact, feet, legs	0.63%	Intact, residual, lower face, legs	0.03%
Intact, torso	0.29%	Intact, residual, lower face	0.16%	Intact, residual, lower face, feet	0.0024%

Chapter 4: Embodied experience and problem solving in childhood: innovation and Imitation in children with upper limb differences

Abstract

Children with congenital upper limb differences grow up navigating a world designed for two-handed individuals, requiring them to develop alternative motor strategies for everyday tasks through self-guided exploration rather than direct imitation. These adaptations may extend beyond motor skills, potentially influencing broader cognitive processes such as innovation and imitation. However, little is known about how physical differences shape children's approach to these skills. This study examined whether differences in motor experience influenced cognitive strategy, focusing on tool innovation and imitation fidelity. Children aged 4-9 years with (n = 30) and without (n = 50) congenital upper limb differences completed two tasks: (1) the hook task, which required retrieving a small basket from a vertical tube using a pipe cleaner and string, to assess innovation, and (2) a puzzle box task to measure imitation fidelity. General intelligence was also assessed using the Raven's Coloured Progressive Matrices. Results showed that innovation success was predicted by age and general intelligence across all participants. There were no significant group differences in overall innovation performance or imitation fidelity. However, in children with upper limb differences, higher imitation fidelity was associated with lower innovation success – an pattern reversed in two-handed children, where greater imitation predicted better outcomes. These findings are discussed in the context of embodied cognition and cognitive flexibility, suggesting developmental equivalence in core abilities but potential differences in strategy. For children with upper limb differences, imitation may serve more affiliative or social functions, rather than directly supprting problem-solving.

Introduction

Children with congenital upper limb differences face a unique set of challenges daily as they learn to navigate a world designed for individuals with two fully functional hands. While most people take for granted everyday actions such as zipping up a jacket or tying shoelaces, children whose conditions range from fused or partial digits to the complete absence of one or both arms, cannot complete these tasks in the same way two handed people do. Instead, these children must develop alternative motor strategies through self-guided exploration and trial-and-error. They cannot often rely on direct imitation (Tucciarelli et al., 2024), which is a very common strategy for learning about the world in two-handed children (Want & Harris, 2001). Importantly, these adaptations may extend beyond physical skills, intersecting with broader areas of cognitive development, such as problem-solving, imitation, and flexible thinking. As such children with congenital upper limb differences may develop advanced cognitive flexibility and innovative problem-solving skills. This raises an important question: does growing up with an upper limb difference shape how children approach novel problem-solving tasks or the extent to which they imitate others? The present study addresses this by comparing the performance of children with and without upper limb differences on tasks designed to assess innovative problem-solving and the propensity to imitate. In doing so, we aim to determine whether differences in motor experience translate to differences in cognitive strategy.

To develop these unique motor strategies, successfully compensating for missing hand function, children must think flexibly, evaluating, adapting and refining their actions relative to a desired goal. In developmental psychology, such problem-solving abilities are closely tied to the concept of tool innovation (Griffin & Guez, 2014; Rawlings & Reader, 2023), which is broadly defined as the ability to independently generate novel yet functional solutions to unfamiliar problems (Cutting et al., 2011). While humans routinely use hundreds of tools, from toothbrushes to cutlery, creating new tools in the absence of pre-existing solutions involves distinct cognitive processes. Much like motor adaptation, tool innovation is thought to draw upon planning, creativity, causal reasoning, and cognitive flexibility, all of which are late developing skills (Davis et al., 2022). Crucially, it also requires purposeful exploration, enabling children to evaluate each attempt and adapt in response to failure (Burdett & Ronfard, 2023; Evans et al., 2021; Evans & Jirout, 2023). Before physically constructing a novel tool, children must first recognise the end-goal and mentally represent how the available materials could be transformed or combined to achieve it (Cutting et al., 2011; Rawlings & Legare, 2021).

What do we know about tool innovation in two-handed children?

A growing body of research has established that young children born with two hands often struggle to innovate novel tools. Foundational research using the “hook task”, a problem-solving task in which children must retrieve a small bucket from the bottom of a vertical tube using only string or a pipe cleaner, showed that around 90% of children under the age of five failed to independently generate a functional solution (Beck et al., 2011; Cutting et al., 2011; Nielsen et al., 2014). Even when prompted to try different strategies, success only rises to around 15% (Chappell et al., 2013). Successful innovation required participants to bend the pipe cleaner into a hook shape, a solution that does not consistently emerge until around the age of eight (Beck et al., 2011; Cutting et al., 2011). Subsequent studies have replicated these findings using other innovation tasks. For example, fewer than 15% of 4-year-olds were able to independently solve a problem that required them to fill a vertical tube with water to retrieve a toy (Hanus et al., 2011; Nielsen, 2013). However, success rates significantly increased with age, with 7- to 8-year-olds solving such problems around 50-60% of the time (Ebel et al., 2019; Hanus et al., 2011). Comparable trends have also been observed in tasks requiring children to straighten a pipe cleaner to push a ball through a horizontal tube (Chappell et al., 2013; Cutting et al., 2011), or to create a loop from wooden wool to retrieve a sticker on a platform behind a mesh screen (Tennie et al., 2009). These findings collectively indicate that the ability to innovate tools develops gradually and is typically limited in early childhood.

Despite failing to independently innovate a functional solution to the hook task, children as young as 4 years were able to successfully complete the task when given the option of choosing between a pre-made hooked pipe cleaner and a straight one (Beck et al., 2011). This suggests that the primary challenge does not lie in using the tool itself, but rather in mentally visualising the range of possible solutions (Harris, 2021). Supporting this view, recent findings suggest that difficulties in tool innovation may be rooted in prospective perception, the ability to anticipate how objects can be modified and used to achieve a goal (Colbourne et al., 2024). Specifically, young children may struggle to anticipate the spatial relations between the available materials and the end goal. In the hook task for example, success depends on recognising that bending the pipe cleaner into a hook will allow it to catch the handle of the basket so it can be pulled from the tube.

As children mature, they gradually develop the capacity to coordinate multiple high-level cognitive processes, including planning, creativity, and causal reasoning (Rawlings & Legare, 2021). These abilities enable them to assess the properties of the available materials, how they might interact with the environment, and switch strategies when initial attempts are unsuccessful. While these cognitive developments align with age-related improvements in tool innovation (Rawlings, 2022), the relationship remains complex. For instance, a recent study found that neither executive functioning nor divergent thinking predicted tool innovation success. However, they did find a relationship between receptive vocabulary and innovation, suggesting that receptive language may serve as a proxy for general intelligence. It is important to note, however, that these findings are based on a relatively small sample of 6- to 8-year-olds, a group in which innovation success rates are typically low, potentially limiting the likelihood of detecting significant effects. Conversely, inhibitory control has been found to predict successful tool innovation in 3- to 6-year olds (Gönül et al., 2018). Given these mixed findings, the present study will instead focus on general intelligence using Raven's Coloured Progressive Matrices, a spatial reasoning measure, to extend previous findings on receptive vocabulary, by investigating a potential link between intelligence and tool innovation (Beck et al., 2016).

Learning through imitation

While innovation tasks highlight limitations in children's independent problem-solving abilities, children demonstrate extremely strong capabilities when learning from others. From an early age, children show a natural inclination to learn socially, seeking information through both explicit instruction and passive observation (Csibra & Gergely, 2009; Tomasello, 1999; Tomasello et al., 2005). Recent research revealed that most 3-5-year-old children will switch from an efficient method of solving a puzzle box to a less efficient one after observing a demonstration (Davis et al., 2022), whereas chimpanzees tend to stick with their established strategies unless their current method becomes less effective. In such cases, they adopt a more efficient solution by combining their own behaviours with socially-acquired information (Davis et al., 2016).

This strong reliance on imitative learning may help to explain the low levels of independent innovation observed in early childhood; children may simply prioritise social information at the expense of exploratory problem-solving. Although young children often fail to independently innovate a novel tool, almost all succeed after observing a single demonstration (Beck et al., 2011; Cutting et al., 2011). Similarly, in a study using the Multiple-Methods Box, a puzzle box from which a reward can be retrieved in multiple ways, over 90% of children engaged in some level of imitation, with this tendency being most pronounced among 4- to 5-year-olds (Carr et al., 2015). Moreover, when given the choice between attempting a novel innovation task independently or watching someone else solve it first, the majority of children aged 4 to 11 years, opt for a social demonstration, underscoring their strong preference for social information over independent problem-solving (Flynn et al., 2016; Rawlings et al., 2022). Notably, this tendency to rely on social learning is not limited to early childhood, it has also been observed in both older children and adults (Van Leeuwen et al., 2014; Whiten et al., 2016).

While children typically favour copying relevant goal-directed actions (Want & Harris, 2001), they also show a propensity to 'overimitate', reproducing actions that are causally irrelevant or redundant (Carr et al., 2015; Lyons et al., 2007; Nielsen et al., 2012). Research suggests that imitation can serve two functions: it can be instrumental, helping children learn how to achieve a goal, or conventional, used to signal affiliation with others or conform to perceived social conventions (Legare & Nielsen, 2015). This tendency to imitate all actions, whether causally relevant or not, has been interpreted as a strategy to fulfil the latter function, particularly when actions are perceived as socially normative rather than necessary for skill acquisition. Children must learn to balance their inclination to imitate with their capacity to innovate, especially since copying others is often an effective method of acquiring information.

In a recent study, children who chose to attempt the Multiple-methods puzzle box without first observing a demonstration were more likely to generate innovative solutions in the hook task (Rawlings et al., 2022). Notably, younger children were more likely to opt for the demonstration rather than attempting the task independently. These findings provide an evidence base for an inverse relationship between imitation fidelity and tool innovation in early childhood. While younger children rely more heavily on social learning to acquire foundational knowledge about the world, with age, they develop a stronger understanding of causal relationships and improved executive functioning, and as such they become more capable of exploring independently and innovating new solutions.

Congenital upper limb differences

To understand whether these processes differ in children with upper limb differences, we now turn to the concept of embodiment. Theories of embodied cognition propose that cognitive processes are fundamentally shaped by physical experiences, specifically the form and function of the body (Wilson, 2002). From this perspective, a child’s physical capabilities, and the actions they can or cannot perform, shape how they perceive and interact with the world, influencing their problem-solving strategies and learning mechanisms.

Due to the rarity and variability of upper limb differences, these children are unlikely to encounter models with similar motor abilities in everyday life. Therefore, direct imitation may be impractical or unfeasible, requiring them to engage in self-guided exploration to adapt observed actions or to acquire novel motor strategies. It is plausible that these interactions may foster greater cognitive flexibility, stronger causal reasoning, and more reflective planning. Supporting this idea, recent research suggests that both children and adults with upper limb differences adopt different cognitive approaches to problem-solving compared to their two-handed peers, tending to spend more time thinking before acting, even when motor constraints are equated (Allen et al., 2024). This may reflect a broader shift in cognitive strategy, potentially an adaptive response to limited direct motor imitation opportunities. This raises important questions: do children with upper limb differences imitate less frequently than their two-handed peers due to functional constraints, or do they imitate to a similar or even greater extent to conform to social norms and foster social affiliation?

The present study investigates tool innovation abilities and imitation fidelity in 30 children aged 4-9-years with congenital upper limb differences, a large sample for a specialised population, and 50 age-matched two-handed controls. Participants completed two primary tasks: the hook task to assess tool innovation, and a puzzle box task to measure imitation fidelity. General intelligence was measured using the Raven's Coloured Progressive Matrices. This could extend previous findings suggesting that the observed relationship between intelligence and innovation success may reflect underlying general cognitive ability but using an arguably more appropriate measure of visuospatial ability rather than receptive vocabulary. We aim to: (1) replicate established age-related improvements in tool innovation, and the inverse relationship between imitation fidelity and innovation (Beck et al., 2011; Rawlings et al., 2022); and (2) explore whether children with upper limb differences demonstrate enhanced cognitive flexibility or whether their performance reflects developmental equivalence with their two-handed peers. Specifically, we hypothesise that children with upper limb differences will show reduced imitation fidelity and enhanced innovation success, reflecting daily embodied problem-solving to achieve functional adaptations, and limitations on their ability to directly imitate the actions of others.

Method

Participants

Eighty children aged 4-9 years were split across two groups: 30 children with a congenital upper limb difference (*M* = 6.71 years, *SD* = 1.84; 11 female) and 50 age-matched two-handed children (*M* = 7.03 years, *SD* = 1.66; 27 female). To focus the analysis on the effects of limb differences, two additional children with neurodevelopmental conditions were excluded.

Children with upper limb differences were recruited through two UK-based limb difference support charities. This study included children born with an upper limb difference affecting one or both arms. Limb anomalies varied among participants, ranging from partial hands to complete absence of the lower arm (Table 4.1). While not all children had received a formal clinical diagnosis, reported diagnoses included symbrachydactyly, radial dysplasia, transverse arrest, and amniotic band syndrome. Details of specific limb anomalies were self-reported by parents and caregivers and validated during in-person testing. Of the 30 children, 25 had never been fitted with or did not use a prosthesis, one child reported recent weekly use of a new prosthetic, and four children reported monthly use for specific activities, e.g., sports.

Age-matched, two-handed control children were recruited through primary schools, holiday camps, and a local science festival. Of the 50 children, 43 were right-handed.

This study was approved by the ethics committee at Durham University (PSYCH-2019-08- 30T10_08_45-mnvj24).

Table 4.1. Participant demographics for the sample of children with congenital upper limb differences.

ID	Age	Affected limb(s)	Level of limb difference	
			Right	Left
1	7.78	Right, left	3 digits	1 digit
2	4.39	Right, left	5 digits, no pincer	5 digits, no pincer
3	4.73	Right	Partial hand, 0 digits	-
4	7.81	Right	Absent lower forearm	-
5	5.87	Right	Partial hand, 0 digits	-
6	6.18	Left	-	Partial hand, 0 digits
7	9.95	Left	-	Absent above elbow
8	5.52	Right, left	3 partial digits	Partial hand, 0 digits
9	5.92	Left	-	2 digits, no pincer
10	9.57	Left	-	Absent lower forearm
11	6.98	Right, left	5 partial digits	5 partial digits
12	5.68	Right	Partial hand, 0 digits	-
13	9.15	Left	-	Absent below elbow
14	8.89	Right	Absent below elbow	-
15	4.21	Right	Partial hand, 0 digits	-
16	4.81	Left	-	4 digits, no pincer
17	4.83	Left	-	Absent lower forearm
18	8.25	Left	-	2 digits, pincer
19	6.44	Left	-	Absent below elbow
20	6.07	Left	-	1 digit, no pincer
21	4.42	Right	4 digits, pincer	-
22	5.23	Left	-	Absent below elbow
23	6.41	Left	-	3 digits, pincer
24	4.41	Right	Partial hand, 0 digits	-
25	9.2	Right	Absent lower forearm	-
26	9.8	Right, left	3 digits, pincer	3 digits, limited pincer
27	9.3	Right	5 digits, no pincer	-
28	7.22	Left	-	Absent lower forearm
29	6.47	Left	-	2 partial digits, pincer
30	5.71	Right	Absent lower forearm	-

Note. Participant 19 has an additional lower limb difference, bilateral fibula hemimelia resulting in bilateral foot amputation

Task and Procedure

Innovation - Hook task

To assess children's innovative problem solving abilities, participants completed the hook task (Beck et al., 2011). Seated at a table opposite the researcher, each participant was presented with a transparent plastic tube measuring 19.5cm in height and 6cm in diameter. At the base of the tube was a small basket containing a sticker, Figure 4.1. The experimenter presented a 30cm pipe cleaner, demonstrated bending it in half and then straightening it, before placing it beside the tube. This demonstration was repeated with a 30cm length of string. Participants were then instructed: "Can you see the sticker inside this tube? Get it out any way you like". To prevent retrieval by simply lifting the tube, the experimenter placed their hands on its base. If the participant did not begin attempting to retrieve the basket they were systematically prompted with the phrase: "You can try anything you like". If the participant successfully retrieved the basket within three minutes, both the time taken and method used were recorded. If the task was not completed within the time limit, the trial was recorded as unsuccessful. The experimenter then demonstrated the solution by forming a hook from the pipe cleaner and retrieving the basket. Participants were subsequently given a second opportunity to replicate the solution and complete the task.

Figure 4.1. Two children participating in the hook task, in which they attempt to retrieve a basket containing a sticker from the bottom of a transparent plastic tube using a pipe cleaner and string. Left: A child with two hands is shown retrieving the basket using a hook-shaped tool made from a pipe cleaner. Right: A child with a congenital upper limb difference affecting the right hand is shown constructing a hook out of a pipe cleaner.

Imitation fidelity

To assess children's propensity to imitate, participants completed the imitation fidelity puzzle box. While seated at a table, the puzzle box was positioned in front of the experimenter, with the surface marked with an "X" oriented on the top face of the box and a small door located on the front face (Figure 4.2).

Figure 4.2. Setup of the imitation fidelity puzzle box task. The image shows a researcher demonstrating the task to a child with two hands. The child observes as the researcher performs a sequence of actions to open the puzzle box and retrieve a reward inside.

Once the participant's attention was secured by saying: "Look at this," the experimenter picked up a rod with their right hand, traced the "X" on the top of the box, and then tapped the centre of the box three times. The rod was then placed on the table while the experimenter opened the small door at the front-facing side of the puzzle box. Next, the experimenter inserted the rod into the opening and used the Velcro tip to a retrieve a smaller box contained inside. The experimenter removed a toy from the small box, showed it to the participant, and said, "Look at this," before returning the small box to its original position in the puzzle box. The experimenter then repositioned the puzzle box in front of the participant and said, "Now it's your turn."

Imitation fidelity was scored as per Whiten et al (2016). The total score was out of 10. A maximum of 4 points were given for imitation of relevant actions, such as opening the box and retrieving the reward. Up to 6 points were given for overimitation, instances of imitating irrelevant actions including tracing the "X" and tapping the top of the box prior to opening (Table 4.2). Higher scores reflect greater imitation fidelity.

Table 4.2. Scoring criteria for the puzzle box task. Imitation fidelity was scored out of 10, inclusive of both relevant and irrelevant actions.

Action	Relevance	Scoring criteria
X traced	Irrelevant	- Traced both directions = 2 - One direction only = 1 - Traced X more than once = 1 - Traced alternative pattern = 1 - Not traced = 0
Number of box taps	Irrelevant	- 3 taps = 2 - Any number other than 0 or 3 = 1 - 0 taps = 0
Box opened	Relevant	- Yes = 2 - No = 0
Used stick to retrieve the reward	Irrelevant	- Yes = 2 - No = 0
Reward retrieved	Relevant	- Yes = 2 - No = 0

General Intelligence - Raven's Coloured Progressive Matrices

To assess general intelligence, participants completed the Raven's Coloured Progressive Matrices (Raven et al., 1990), a non-verbal cognitive test that measures abstract reasoning and problem-solving ability. For each item, children were asked to select one of six options to correctly complete a visual pattern. Responses were scored as correct or incorrect, with a maximum raw score of 36. Raw scores were converted to age-normed standard scores using published normative data.

Statistical analyses

We first examined the success rate in the hook task by inspecting the proportion of participants in each group who successfully completed the task within the time limit. To formally assess the predictors of success, we conducted a binomial logistic regression with task success (pass/fail) as the dependent variable. Predictor variables included group, age in years, intelligence as measured by standardised Raven's scores, and imitation fidelity (score out of 10 as above). Interactions between group and each predictor were also included to assess for potential group differences in these effects. Due to one missing datapoint in the intelligence domain, one child with an upper limb difference was excluded from this analysis, resulting in a final sample size of N = 79.

Results

Overall, of the 80 children who participated in this study, 41.25% (*n* = 33) successfully retrieved the basket from the tube in the hook task. All successful children attempted to modify the pipe cleaner into a hook, except for two children with upper limb differences, who employed an alternative strategy, twisting the pipe cleaner into a spiral to retrieve the basket.

One child with two hands successfully constructed a hook but was unable to retrieve the basket within the time limit and was therefore scored as unsuccessful. Additionally, three children with upper limb differences and two children with two hands successfully retrieved the basket using the "dragging" technique (Beck et al., 2014; Rawlings et al., 2022), in which an unmodified, straight pipe cleaner was wedged into the weave of the basket weave and used to drag it out of the tube. As this technique did not involve tool innovation, it was scored as unsuccessful. All children who failed to complete the hook task could successfully create a hook and retrieve the basket after a demonstration by the researcher.

A binary logistic regression was conducted to examine the effects of group, age, intelligence, and imitation fidelity on the likelihood of success in the hook task. The model was statistically significant, $\chi^2(7, N = 79) = 37.31$, $p < .001$, indicating that the predictors collectively distinguished between those who succeeded and those who failed. The model showed a good fit, with a Tjur's R^2 of .407, indicating moderate discriminative ability. Classification accuracy was 74.7%, correctly predicting 66.7% of successes and 80.4% of failures.

Contrary to our prediction, there was no significant main effect of group (p = .74), suggesting that the probability of success did not differ between children with upper limb differences and their two-handed peers (Figure 4.3). Further analysis confirmed that there was also no significant group difference in time to success (U = 170.00, p = .103).

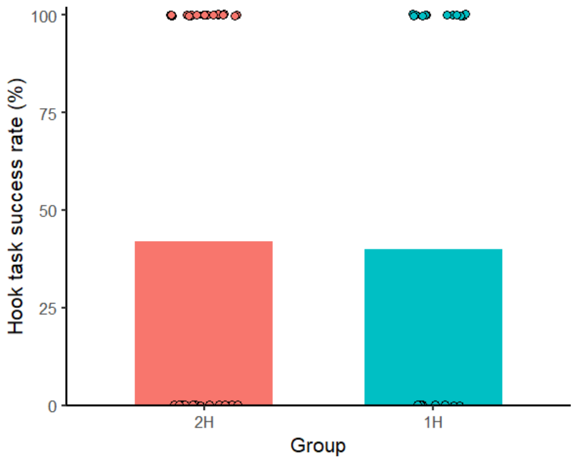


Figure 4.3. Percentage of children with upper limb differences and two-handed controls who successfully completed the hook task.

However, consistent with our predictions, success on the hook task was significantly predicted by age (β = 0.76, SE = 0.27, Wald = 7.91, p = .005, OR = 2.14), such that for every year of age, children were 2.14 times more likely to solve the hook task (Figure 4.4). This effect did not significantly differ between groups (p = .23).

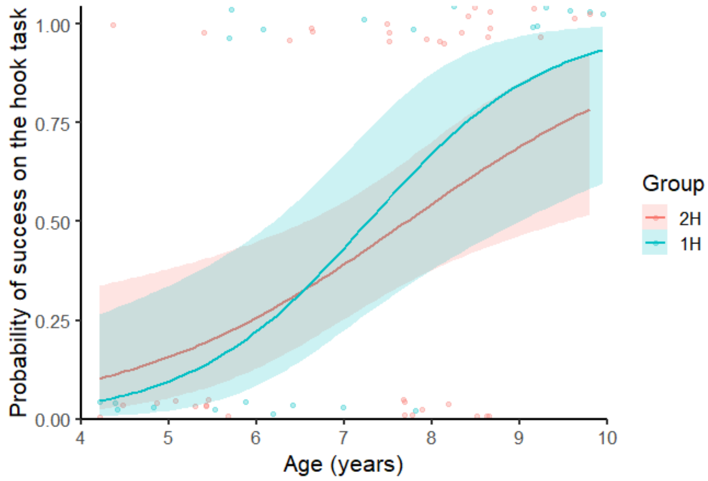


Figure 4.4. Predicted probability of success on the hook task as a function of age for children with upper limb differences (1H) and children with two hands (2H). Solid lines show logistic regression fits for each group, with shaded ribbons representing 95% confidence intervals.

Intelligence was also positively associated with success (β = 0.05, SE = 0.02, Wald = 6.02, p = .014, OR = 1.05), indicating that children with higher non-verbal intelligence were more likely to solve the hook task (Figure 4.5). This effect did not interact with group (p = .56).

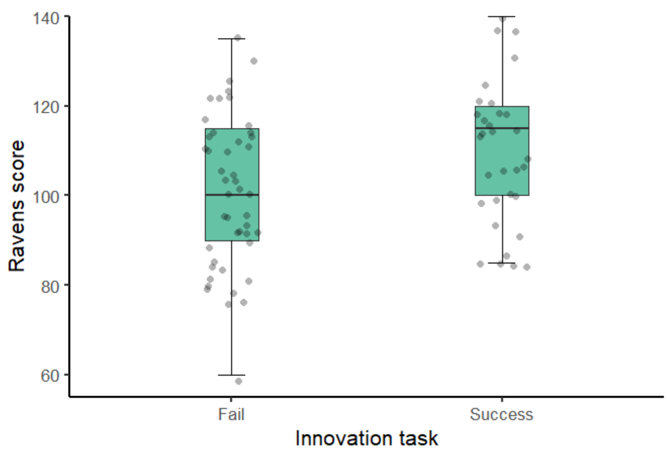


Figure 4.5. Distribution of standardised Raven's scores by hook task success.

Although imitation fidelity did not show a significant main effect (p = .34), there was a significant interaction between imitation fidelity and group (β = -0.75, SE = 0.37, Wald = 4.08, p = .043, OR = 0.47). For children with upper limb differences, higher imitation fidelity was associated with lower success on the hook task. In contrast, for children with two hands, higher imitation fidelity was associated with a greater likelihood of success (Figure 4.6).

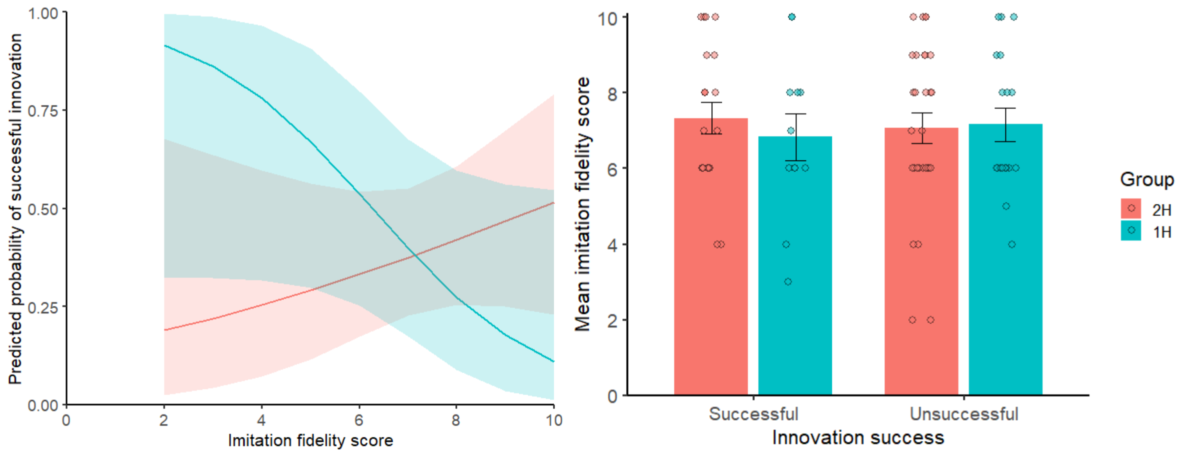


Figure 4.6. Left: Predicted probability of success on the hook task as a function of imitation fidelity score for children with upper limb differences (1H) and children with two hands (2H). Solid lines showlogistic regression fits for each group, with shaded ribbons representing 95% confidence intervals. Right: Mean imitation fidelity scores for children who were successful vs. unsuccessful on the hook task, plotted separately for each group. Bars represent group means, with error bars indicating standard errors.

To explore whether this interaction reflected overall group differences in imitation behaviour, a Mann-Whitney U test was conducted to compare the propensity to imitate between children with upper limb differences and two-handed controls. The results showed no significant difference between groups, U = 6.98, p = .598. Children with upper limb differences (M = 7.03, SD = 1.94) and two-handed children (M = 7.18, SD = 2.07) displayed similar levels of imitation fidelity, suggesting that both groups were equally likely to copy both relevant and irrelevant actions in the puzzle box task.

Discussion

This study explored whether embodied motor experience influence's children's problem-solving abilities and reliance on social learning, by comparing tool innovation success and imitation fidelity in children with congenital upper limb differences and age-matched two-handed controls. To our knowledge, this is the first study to examine how embodied motor experience shapes the relationship between imitation and innovation in childhood, providing new insights into how cognitive strategies may adapt in response to physical constraints. Consistent with previous findings, innovation success was predicted by age (Beck et al., 2011, 2016; Cutting et al., 2011; Nielsen et al., 2014). However, contrary to our hypothesis, children with upper limb differences did not outperform their two-handed peers on the tool innovation task, nor did they exhibit reduced imitation fidelity.

Given the vastly different embodied experiences of children born with upper limb differences, the absence of overall group differences in innovation success was unexpected. However, while these children did not demonstrate enhanced innovation success, crucially they also showed no deficits. All children who initially failed the hook task successfully completed it following a demonstration, suggesting that motor constraints did not inhibit task completion. These findings suggest a pattern of developmental equivalence, whereby similar outcomes are achieved via different physical strategies. Notably, the performance of two-handed children in our study closely mirrors findings reported by Colbourne et al., (2024), who summarised 19 published studies on the hook task, where average innovation success for this age group was similar to the current study, reinforcing consistent developmental trajectories in innovation.

One potential explanation for the similar performance across groups is general intelligence, which was a consistent predictor of success on the hook task in across groups. Regardless of motor experience, children with high general intelligence scores were more likely to solve the hook task, suggesting that core cognitive abilities play a foundational role in innovation success. This extends previous findings which identified a link between innovation success and receptive vocabulary, which was proposed to serve as a proxy for general intelligence (Beck et al., 2016).

However, it is possible that the convergent nature of the hook task may have masked differences in problem-solving abilities driven by embodied experience. Children with upper limb differences routinely develop unique motor strategies to navigate everyday motor challenges, such as tying shoelaces or zipping up a jacket. This embodied experience likely extends beyond motor adaptation, but also divergent thinking – the ability to generate multiple or novel solutions to a problem. Such cognitive flexibility may not be fully captured by a task designed with only one correct solution. Two children with upper limb differences in our study solved the hook task using a novel spiral technique - a strategy not observed in any of the two-handed children. This suggests that embodied experience may influence how children approach a problem, enabling them to generate a novel solution even when a task is designed to elicit a single correct response.

This observation reinforces the value of alternative open-ended tasks such as the Multiple Methods Box that allow for variation in tool use and solution strategies. Such tasks could provide a more sensitive measure of creativity and innovation by providing a space for diverse approaches. Further research using these paradigms could help determine whether the developmental trajectory of innovation is truly consistent across groups, or whether meaningful differences emerge when children are given more opportunities to explore.

Supporting this idea, recent findings have highlighted the importance of purposeful exploration in innovation (Burdett & Ronfard, 2023; Evans et al., 2021). Children who adapted or refined their previous failed attempts, by adding, removing, or modifying materials, were more likely to succeed than those who discarded their attempt and started from scratch after each failure. The rigid structure of the hook task may not have provided sufficient opportunities to showcase this kind of exploration and given the adaptive nature of their everyday motor behaviour children with upper limb differences are likely to be particularly adept at this.

Like innovation, imitation fidelity did not differ between groups. This is notable given that direct imitations in daily life are often impractical or unfeasible for children with upper limb differences due to motor constraints. Nevertheless, in our puzzle box task imitation was possible for all participants given that all demonstrated actions were performed with a single hand. The absence of group differences in these areas points towards shared core abilities between the two groups but is indicative of differences in cognitive strategies. These findings reflect those of a recent study where children and adults with an upper limb difference performed similarly in an online problem-solving game in which physical constraints were equalised, but used different cognitive strategies – taking more time to think and solving puzzles using fewer attempts (Allen et al., 2024). These findings collectively suggest that motor differences do not impair problem-solving or innovation abilities but may foster alternative cognitive strategies characterised by more planning and exploration.

Despite these surface similarities, the relationship between imitation and innovation diverged between groups. Among two-handed children, higher imitation fidelity on the puzzle box was associated with greater innovation success in the hook task, a finding that contrasts with prior claims that imitation may constrain tool innovation (Legare & Nielsen, 2015). For example, children who opted to solve a novel puzzle box individually by foregoing a demonstration were more likely to successfully solve the hook task, suggesting that innovation is supported by independent problem-solving rather than social learning (Rawlings et al., 2022). However, in the present study, children who more closely imitated the observed demonstration in the puzzle box task, relying on social learning, also tended to perform better on the hook task. In this context, imitation does not constrain innovation in two-handed children but rather support effective innovative strategies.

In contrast, for children with upper limb differences, higher imitation fidelity was associated with lower innovation success. This reversal suggests that imitation may serve a different cognitive or social significance in this group. Rather than facilitating instrumental learning, such that imitation is used as a means of acquiring the necessary skills to achieve a goal, imitation may be more affiliative, driven by a desire to conform or align socially with others in the face of their physical differences. While two-handed children show a natural inclination for learning through imitation from an early age, congenital hand anomalies typically prevent direct imitation of motor actions. Instead, these children typically rely on self-guided exploration or modifying observed behaviours to fit their motor capabilities. Over time, this likely fosters a learning style grounded in cognitive flexibility and independent exploration. The inverse relationship between imitation and innovation observed in this group may reflect a tension between exploratory problem-solving and a need to fit in. Children with a higher propensity to imitate may be temporarily suppressing their typical exploratory problem-solving strategies in favour of social conformity.

Strikingly, children with upper limb differences who exhibited low imitation fidelity (a score of 2) had a predicted success rate of 92%, far exceeding the best-performing two-handed children, whose success rate peaked at 51% for those with maximum imitation fidelity (a score of 10). This suggests that for children with upper limb differences, selective imitation, focusing on relevant actions and filtering out redundant information, can be a powerful advantage, enabling them to outperform their two-handed peers on innovation tasks. Rather than passively replicating observed actions, or ‘overimitating’, greater innovation success in these children requires adaptation through a combination of replicating necessary actions and self-guided exploration. In this sense, motor constraints may promote more efficient goal-directed learning.

There are several limitations for this study that should be acknowledged. First, the convergent task design may have underestimated the innovation capabilities of children with upper limb differences, who showed some novel strategies despite the single-solution design. Future research should employ more divergent innovation tasks with multiple solution paths, allowing for repeated opportunities for innovation, which will either confirm the developmental equivalence between the two groups, or alternatively highlight differences in exploratory problem-solving abilities resulting from embodied experience. Second, the role of social motivation in imitation remains speculative. Direct measures of social affiliation or conformity would clarify whether imitation is primarily socially or instrumentally motivated in each group.

Finally, further assessment of cognitive processes beyond general intelligence is warranted. Although prior work has shown mixed results regarding executive functions and innovation (Beck et al., 2016; Gönül et al., 2018), assessing components such as cognitive flexibility, planning, and working memory could help to clarify whether differences in embodied motor experience shape the underlying strategies used in problem-solving.

In conclusion, we found that children with congenital upper limb differences demonstrated equivalent levels of imitation and innovation as their two-handed peers. However, the strategies they used to achieve these outcomes markedly differed. For children with upper limb differences, high imitation fidelity appeared to suppress innovation success, suggesting that imitation in this group may be motivated more by social affiliation than by instrumental learning. Conversely, children who imitated less, and likely relied more on exploratory strategies, demonstrated superior problem-solving abilities, outperforming their two-handed peers. These findings support the view that cognitive development is shaped by embodied experience and highlights the importance of examining how children solve problems, not just whether they succeed.

References

Allen, K. R., Smith, K. A., Bird, L.-A., Tenenbaum, J. B., Makin, T. R., & Cowie, D. (2024). Lifelong learning of cognitive styles for physical problem-solving: The effect of embodied experience. *Psychonomic Bulletin & Review*, *31*(3), 1364–1375. https://doi.org/10.3758/s13423-023-02400-4

Beck, S. R., Apperly, I. A., Chappell, J., Guthrie, C., & Cutting, N. (2011). Making tools isn't child's play. *Cognition*, *119*(2), 301–306. https://doi.org/10.1016/j.cognition.2011.01.003

Beck, S. R., Cutting, N., Apperly, I. A., Demery, Z., Iliffe, L., Rishi, S., & Chappell, J. (2014). Is tool-making knowledge robust over time and across problems? *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.01395

Beck, S. R., Williams, C., Cutting, N., Apperly, I. A., & Chappell, J. (2016). Individual differences in children's innovative problem-solving are not predicted by divergent thinking or executive functions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150190. https://doi.org/10.1098/rstb.2015.0190

Burdett, E. R. R., & Ronfard, S. (2023). Tinkering to innovation: How children refine tools over multiple attempts. *Developmental Psychology*, *59*(6), 1006–1016. https://doi.org/10.1037/dev0001512

Carr, K., Kendal, R. L., & Flynn, E. G. (2015). Imitate or innovate? Children's innovation is influenced by the efficacy of observed behaviour. *Cognition*, *142*, 322–332. https://doi.org/10.1016/j.cognition.2015.05.005

Chappell, J., Cutting, N., Apperly, I. A., & Beck, S. R. (2013). The development of tool manufacture in humans: What helps young children make innovative tools? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 20120409. https://doi.org/10.1098/rstb.2012.0409

Colbourne, J. A. D., Auersperg, A. M. I., & Beck, S. R. (2024). Children's limited tooling ability in a novel concurrent tool use task supports the innovation gap. *Scientific Reports*, *14*(1), 21374. https://doi.org/10.1038/s41598-024-71686-8

Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences*, *13*(4), 148–153. https://doi.org/10.1016/j.tics.2009.01.005

Cutting, N., Apperly, I. A., & Beck, S. R. (2011). Why do children lack the flexibility to innovate tools? *Journal of Experimental Child Psychology*, *109*(4), 497–511. https://doi.org/10.1016/j.jecp.2011.02.012

Davis, S., Rawlings, B., Clegg, J. M., Ikejimba, D., Watson-Jones, R. E., Whiten, A., & Legare, C. H. (2022). Cognitive flexibility supports the development of cumulative cultural learning in children. *Scientific Reports*, *12*(1), 14073. https://doi.org/10.1038/s41598-022-18231-7

Davis, S., Vale, G. L., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2016). Foundations of cumulative culture in apes: Improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (Pan troglodytes). *Scientific Reports*, *6*(1), 35953. https://doi.org/10.1038/srep35953

Ebel, S. J., Hanus, D., & Call, J. (2019). How prior experience and task presentation modulate innovation in 6-year-old-children. *Journal of Experimental Child Psychology*, *180*, 87–103. https://doi.org/10.1016/j.jecp.2018.12.004

Evans, N. S., & Jirout, J. J. (2023). Investigating the relation between curiosity and creativity. *Journal of Creativity*, *33*(1), 100038. https://doi.org/10.1016/j.yjoc.2022.100038

Evans, N. S., Todaro, R. D., Schlesinger, M. A., Golinkoff, R. M., & Hirsh-Pasek, K. (2021). Examining the impact of children's exploration behaviors on creativity. *Journal of Experimental Child Psychology*, *207*, 105091. https://doi.org/10.1016/j.jecp.2021.105091

Flynn, E., Turner, C., & Giraldeau, L.-A. (2016). Selectivity in social and asocial learning: Investigating the prevalence, effect and development of young children's learning preferences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150189. https://doi.org/10.1098/rstb.2015.0189

Gönül, G., Takmaz, E. K., Hohenberger, A., & Corballis, M. (2018). The cognitive ontogeny of tool making in children: The role of inhibition and hierarchical structuring. *Journal of Experimental Child Psychology*, *173*, 222–238. https://doi.org/10.1016/j.jecp.2018.03.017

Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms. *Behavioural Processes*, *109 Pt B*, 121–134. https://doi.org/10.1016/j.beproc.2014.08.027

Hanus, D., Mendes, N., Tennie, C., & Call, J. (2011). Comparing the Performances of Apes (Gorilla gorilla, Pan troglodytes, Pongo pygmaeus) and Human Children (Homo sapiens) in the Floating Peanut Task. *PLOS ONE*, *6*(6), e19555. https://doi.org/10.1371/journal.pone.0019555

Harris, P. L. (2021). Early Constraints on the Imagination: The Realism of Young Children. *Child Development*, *92*(2), 466–483. https://doi.org/10.1111/cdev.13487

Legare, C. H., & Nielsen, M. (2015). Imitation and Innovation: The Dual Engines of Cultural Learning. *Trends in Cognitive Sciences*, *19*(11), 688–699. https://doi.org/10.1016/j.tics.2015.08.005

Lyons, D. E., Young, A. G., & Keil, F. C. (2007). The hidden structure of overimitation. *Proceedings of the National Academy of Sciences*, *104*(50), 19751–19756. https://doi.org/10.1073/pnas.0704452104

Nielsen, M. (2013). Young Children's Imitative and Innovative Behaviour on the Floating Object Task. *Infant and Child Development*, *22*(1), 44–52. https://doi.org/10.1002/icd.1765

Nielsen, M., Moore, C., & Mohamedally, J. (2012). Young children overimitate in third-party contexts. *Journal of Experimental Child Psychology*, *112*(1), 73–83. https://doi.org/10.1016/j.jecp.2012.01.001

Nielsen, M., Tomaselli, K., Mushin, I., & Whiten, A. (2014). Exploring tool innovation: A comparison of Western and Bushman children. *Journal of Experimental Child Psychology*, *126*, 384–394. https://doi.org/10.1016/j.jecp.2014.05.008

Raven, J. C., Court, J. H., & Raven, J. (1990). *Raven's coloured progressive matrices*. Oxford Psychologists Press.

Rawlings, B. (2022). After a decade of tool innovation, what comes next? *Child Development Perspectives*, *16*(2), 118–124. https://doi.org/10.1111/cdep.12451

Rawlings, B., Flynn, E. G., & Kendal, R. L. (2022). Personality predicts innovation and social learning in children: Implications for cultural evolution. *Developmental Science*, *25*(1), e13153. https://doi.org/10.1111/desc.13153

Rawlings, B., & Legare, C. H. (2021). Toddlers, Tools, and Tech: The Cognitive Ontogenesis of Innovation. *Trends in Cognitive Sciences*, *25*(1), 81–92. https://doi.org/10.1016/j.tics.2020.10.006

Rawlings, B., & Reader, S. M. (2023). What Is Innovation? A Review of Definitions, Approaches, and Key Questions in Human and Non-Human Innovation. In J. J. Tehrani, J. Kendal, & R. Kendal (Eds.), *The Oxford Handbook of Cultural Evolution*. Oxford University Press. https://doi.org/10.1093/oxfordhb/9780198869252.013.11

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2405–2415. https://doi.org/10.1098/rstb.2009.0052

Tomasello, M. (1999). *The Cultural Origins of Human Cognition*. Harvard University Press.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, *28*(5), 675–691. https://doi.org/10.1017/S0140525X05000129

Tucciarelli, R., Bird, L., Straka, Z., Szymanska, M., Kollamkulam, M., Sonar, H., Paik, J., Clode, D., Hoffmann, M., Cowie, D., & Makin, T. R. (2024). *Shaping the developing homunculus: The roles of deprivation and compensatory behaviour in sensory remapping* (p. 2024.11.26.624817). bioRxiv. https://doi.org/10.1101/2024.11.26.624817

Van Leeuwen, E. J. C., Call, J., & Haun, D. B. M. (2014). Human children rely more on social information than chimpanzees do. *Biology Letters*, *10*(11), 20140487. https://doi.org/10.1098/rsbl.2014.0487

Want, S. C., & Harris, P. L. (2001). Learning from Other People's Mistakes: Causal Understanding in Learning to Use a Tool. *Child Development*, *72*(2), 431–443. https://doi.org/10.1111/1467-8624.00288

Whiten, A., Allan, G., Devlin, S., Kseib, N., Raw, N., & McGuigan, N. (2016). Social Learning in the Real-World: 'Over-Imitation' Occurs in Both Children and Adults Unaware of Participation in an Experiment and Independently of Social Interaction. *PLOS ONE*, *11*(7), e0159920. https://doi.org/10.1371/journal.pone.0159920

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review*, *9*(4), 625–636. https://doi.org/10.3758/BF03196322

Chapter 5: Feedforward motor learning in childhood: a developmental insight into implicit and explicit contributions to learning

Abstract

People have a remarkable capacity to behave flexibly, adapting their motor actions to achieve a desired end-goal. To successfully adapt their behaviour individuals must update their internal model of how their motor commands affect the environment. This is achieved by using sensory information to map the updated spatial relationship between the body and the desired target. Whilst historically sensorimotor adaptation was thought to be an implicit process, recent findings suggest adults can use explicit strategies to facilitate this learning process. Despite being studied extensively in adults, our understanding of sensorimotor adaptation in childhood is limited. Here we use a classical error-based learning task in which participants were required to overcome a 45-degree rotation using ballistic reaches. Ninety-four children (5-9 years) and thirty-five adults were split into two conditions: visual landmarks and no landmarks. Before reaching to the target using a digital pen and tablet, participants in the visual landmarks condition were asked to verbally report their aiming direction. Despite no differences in baseline performance, results showed significant differences between the two conditions. Participants in the visual landmarks condition showed significantly higher adaptation than those in the no landmarks condition. Furthermore, while children adapted less than adults overall, both adults and children used implicit and explicit mechanisms to scaffold their learning and successfully updated their internal model of motor control as evidenced by comparable aftereffects. We included an additional group of children with congenital upper limb differences, who contrary to our expectations performed comparably to age-matched two-handed children, suggesting that while sensorimotor experience did not enhance internal model updating, it did not impede it either. Findings are discussed in relation to our existing understanding of these learning mechanisms based on online feedback-control.

Introduction

In an ever-changing world, we rarely stop to consider the subtle adaptations we make throughout the day, from altering how we reach for objects of different sizes to adjusting how we walk across uneven terrain (Darici & Kuo, 2022; von Hofsten & Rönnqvist, 1988). Though these everyday adaptations feel effortless, they rely on a remarkably sophisticated system of sensorimotor learning, the process by which individuals adapt their movements in response to sensory feedback (Wolpert et al., 2011). Consider a child navigating their environment; whether they are learning to ride a bike or simply reaching for a toy, their movements are continuously refined by sensory signals such as vision, touch, and proprioception. Over time, this feedback allows children to update their internal model of how their actions affect the environment, improving the speed, accuracy, and coordination of their movements (Krakauer & Mazzoni, 2011). This adaptive process is driven by the dynamic interplay between implicit and explicit learning mechanisms (Bond & Taylor, 2015; Taylor et al., 2014; Tsay et al., 2024). Implicit learning is driven by sensory-prediction errors, which occur when there is a discrepancy between predicted and actual outcomes, leading to unconscious changes in motor behaviour. In contrast, explicit learning is driven by target error and involves conscious strategies, such as aiming towards visual landmarks, to reduce movement error (Taylor et al., 2014). In adults, implicit learning involves slow, gradual changes to internal models, whereas explicit adaptation is a relatively fast process, characterised by an initial phase of large exploratory movements followed by smaller, fine-tuned adjustments (Taylor et al., 2014). However, our understanding of how children engage these mechanisms to support motor learning remains limited. As their motor systems are still developing, their use of implicit and explicit learning mechanisms may differ from that of adults. This study aims address these outstanding questions by investigating how children aged 5-9 years engage with implicit and explicit learning mechanisms during visuomotor adaptation compared to adults, offering new insights into the developmental trajectory of motor control.

Sensorimotor adaptation is classically studied using error-based learning paradigms that create a conflict between visual and proprioceptive feedback. A widely used example is the visuomotor rotation task, in which the visual feedback of a cursor is rotated relative to actual hand movements (Taylor et al., 2014; Wang et al., 2022). This manipulation creates an incongruence between vision and proprioception. In such tasks, implicit learning is typically inferred from aftereffects, the residual errors observed in reaching movements when feedback is removed and participants are instructed to aim directly towards the target. These errors reflect unconscious changes in motor actions. In contrast, explicit learning is often assessed through verbal reports of aiming direction made possible by the inclusion of visual landmarks. These reports are used to infer the conscious strategies being used to reduce error.

Recent theoretical work suggests that sensorimotor learning in adults unfolds through three fundamental processes: reasoning, refinement, and retrieval (Tsay et al., 2024). In the reasoning phase of learning a new motor skill, learners use explicit cognitive strategies to interpret the task and explore possible solutions based on internal models of motor behaviour. During the refinement phase, these behaviours are optimised through implicit learning mechanisms reducing motor error. Finally, in the retrieval phase, learned behaviours shift from intentional to automatic, meaning that they can be utilised effectively without the need for continuous recalibration or strategic control.

Building on this framework highlighting key differences in the role implicit and explicit learning mechanisms, research has demonstrated further distinctions in feedback sensitivity. Specifically, adaptation rate and the implicit component of learning are enhanced when feedback is presented continuously or when endpoint feedback is presented earlier in the movement (e.g., when the hand is halfway to the target), rather than after the full reach is completed (Wang et al., 2022). In contrast, explicit learning mechanisms demonstrate greater temporal robustness, remaining effective even when feedback is delayed until after the reach has finished (Tsay et al., 2023). Given these distinctions, it is unsurprising that in adults, explicit strategies often account for a larger proportion of error reduction compared to implicit learning mechanisms (Bond & Taylor, 2015; Maresch et al., 2021; Wilterson & Taylor, 2021).

Research on aging populations has further illuminated the sensitivity of these processes, specifically how they change across the lifespan. Findings have consistently shown a decline in visuomotor adaptation with age, characterised by slower and less accurate performance (Cisneros et al., 2024; Li et al., 2021, 2023). However, this decline appears to be primarily driven by changes in explicit strategy use: while implicit learning appears to be preserved, occurring at a similar or even enhanced level in older adults, the ability to employ explicit strategies declines with age (Cisneros et al., 2024; Heuer et al., 2011; Ruitenberg et al., 2023; Vandevoorde & Orban de Xivry, 2020). This age-related decline has been linked more closely to reductions in cognitive functions like working memory, anticipation, and motor execution, than to chronological age alone (Li et al., 2023). Collectively, these findings illustrate that implicit and explicit learning mechanisms follow distinct developmental trajectories across the lifespan. While much of this research has focused on adulthood and aging, comparatively little is known about how these mechanisms emerge in childhood. Investigating how young children engage with sensorimotor adaptation offers a valuable opportunity to explore the foundations of motor learning, specifically the extent to which skill acquisitions relies on implicit and explicit learning mechanisms.

Developmentally, children as young as 4 years old have demonstrated the ability to adapt to visual perturbations in error-based learning tasks (Clayton et al., 2024; Ferrel-Chapus et al., 2002; Gómez-Moya et al., 2016; King et al., 2009; Tahej et al., 2012). However, their adaptations tend to be less refined, with younger children exhibiting larger initial direction errors, greater variability, slower movement speeds, and in some cases a lower magnitude of adaptation, compared to older children and adults who demonstrate smoother, faster, and more direct movements (Contreras-Vidal et al., 2005; Deng et al., 2019; Gómez-Moya et al., 2016; King et al., 2009; Tahej et al., 2012).

Although children are capable of counteracting visual perturbations from an early age, it remains unclear whether their adaptations reflect the same level of forward model adaptation seen in adults. While some studies report adult-like aftereffects in early childhood, suggesting successful recalibration of their internal models of motor control (Clayton et al., 2024; Deng et al., 2019; Gómez-Moya et al., 2016; King et al., 2009), others find that such aftereffects do not emerge until around 8 years old (Contreras-Vidal et al., 2005). This discrepancy may stem from methodological differences, particularly the duration of perturbation exposure, which varies widely across studies. While some studies use 126 trials of perturbation exposure, others only use 60 (Contreras-Vidal et al., 2005; King et al., 2009). It is possible that younger children require prolonged exposure to fully update their internal models, which could explain these inconsistencies, including why aftereffects were only seen in one of two studies in 5-year-old children.

To further understand how children adapt, research has explored the roles of implicit and explicit learning mechanisms during development. Mirroring the adult literature, this is typically assessed by asking participants to verbally report their aiming direction using visual landmarks before reaching to the target. Findings indicate that while both implicit and explicit learning mechanisms are engaged in visuomotor adaptation, they mature at different rates in childhood. Implicit processes are thought to mature earlier, as evidenced by adult-like aftereffects in children following adaptation to a visual perturbation (Deng et al., 2019; Tahej et al., 2012; Gomez-Moya et al., 2016, King et al, 2008; Clayton et al., 2024), whereas the ability to use explicit strategies improve with age (Ruitenberg et al., 2023; Tahej et al., 2012). For example, while 6-year-old children rely more heavily on implicit adaptation, 8- and 11-year-old children show a more efficient balance of implicit and explicit strategies (Deng et al., 2019). Prism adaptation studies echo these findings, suggesting that children as young as 4 years can adapt to visual perturbations, but only around 8 years do they begin to demonstrate adult-like strategic compensation (Gómez-Moya et al., 2016).

However, a key limitation of many developmental studies investigating visuomotor adaptation is the lack of time constraints on reaching movements. For example, Deng and colleagues (2019) allowed participants up to 2000ms to complete a 7cm reach. They found that 6-year-old children performed their reaches more slowly than older children and adults. Furthermore, in Contreras-Vidal (2005), the longest reaching times during the perturbation were observed in 8-year-old children, the only group in this study who showed adult-like aftereffects. These findings raise a critical question: when young children successfully counteract visual perturbations, are they adapting internal models, or are they relying on online visual feedback to make real-time corrections during the movement? While the presence of aftereffects is typically taken as evidence of internal model updating, longer movement durations could allow children to use visual feedback mid-movement to correct their trajectory in real-time, gradually refining performance across trials without engaging feedforward adaptation mechanisms. Although Deng et al. (2019) attempted to minimise the influence of online corrections by measuring reach angle at the midpoint of the trajectory, the generous time window (up to 2000ms) still leaves room for slow, feedback-based corrections before the midpoint is reached. Without preventing such corrections through stricter time constraints, it remains difficult to distinguish between the relative contributions of real-time correction and genuine internal model adaptation.

A recent study attempted to address this by limiting opportunities for online correction. It found that young children, particularly those around 3-4 years old, rely heavily on real-time feedback control, gradually shifting towards feedforward control and internal model updating over the course of development. By around age 13, children primarily relied on feedforward adaptation to counteract perturbations (Malone et al., 2025). While this study successfully constrained online corrections, allowing for clearer measures of internal model adaptation, it employed a gradual perturbation due to high frustration and early dropout in pilot testing when an abrupt perturbation was used. The authors acknowledged that this introduced two new limitations. First, gradual perturbations can mask the learning process and obscure age-related differences in adaptation, as small incremental errors may fail to elicit clear error-driven learning responses. Therefore, the speed and effectiveness of adaptation cannot be truly analysed. Second, gradual perturbations are thought to encourage implicit adaptation rather than explicit, target error-driven strategies. As such, further work is needed to track the development of implicit and explicit adaptation across development, combining abrupt perturbations, suppression of online correction, and direct measurement of both implicit and explicit components of learning.

The current study aims to address these limitations by using abrupt visuomotor perturbations alongside ballistic reaching movements which prevent real-time corrections, to enhance our understanding of how feedforward adaption develops in childhood. Furthermore, by assessing both verbal aiming reports and aftereffects, this study will isolate the distinct contributions of implicit and explicit learning mechanisms under these conditions.

While much of the existing research focuses on typical sensorimotor learning, less attention has been given to how these processes are influenced by physical differences that alter typical motor trajectories, such as those seen in children with congenital upper limb differences. Importantly, these children have no known cognitive impairments (Allen et al., 2024), allowing us to explore the developmental trajectory of sensorimotor learning in the context of isolated physical differences. Children with congenital upper limb differences must develop alternative motor behaviours to overcome challenges completing everyday bimanual motor tasks, like tying shoelaces. Because these conditions are rare, these children cannot rely on traditional methods of learning through imitation or mimicry. Instead, they must devise their own motor solutions through self-guided sensorimotor exploration (Tucciarelli et al., 2024). This dynamic and evolving repertoire of compensatory behaviours necessitates the rapid acquisition and continual updating of motor strategies. In this sense, their learning process is distinct, shaped by the need to find alternative motor solutions for tasks that two-handed children typically perform with both hands.

The adaptation of sensorimotor learning in children with upper limb differences may differ significantly from that of two-handed children. While research in adults with unilateral upper limb differences has reported mild bimanual motor deficits (Phillip et al., 2015), these individuals also develop a remarkable repertoire of adaptive behaviours (Dempsey-Jones et al., 2019; Hahamy et al., 2017; Tucciarelli et al., 2024). These compensatory processes may cultivate meta-learning skills – strategies that facilitate more efficient and flexible adaptive learning. Such distinctions could shape how children with congenital upper limb differences respond to motor challenges, including visual perturbations. This process may be further supported by heightened brain plasticity in response to sensory or motor impairments (Oudeyer & Smith, 2016), which could enhance the ability to update internal motor representations, a key mechanism underlying effective visuomotor adaptation. Together, these motor adaptations combined with neural plasticity suggests that children with upper limb differences might possess a unique advantage in adapting to visual perturbations, potentially enabling faster or more robust adaptation to novel visuomotor transformations compared to their two-handed peers.

The rationale for this study is therefore twofold. First, we aimed to understand whether the development of compensatory strategies through self-guided exploration supports more flexible and adaptive motor learning in children with congenital limb differences. Second, in reviewing the literature, it became clear that a robust baseline for visuomotor adaptation in two-handed children was lacking. Existing studies vary considerably in movement constraints, perturbation exposure, and the extent to which explicit strategies are assessed, making it difficult to compare across findings or isolate the underlying mechanisms of learning. As such, a foundational aim of this study was to first establish a clear, age-sensitive baseline of how implicit and explicit learning mechanisms operate in two-handed children.

In this study we investigated visuomotor adaptation using ballistic reaching movements that prohibited the use of online feedback control, specifically focusing on the development of implicit and explicit contributions to visuomotor adaptation. We tested three age groups: 5-7-year-olds, 8-9-year-olds, and adults. These age ranges were selected to reflect a proposed developmental shift in internal model updating: while some studies report adult-like aftereffects in children as young as 5, others suggest that consistent and reliable internal model adaptation does not emerge until around 8 years of age (Contreras-Vidal et al., 2005; Deng et al., 2019). By dividing the children into 5–7 and 8–9-year-olds, we aimed to capture this potential developmental transition and clarify whether there is a meaningful shift in the use of implicit and explicit learning mechanisms across this age range. Participants were split into two aiming conditions: one involving explicit strategies (aiming using visual landmarks) and one without explicit aiming (no landmarks). Explicit contributions were measured through verbal aiming reports, while implicit adaptation was assessed through residual aftereffects once the perturbation was removed (Taylor et al., 2014). The aiming condition also allowed us to further assess the implicit and explicit contributions to learning during forward model adaptation by examining the difference between the reported aim and actual reaching trajectory. Additionally, the inclusion of 5-7-year-old children with congenital upper limb differences in the no-landmarks condition provided insight into how physical variations influence the learning of motor tasks and how these children implicitly adapt to visual perturbations compared to their two-handed peers.

We hypothesised that younger children (5-7 years) would struggle with the ballistic movement constraint due to less developed internal models, resulting in less effective adaptation and smaller aftereffects compared to older children and adults (Contreras-Vidal et al., 2005; Malone et al., 2025). We also expected that younger children would also rely more on implicit adaptation in the visual landmarks condition, as they are still developing the cognitive skills to engage in explicit strategies effectively (Deng et al., 2019; Ruitenberg et al., 2023). We predicted that children aged 8-9 years would show some ability to rely on both implicit and explicit strategies, while adults would adapt efficiently under both conditions, engaging a balance of implicit and explicit strategies. Finally, we expected that children with upper limb differences would engage in demonstrate faster and more robust adaptation compared to two-handed 5-7-year-olds, as evidenced by increased aftereffects.

Method

Participants

A total of 129 participants were recruited for this study, across three age groups: 50 children aged 5-7 years, 44 children aged 8-9 years, and 35 adults. Demographics are summarised in Table 5.1. Within the sample, 109 participants were right-handed, all participants had no known neurodevelopmental conditions and normal or corrected-to-normal vision. Children were recruited though local schools and a database of volunteer families, while adults were recruited from the university's study participant pool. Data from two additional children aged 5-7 years were excluded due to inattentiveness.

Table 5.1. Participant demographics by condition and age group, including number of participants, gender distribution, and mean age.

Condition	Age Group	N (Female)	Mean age (SD)
Aiming	5-7 years	25 (13)	6.15 (.71)
	8-9 years	20 (12)	9.17 (.57)
	Adults	15 (12)	20.85 (2.95)
Non-aiming	5-7 years	25 (9)	6.47 (.73)
	8-9 years	24 (15)	9.02 (.65)
	Adults	20 (18)	20.67 (1.10)

Additionally, 9 children with congenital upper limb differences, aged 5-7 years (M = 6.41, SD = .79) were recruited in the non-aiming condition. Details of each child's limb difference, summarised in table 5.2, were self-reported by parents and caregivers and verified during in-person testing. Participants were recruited through two UK-based charities, Reach and LimbBo, who support individuals with upper limb differences. All children completed the task using their dominant limb as reported in table 5.2. For seven children, this was an anatomically intact hand; for the remaining two, it was a partial hand capable of gripping a pen. There were no significant differences in baseline performance between these children and age-matched two-handed controls, confirming that they were able to complete the task successfully (p = .140).

Table 5.2. Details of upper limb anatomy and functional characteristics for children with upper limb differences. The dominant limb specifies which hand participants completed the task with.

ID	Limb difference				Dominant limb
	Left	Pincer	Right	Pincer	
1	Intact	Yes	Partial hand, 3 digits	Yes	Left
2	Radial deviation	Weak	Radial deviation	Weak	Left
3	Intact	Yes	Partial hand, 0 digits	No	Left
4	Intact	Yes	Partial hand, 0 digits	No	Left
5	Partial hand, thumb	No	Intact	Yes	Right
6	Partial hand, 3 digits	Yes	Partial hand, 4 digits	Yes	Left
7	Absent below elbow	No	Intact	Yes	Right
8	Partial hand, thumb & 1 partial digit	Yes	Intact	Yes	Right
9	Intact	Yes	Absent below elbow	No	Left

Task and apparatus

Participants were seated in front of a 22” monitor (iiyama T2252MSC-B1) mounted horizontally 25cm above a Huion Inspiroy drawing tablet (Figure 5.1). Using a digital pen in their dominant hand, participants made reaching movements from a central circle (5mm in diameter) to one of four targets displayed on the screen.

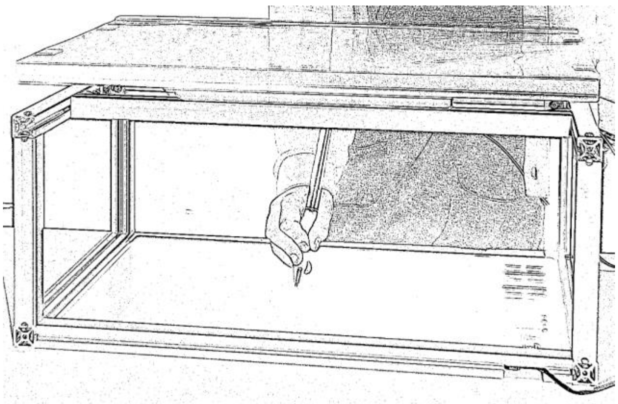


Figure 5.1. Schematic drawing of the experimental setup. Participants sat in front of a monitor mounted horizontally above a drawing tablet, obscuring the view of their hands.

Procedure

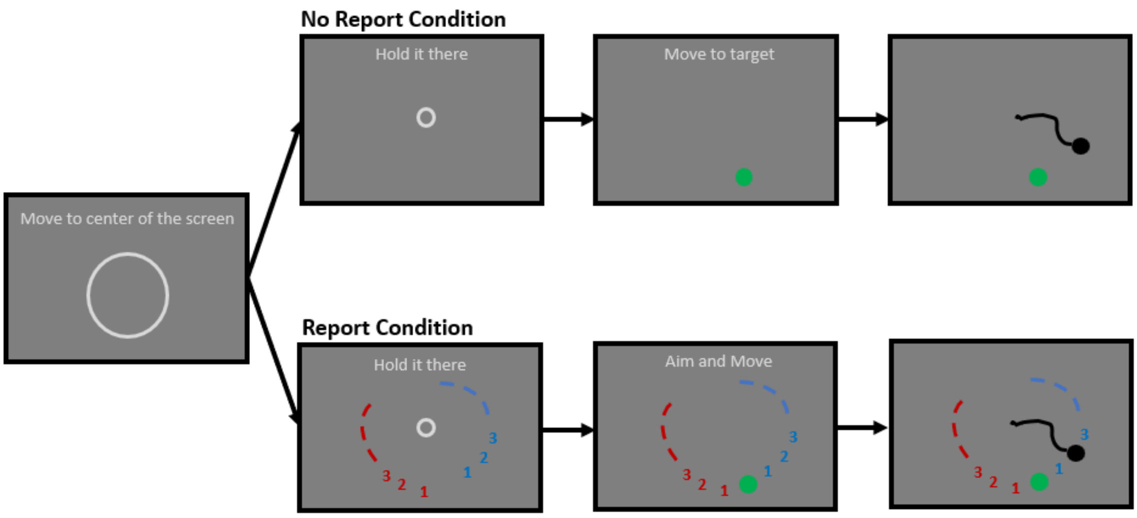
This study used a visuomotor adaptation paradigm adapted from Taylor, Krakauer & Ivry (2014). At the beginning of each trial, participants were guided to the centre of the screen by a white ring which reduced in size as they moved towards the central starting position. Once the participant reached the centre, they waited for 1 second before a 7mm green target circle appeared at one of four locations: 45°, 135°, 225°, and 315° on an unseen circle with a radius of 7cm. Target location was pseudorandomised so that each location was presented once every four trials.

Participants were instructed to make fast reaching movements, drawing a straight line through the target. All participants received online feedback, allowing them to see their trajectory while drawing. As per Taylor and colleagues (2014), a 500ms time limit was enforced, beginning once the participant had moved 1cm away from the starting position. This approach ensured that the timer was not accidentally triggered by minor movements or wobbling at the start point. If participants did not reach the target within this time limit, the cursor would freeze. To further encourage ballistic movements, participants were provided with an auditory cue in the form of a whooshing sound and were encouraged to complete their reach before the sound stopped. If participants successfully completed the 7cm reach within the time limit, they heard a “ding” and were rewarded with stars based on their performance: three stars for hitting the target, two stars if they were within 1cm of the target, and one star if they were within 2cm of the target. To enforce these contingencies during the task, the distance from the target was calculated at each frame as a straight line between the endpoint of their movement and the target location. A sample trial can be seen in Figure 5.2A.

The experiment was divided into five blocks: Familiarisation, Baseline, Rotation, No Feedback, and Washout (Figure 2B). During the Familiarisation block, participants completed up to five blocks of four trials each (maximum of 20 trials) with veridical feedback. This phase was designed to ensure participants understood the task instructions and had sufficient opportunity to practice making ballistic movements. If a participant earned at least two stars on three out of four trials within a single block, the familiarisation phase was considered complete, and they proceeded to the Baseline block. The Baseline block consisted of 24 trials with veridical feedback. In the Rotation block, participants completed 96 trials, with perturbed feedback. The perturbation was a 45° or -45° rotation, counterbalanced across participants. Throughout the block participants were reminded that the goal of the task was to reach the green target. In the No feedback block, participants completed 24 trials in which they were instructed to draw directly towards the target with all visual and auditory feedback removed. Although no performance-related feedback was provided, a neutral knocking sound indicated when the reach was completed within the time limit. This sound did not convey any information about movement accuracy. The final Washout block mirrored the Baseline block, also consisting of 24 trials with veridical feedback reinstated. During this block, participants once again received visual and auditory feedback (e.g., stars and “ding”) to reinforce accurate and timely movements.

Within each age group, participants were randomly assigned to one of two conditions: aiming and non-aiming. Participants in both conditions completed all five blocks with the goal of drawing a line to the green target. In the aiming condition, after the Baseline block participants completed an additional block coined Baseline Report, consisting of four trials with veridical feedback. During both the Baseline Report and Rotation blocks, the green target was presented as part of a circle of 63 numbered landmarks spaced 5.625° apart. The target always appeared at 0°. Before each movement, participants were asked to verbally report the colour and number of the landmark they planned to draw to in order to reach the green target, e.g., red 5.

A.



B.

Baseline (24 trials)	Baseline Report (4 trials)	Rotation (96 trials)	No Feedback No Landmarks (24 trials)	Washout (24 trials)

Figure 5.2. A. Sample trial during the Rotation block under the report and no report conditions. B Overview of the sequence of blocks administered during the experiment following the familiarisation phase.

Statistical analyses

Prior to analysis, data were screened to eliminate any trials in which reaching time exceeded 500ms. Approximately 90% of the data were retained for analysis (19,326/21,672 trials).

To assess performance, our analyses focused on the heading angle of each reach. The heading angle was calculated by first identifying two referent points along the trajectory of the reach, positioned at 1 and 3cm from the starting point. A straight line was drawn between these two points, and the angle relative to a reference axis with the target at 0° was computed. For participants exposed to the 45-degree rotation, all heading angles following the baseline block were multiplied by -1 to standardise the perturbation direction. Positive heading angles indicate a clockwise deviation from the target, while negative angles indicate a counterclockwise deviation. This method allows us to quantify learning while controlling for the influence of online feedback corrections.

Baseline performance

To confirm that children were able to perform the task comparably to adults, we assessed baseline performance using the average heading angle from the final four trials of the baseline block (i.e., one trial at each target location), as per Taylor et al (2014). Group differences were analysed using a two-way ANOVA was conducted with age group (5-7 years, 8-9 years, and adults) and aiming condition (visual landmarks vs. no landmarks) as between-subjects factors.

Learning to counter a visual perturbation

To quantify learning, we examined changes in heading angle during early and late phases of the rotation block. This distinction follows previous work, capturing both the speed and overall magnitude of learning (Taylor et al., 2014). Subsequent analyses will explore the extent to which implicit and explicit processes contribute to these changes. Early rotation was defined as the average heading angle from the first four trials of the rotation block, minus the average from the last four trials of the baseline block, capturing initial adjustments in movement trajectories in response to the perturbation. Late rotation was defined as the average heading angle from the last four trials of the rotation block, minus the average from the last four trials of the baseline block and was used to assess the overall magnitude of adaptation. Two separate two-way ANOVAs were conducted for early and late rotation, including age group and aiming condition as between-subjects factors. These analyses assessed the rate and amount of learning across age groups and conditions.

Implicit and explicit contributions to learning

The visual landmarks condition allowed us to quantify implicit and explicit contributions to learning during adaptation. The data from 60 participants across the three age groups were analysed. Explicit contributions were calculated using the reported aiming location for each trial in the rotation block. Reported aims were converted to degrees by multiplying the selected landmark by 5.625°, the spacing constant between visual landmarks. Red landmarks were treated as positive values and blue landmarks were treated as negative (Figure 5.2a). Implicit contributions were estimated by subtracting the reported aiming direction from the initial heading angle of each reach, isolating the component of learning that was not accounted for by explicit aiming. Separate one sample t-tests were conducted for each group to assess the presence of implicit and explicit contributions in both early and late rotation. Subsequently, separate one-way ANOVAs, with age group as a factor, were conducted for early and late rotation to assess the rate and amount of each type of adjustment.

Relative contributions of implicit and explicit adaptation

To examine how adults and children rely on implicit and explicit contributions during motor learning, we analysed their relative contributions using a repeated measures ANOVA during early and late rotation, with age group as factor.

Aftereffects

Aftereffects were measured to quantify implicit adaptation, since they represent the residual reaching error when participants aim directly to the target after the rotation is removed. The aftereffect was computed as the average heading angle computed over the first four trials of the no-feedback block minus the average heading angle of last four trials in the baseline block. A one sample t-test was conducted for each group to assess the presence of this aftereffect. Subsequently, a two-way ANOVA was performed with age group and aiming condition as factors to examine potential group differences in the magnitude of aftereffects.

Visuomotor adaptation in children with upper limb differences

Children with congenital upper limb differences were compared to age-matched two-handed children (aged 5-7 years) on their visuomotor adaptation performance in the no landmarks condition. The analysis focused on baseline performance, early and late rotation phases to quantify the rate and amount of learning, and aftereffects to assess implicit adaptation of the forward model. One sample t-tests were used to assess within-group differences, specifically the presence of aftereffects, while independent samples t-tests or Mann-Whitney U tests were conducted, depending on data distribution, to compare group differences across baseline performance, learning phases, and aftereffects.

Results

Baseline performance

A two-way ANOVA was conducted to ensure that children were able to perform the task similarly to adults at baseline. The results revealed no significant main effect of age ($F(2, 123) = 2.19$, $p = .116$) or aiming condition ($F(1, 123) = 0.99$, $p = .321$), and no significant interaction between age and condition ($F(2, 123) = 0.42$, $p = .660$). Any subsequent differences observed in later blocks can therefore be attributed to the experimental manipulations rather than differences in baseline performance.

Learning to counter a visual perturbation

To quantify the rate and amount of learning, we focused our analysis on the average heading angles during early and late rotation. All groups exhibited a stereotypical learning curve (Figure 5.3).

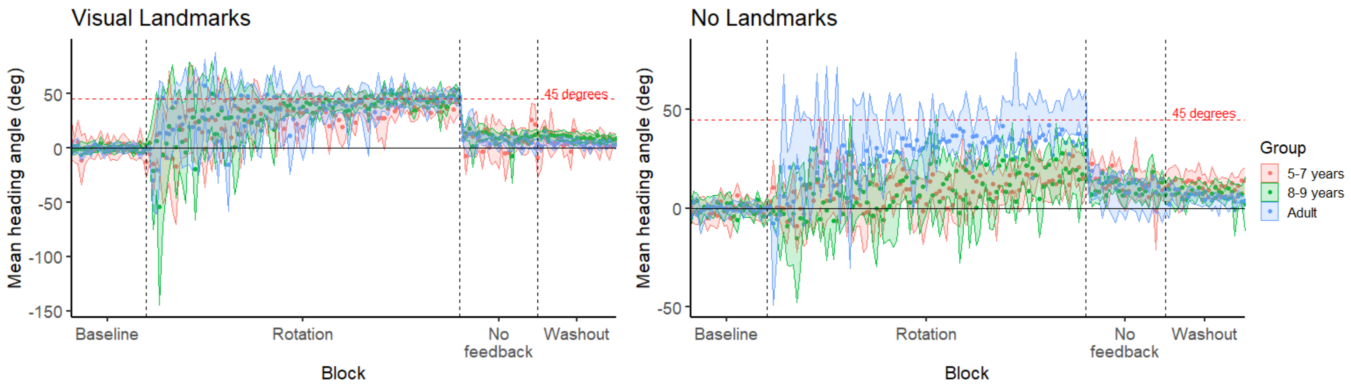


Figure 5.3. Average heading angle for adults and children in the visual landmarks and no landmarks conditions.

In early rotation, a two-way ANOVA revealed no significant differences in age ($F(2, 120) = 1.77$, $p = .176$), aiming condition ($F(1, 120) = 0.04$, $p = .850$), or the interaction between age and condition ($F(2, 120) = 0.08$, $p = .920$). Early adaptation was therefore similar across age groups, regardless of whether visual landmarks were present. Specifically, children aged 5-7 years showed a mean heading angle of 5.57° with visual landmarks and 5.36° with no landmarks, children aged 8-9 had means of -8.72° and -4.38°, respectively, and adults showed a mean of -3.04° with visual landmarks and -3.93° with no landmarks (Figure 5.4, leftmost bars in each plot).

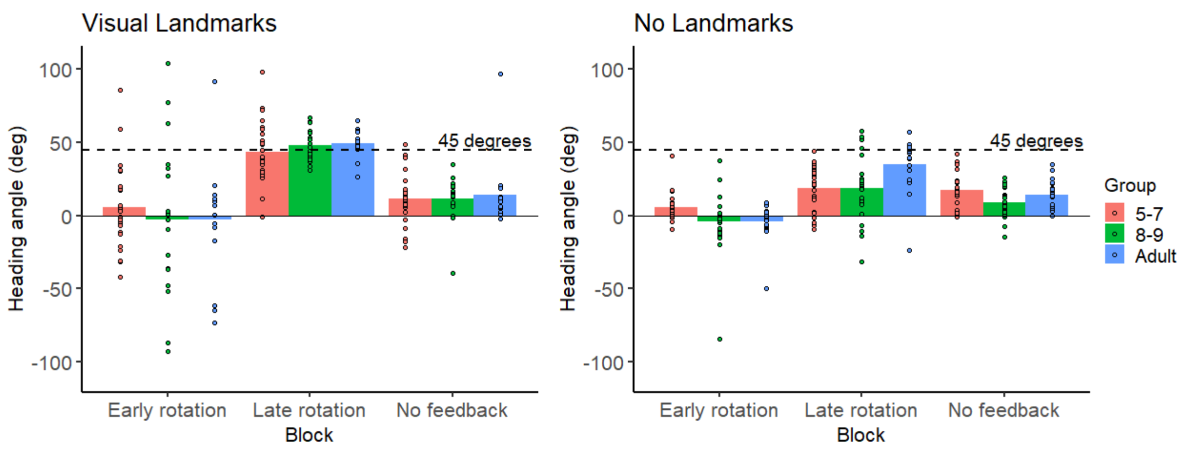


Figure 5.4. Average heading angle in early rotation, late rotation, and the no feedback block relative to baseline performance for each age group in the visual landmarks and no landmarks conditions.

To fully compensate for the -45° perturbation, participants were required to adjust their heading angle by approximately +45°. The baseline-corrected early rotation adjustments observed were close to 0, suggesting that initial adjustments to the perturbation were minimal. The absence of group or condition differences further indicates that suggests that early adaptation was similarly limited across all participants.

In contrast, in late rotation, a significant main effect of aiming condition ($F(1, 123) = 51.60$, $p < .001$) was observed, along with a significant effect of age ($F(2, 123) = 3.32$, $p = .039$), though their interaction was not significant ($F(2, 123) = 1.72$, $p = .183$). The presence of visual landmarks led to significantly greater learning, with mean heading angles of 47.51° in the landmark condition and 23.50° without. Adaptation also improved with age: children aged 5-7 years showed a mean of 32.50°, children aged 8-9 years had a mean of 31.92°, while adults demonstrated the most learning with a mean of 41.22°. These findings indicate that while early responses to the perturbation were limited, extended exposure led to more robust adaptation, particularly in adults who showed near-perfect adaptation.

Implicit and explicit contributions to learning

We estimated *explicit* contributions to learning, shown in figure 5.5A, by converting participants' reported aiming locations into degrees. Each visual landmark corresponded to a fixed spatial location spaced 5.625° apart; reported landmark values were multiplied by this spacing constant to quantify explicit re-aiming strategies. To assess the rate and magnitude of explicit adaptation, we analysed the average reported aims in the first and last epicycles of the rotation block. One sample t-tests, or Wilcoxon signed rank test where assumptions were violated, were first conducted to determine whether explicit contributions were significantly greater than zero. In early rotation, explicit contributions were observed in 8–9-year-old children ($t(18) = 2.93$, $p = .009$), but not in 5-7-year-old children ($W = 55.50$, $p = .209$) or adults ($W = 30.50$, $p = .798$). A one-way ANOVA subsequently revealed a significant main effect of group ($F(2, 54) = 4.30$, $p = .018$). Post-hoc comparisons confirmed that children aged 8-9 years exhibited a significantly higher rate of explicit adaptation than adults (adjusted $p = .021$), and marginally higher rate than children aged 5–7 years (adjusted $p = .08$; Figure 5.5B).

In late rotation, one-sample t-tests confirmed that all groups showed significant explicit adaptation (5-7 years: $W = 300.00$, $p < .001$; 8-9 years: $W = 210.00$, $p < .001$; and adults: $W = 120.00$, $p < .001$). A one-way ANOVA subsequently revealed no significant main effect of group ($F(2, 57) = 0.43$, $p = .654$), suggesting that the magnitude of explicit adaptation by the end of the rotation block did not differ by age.

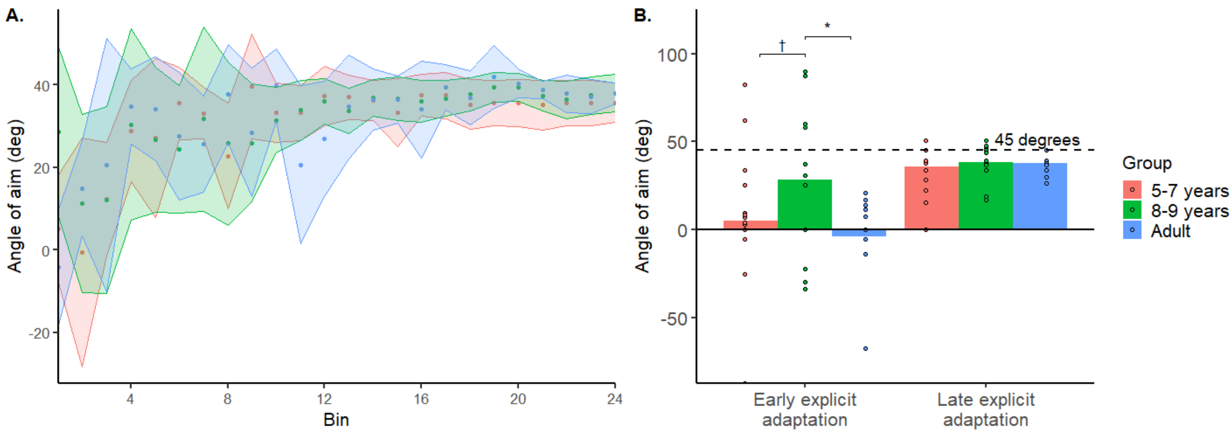


*Figure 5.5. A. Average explicit learning curve in the rotation phase for each group in the visual landmarks condition. The y-axis represents the angle of aiming location, calculated by multiplying the reported landmark number by a spacing constant of 5.625°. The x-axis shows trial bins, with each bin representing four consecutive trials. Shaded areas represent the 95% confidence interval. B. Average explicit aim in early and late rotation phases for each age group, defined by the first and last trial bin, respectively. Significant differences are denoted by * (p < .05), and marginal significance by † (p = .08).*

We also estimated the contributions of *implicit* learning during the rotation block in the aiming condition, by calculating the difference between the reported aiming location and the heading angle. The time course for each group is shown in Figure 5.6A. One sample t-tests, or Wilcoxon signed rank test where data violated test assumptions, were used to determine whether implicit contributions were significantly greater than zero. In early rotation, no group showed significant implicit contributions to learning. Specifically, implicit contributions did not differ from zero in 5-7-year-old children ($t(22) = .35$, $p = .732$), 8-9-year-olds ($W = 120.00$, $p = .332$), or adults ($W = 52.00$, $p = .679$).

By contrast, in late rotation, implicit learning was evident in the two older groups. Children aged 8-9 years showed robust implicit contributions to learning ($t(19) = 5.75$, $p < .001$), as did adults ($t(14) = 4.99$, $p < .001$). In 5-7-year-olds, the implicit contributions to learning were only marginally difference to zero ($t(24) = 1.89$, $p = .07$), suggesting a trend toward implicit learning. A one-way ANOVA revealed no significant main effect of group ($F(2, 57) = 0.96$, $p = .389$), indicating that the overall magnitude of implicit contributions was comparable across groups by the end of the learning phase (Figure 5.6B).

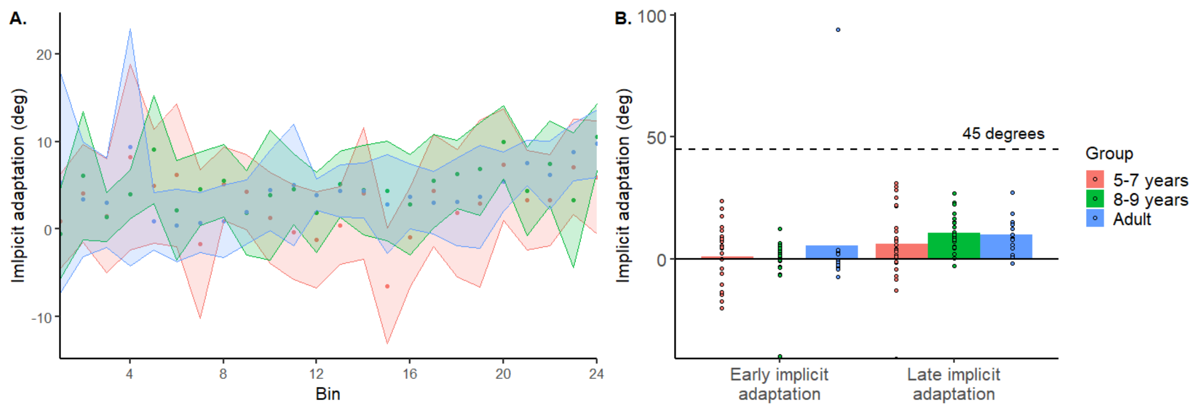


Figure 5.6. A. Average implicit learning curve in the rotation phase for each group in the visual landmarks condition. The y-axis represents the residual error calculated by subtracting the reported aim from the heading angle. The x-axis shows trial bins, with each bin representing four consecutive trials. Shaded areas represent the 95% confidence interval. B. Average implicit aim in early and late rotation phases for each age group, defined by the first and last trial bin, respectively.

Relative contributions of implicit and explicit adaptation

To further assess the relative contributions of implicit and explicit adaptation a repeated-measures ANOVA was conducted. In early rotation, results revealed a significant interaction between group and contribution type ($F(2, 54) = 5.19$, $p = .009$). Post-hoc analyses confirmed that no differences were observed between implicit and explicit contributions in 5–7-year-olds (adjusted $p = 1.00$) or adults (adjusted $p = 1.00$), but 8-9-year-olds showed significantly higher explicit than implicit contributions (adjusted $p = .013$).

In late rotation, a significant main effect of contribution type ($F(1, 57) = 173.01$, $p < .001$), revealed that explicit contributions to learning ($M = 37.02°$, $SD = 9.54°$) were significantly greater than implicit contributions ($M = 8.41°$, $SD = 11.81°$). There was no significant interaction between group and contribution type ($F(2, 57) = 0.11$, $p = .899$), indicating that the magnitude of this difference did not vary by age.

Aftereffects

As another means of assessing implicit adaption of the forward model, we examined the presence of aftereffects in the no-feedback block across all groups. One sample t-tests, or Wilcoxon signed rank test where data violated test assumptions, were used to determine whether aftereffects were significantly greater than zero. Significant aftereffects were observed in all groups. In the visual landmarks condition, children aged 5-7 years exhibited an aftereffect of 11.53° ($t(24) = 3.31$, $p = .003$), children aged 8-9 years showed an aftereffect of 11.71° ($W = 187.00$, $p < .001$), and adults demonstrated an aftereffect of 14.10° ($W = 118.00$, $p < .001$). In the no landmarks condition, children aged 5-7 years showed an aftereffect of 17.58° ($t(24) = 6.99$, $p < .001$), children aged 8-9 years showed an aftereffect of 8.91° ($t(23) = 4.38$, $p < .001$), and adults showed an aftereffect of 14.29° ($t(20) = 6.52$, $p < .001$; Fig 5.4, rightmost bars).

A two-way ANOVA was conducted to assess group differences in aftereffects. The results revealed no significant main effect of age ($F(2, 123) = 1.10$, $p = .337$) or condition ($F(1, 123) = 0.19$, $p = .667$), and no significant interaction between age and condition ($F(2, 123) = 1.08$, $p = .344$). These findings suggest that the magnitude of aftereffects was not significantly influenced by age or condition.

Visuomotor adaptation in children with upper limb differences

To explore how physical differences impact motor adaptation, we compared the performance of 5–7-year-old children with congenital upper limb differences to age-matched two-handed control children in the no landmarks condition.

For baseline performance, a Mann-Whitney U test revealed no significant differences between the two groups ($W = 74.00$, $p = .140$), suggesting that both groups performed similarly at baseline. This indicates that any subsequent differences observed in learning or aftereffects are likely due to the experimental manipulations rather than inherent differences in baseline capabilities.

Children with upper limb differences showed a stereotypical learning curve, like their two-handed peers, children with limb differences showed improvements over the course of the rotation block (Figure 5.7). In the early rotation phase, a Mann-Whitney U test indicated no significant difference in heading angles between the groups ($W = 81.00$, $p = .231$), demonstrating that both groups adapted at a similar rate during the initial exposure to the perturbation. Likewise, in the late rotation phase, no significant difference in performance was observed between the groups ($t(32) = 0.375$, $p = .710$), suggesting that both groups had similarly adapted by the end of the rotation block, with an average of 21° for children with upper limb differences and 19° for two-handed 5-7-year-olds.

Finally, to assess implicit adaptation of a forward model, aftereffects were measured in the no-feedback block. A one-sample t-test confirmed the presence of aftereffects in children with upper limb differences ($t(8) = 2.90$, $p = .02$). Furthermore, a Mann-Whitney U test revealed no significant difference in the magnitude of aftereffects between the two groups ($W = 93.00$, $p = .465$), suggesting that the implicit adaptation of the forward model was similar across the two groups.

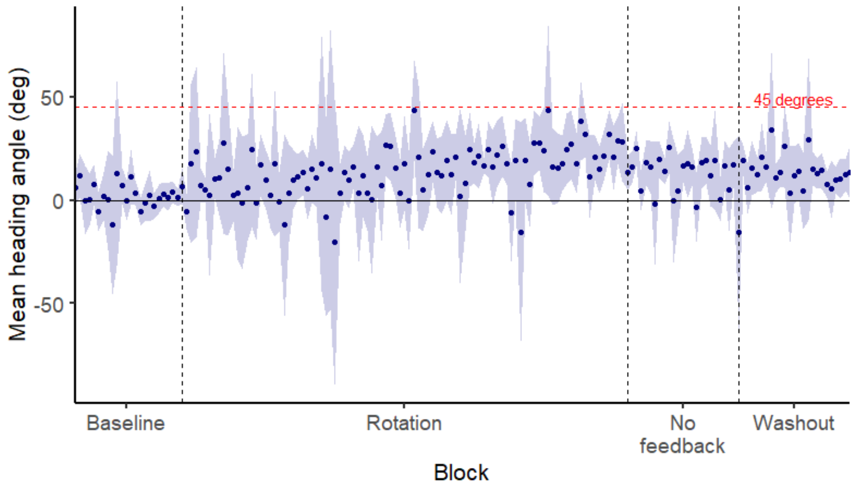


Figure 5.7. Average heading angle for our sample of children with congenital upper limb differences.

Discussion

This study investigated the developmental trajectory of visuomotor adaptation in children, focusing on the relative contributions of implicit and explicit learning mechanisms under ballistic movement constraints. By using a reaching task that limited the use of online feedback control, we aimed to isolate feedforward learning processes to assess the extent to which children could update their internal forward models to counter a visual perturbation. Contrary to our hypothesis, children as young as five demonstrated successful adaptation, even under ballistic constraints, performing comparably to older children. However, both groups of children adapted less than adults, highlighting developmental differences in motor learning. Notably, while implicit contributions remained constant across groups, explicit strategy use varied, such that 8–9-year-olds exhibited greater explicit strategy use in early adaptation than both younger children and adults. However, by the end of the adaptation phase, all groups showed a greater reliance on explicit rather than implicit mechanisms, suggesting a general shift toward strategic scaffolding over time. These findings provide novel insights into the developmental trajectory of motor learning and the interplay between implicit and explicit processes in the absence of online feedback.

The observed differences in overall adaptation are consistent with previous work suggesting that visuomotor adaptation continues to mature throughout childhood, becoming adultlike in early adolescence (Malone et al., 2025). This however contrasts with findings from free-reaching tasks which suggest that children's adaption already mirrors that of adults (Clayton et al., 2024). A likely explanation for this lies in task demands. Free-reaching tasks allow for online feedback control, enabling participants to make mid-reach corrections using visual and proprioceptive input. In contrast, the ballistic task used here required predictive feedforward control, whereby movements had to be pre-planned and executed without real-time adjustments. Feedforward control mechanisms are arguably more cognitively demanding than online feedback strategies, relying on spatial working memory, motor planning, and sustained attention (Anguera et al., 2011; de Oliveira et al., 2022; Kao & Pierro, 2022). It also places greater demands on the developing cerebellum, which supports sensorimotor prediction and internal model updating (Tzvi et al., 2020). Based on these demands, we hypothesised that younger children would struggle with ballistic constraints due to underdeveloped internal models. Surprisingly, however, even five-year-old children demonstrated successful adaptation and robust aftereffects, suggesting a greater capacity for internal model updating than previously recognised.

These findings challenge earlier claims that forward model adaptation does not emerge until around age eight (Contreras-Vidal et al., 2005), suggesting that when online corrections are unavailable, as in our task, children appear capable of engaging predictive control processes. To our knowledge, this is one of the first studies to investigate motor adaptation in children using both ballistic movements and an abrupt perturbation, as such our paradigm may have forced participants to engage cognitive and motor planning mechanisms which are otherwise bypassed in free-reaching movements. In contexts where real-time feedback is available and time constraints are low, young children may typically avoid feedforward strategies. Instead, they may prioritise short-term performance, relying on slower, feedback-based corrections to maximise immediate accuracy rather than updating their existing motor mappings. This is consistent with evidence showing that children often favour immediate performance at the cost of long-term adaptation (Malone et al., 2025).

In our task, however, the use of a strict time limit reduced this strategic flexibility, meaning successful performance required greater engagement of predictive motor planning. As a result, we may have uncovered a greater capacity for internal model-based learning in early childhood than previously reported. Notably, more than half (53%) of the trials exceeding 500ms in movement duration came from the 5-7-year-old group, suggesting that younger children may have attempted to use online feedback-based strategies despite the ballistic constraints of the task. This aligns with theories proposed by Malone and colleagues (2025), who suggest that younger children tend to rely more heavily on feedback-based adjustments. Such findings highlight developmental variability in motor control, and suggest that, despite being capable of feedforward adaptation, young children show a clear preference for online feedback control.

The overall rate of adaptation was influenced by the availability of visual landmarks, but this benefit only emerged in the later stages of learning. In early adaptation, we found no significant differences between conditions, whereas by late rotation, participants with access to visual landmarks showed significantly greater adaptation. This finding contrasts with previous studies which suggest that the use of visual landmarks primarily facilitate early adaptation, providing no significant advantage in overall adaptation (Deng et al., 2019; Taylor et al., 2014). One possible explanation for this discrepancy may lie in analytical procedures. Both of these prior studies used eight target locations and as such measured early and late adaptation in bins of eight trials. To accommodate younger children, we ran a simplified version of the task, exposing participants to, and basing our analysis on four target locations. Given that in the adaptation phase, participants likely spend the first few trials familiarising themselves with the perturbation, our simplified version may not have reliably captured early landmark use. As a result, the apparent shift in when landmarks became beneficial may reflect analytical sensitivity rather than a true difference between conditions. Notably, despite the advantage of visual landmarks in scaffolding learning, we found no direct benefit to forward model adaptation, as evidenced by comparable aftereffects in the landmark and no landmark conditions. This suggests that while visual landmarks enhance learning by supporting explicit strategies, they do so without strengthening the implicit processes involved in updating the internal model. These results mirror those of Taylor et al. (2014) and Deng et al. (2019), who similarly found that explicit cues do not lead to improved implicit adaptation.

To further understand these findings, we examined the relative contributions of implicit and explicit mechanisms during adaptation in the visual landmarks condition. Across both early and late adaptation phases, the magnitude of implicit contributions to learning remained consistent across age groups. This pattern was corroborated by the comparable aftereffects we observed in the no feedback block, suggesting that implicit adaptation is relatively stable across development, aligning with previous findings showing that children can successfully update their forward model using implicit processes to a similar extent as adults (Deng et al., 2019; Tahej et al., 2012; Gomez-Moya et al., 2016, King et al, 2008; Clayton et al., 2024). Although early work proposed that internal model updating is immature before 8-years (Contreras-Vidal et al., 2005), our findings reinforce earlier points suggesting that even young children can update their internal model when contextual constraints force them to engage in feedforward control. Our findings also contrast with adult research suggesting that implicit learning gradually increases over the course of adaptation (Taylor & Ivry, 2011). In our study, we observed no such growth. This may be explained by differences in task design: while our adaptation phase comprised of 96 trials, Taylor and Ivry (2011) exposed participants to a much longer adaptation phase (320 trials). It is therefore possible, that the full trajectory of implicit learning was not captured in the shorter phase used in our study, and that implicit processes may have increased had the duration been extended.

Our findings on explicit contributions to learning however are more nuanced. Unexpectedly, we observed that even 5-7 -year-olds could engage explicit strategies using visual landmarks to scaffold their learning, challenging or initial hypothesis that such strategic use would be limited to older children and adults (Ruitenberg et al., 2023; Tahej et al., 2012). We also found an interesting effect in 8-9 year-old children, who showed a sharp peak in their explicit strategy use within the first four adaptation trials, a pattern not observed in younger children or adults. This early engagement with visual landmarks suggests that they are quick to begin exploring visual landmarks, likely reflecting a developmental shift in the ability to recognise and engage with external cues as potential tools. This interpretation is supported but the tool innovation literature, which shows that children begin to succeed at novel tool innovation tasks around 8 (Beck et al., 2011; Rawlings et al., 2022). In contrast, younger children may not have fully developed the cognitive flexibility or planning skills necessary to utilise these cues effectively, while adults may adopt a more conservative approach, trying to gather information on how to counter the perturbation before adopting an explicit aiming strategy.

In line with previous findings, we observed that in late adaptation explicit contributions dominate learning across groups, suggesting learning was primarily driven by the ability to effectively use visual landmarks to reduce error (Bond & Taylor, 2015; Maresch et al., 2021; Tsay et al., 2024; Wilterson & Taylor, 2021). However, as expected given the greater use of explicit strategies early in the adaptation phase, 8-9 year old children also showed significantly greater explicit adaptation than implicit contributions to learning, while younger children and adults showed no such distinction between implicit and explicit learning mechanisms.

One of the most novel aspects of our study was the inclusion of children with congenital upper limb differences. Unexpectedly, no significant differences were found between these children and their two-handed peers. Contrary to our hypothesis, children with upper limb differences did not demonstrate faster and more robust adaptation. While we anticipated that their daily experience of self-guided sensorimotor exploration would support more efficient internal model updating, these findings suggest that feedforward learning mechanisms may be preserved in the presence of physical differences but not necessarily enhanced. It is possible that these children rely on more explicit strategies in their everyday motor exploration in the process of acquiring unique motor strategies to complete everyday tasks. Future research should expand on out work by including a visual landmarks condition for children with upper limb differences to determine whether their implicit and explicit adaptation strategies mirror those of their two-handed peers. Such research could have important implications for interventions aimed at supporting motor learning and adaptation in children with physical disabilities.

While this study provides valuable insights into visuomotor adaptation across different age groups and motor abilities, there are several limitations to consider. The sample size, particularly for the children with upper limb differences, was small. A larger sample of children with upper limb differences would increase the generalisability of our findings and reduce noise. Additionally, the task design, specifically the rotation block, may not have fully captured the longer-term adaptation processes, particularly regarding implicit learning. Although the length of this block was carefully chosen to balance the time for participants to adapt and maintain concentration in young children, in the no landmarks conditions, adults only adapted to around 35 degrees by the end of the rotation block. Future research could use longer trial blocks to explore how implicit and explicit learning contributions evolve over time in different age groups.

In conclusion, this study demonstrated that children as young as five can successfully adapt to an abrupt visual perturbation engaging both implicit and explicit learning mechanisms. By using a task that minimised the use of online feedback control, we isolated feedforward learning processes and found that all groups exhibited comparable levels of implicit adaptation, as evidenced by similar aftereffects. Notably, when explicit strategies were possible through the use of visual landmarks, they dominated over implicit contributions in all groups, enhancing overall learning but not adaptation of internal models. Contrary to our predictions, children with congenital upper limb differences adapted similarly to their two-handed peers. While we expected enhanced adaptation due to their daily reliance on self-guided motor exploration, these results suggest that the mechanisms of implicit motor adaptation are comparable across diverse sensorimotor experiences. Importantly, by removing the opportunity for online corrections, our study reveals a previously underestimated capacity for predictive motor control in early childhood. Though its use is shaped by task constraints in early childhood, such that when given the option young children prefer to employ online corrections.

References

Allen, K. R., Smith, K. A., Bird, L.-A., Tenenbaum, J. B., Makin, T. R., & Cowie, D. (2024). Lifelong learning of cognitive styles for physical problem-solving: The effect of embodied experience. *Psychonomic Bulletin & Review*, *31*(3), 1364–1375. https://doi.org/10.3758/s13423-023-02400-4

Anguera, J. A., Reuter-Lorenz, P. A., Willingham, D. T., & Seidler, R. D. (2011). Failure to Engage Spatial Working Memory Contributes to Age-related Declines in Visuomotor Learning. *Journal of Cognitive Neuroscience*, *23*(1), 11–25. https://doi.org/10.1162/jocn.2010.21451

Beck, S. R., Apperly, I. A., Chappell, J., Guthrie, C., & Cutting, N. (2011). Making tools isn't child's play. *Cognition*, *119*(2), 301–306. https://doi.org/10.1016/j.cognition.2011.01.003

Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of Neurophysiology*, *113*(10), 3836–3849. https://doi.org/10.1152/jn.00009.2015

Cisneros, E., Karny, S., Ivry, R. B., & Tsay, J. S. (2024). Differential Aging Effects on Implicit and Explicit Sensorimotor Learning. *bioRxiv*, 2024.07.02.601091. https://doi.org/10.1101/2024.07.02.601091

Clayton, H. A., Abbas, S., Hart, B. M. `t, & Henriques, D. Y. P. (2024). Visuomotor adaptation across the lifespan. *PLOS ONE*, *19*(7), e0306276. https://doi.org/10.1371/journal.pone.0306276

Contreras-Vidal, J. L., Bo, J., Boudreau, J. P., & Clark, J. E. (2005). Development of visuomotor representations for hand movement in young children. *Experimental Brain Research*, *162*(2), 155–164. https://doi.org/10.1007/s00221-004-2123-7

Darici, O., & Kuo, A. D. (2022). Humans optimally anticipate and compensate for an uneven step during walking. *eLife*, *11*, e65402. https://doi.org/10.7554/eLife.65402

de Oliveira, D. S. V., Alouche, S. R., de Freitas, S. M. S. F., Oba, G. H., Giangiardi, V. F., & de Sá, C. dos S. C. (2022). Planning and Executing Aiming Movements in Middle Childhood. *Perceptual and Motor Skills*, *129*(5), 1362–1380. https://doi.org/10.1177/00315125221112243

Dempsey-Jones, H., Wesselink, D. B., Friedman, J., & Makin, T. R. (2019). Organized Toe Maps in Extreme Foot Users. *Cell Reports*, *28*(11), 2748-2756.e4. https://doi.org/10.1016/j.celrep.2019.08.027

Deng, K., Chan ,John S. Y., & and Yan, J. H. (2019). Explicit Aiming Strategy Decreases the Differences in Visuomotor Adaptation between Children and Young Adults. *Developmental Neuropsychology*, *44*(7), 495–512. https://doi.org/10.1080/87565641.2019.1675664

Ferrel-Chapus, C., Hay, L., Olivier, I., Bard, C., & Fleury, M. (2002). Visuomanual coordination in childhood: Adaptation to visual distortion. *Experimental Brain Research*, *144*(4), 506–517. https://doi.org/10.1007/s00221-002-1064-2

Gómez-Moya, R., Díaz, R., & Fernandez-Ruiz, J. (2016). Different visuomotor processes maturation rates in children support dual visuomotor learning systems. *Human Movement Science*, *46*, 221–228. https://doi.org/10.1016/j.humov.2016.01.011

Hahamy, A., Macdonald, S. N., van den Heiligenberg, F., Kieliba, P., Emir, U., Malach, R., Johansen-Berg, H., Brugger, P., Culham, J. C., & Makin, T. R. (2017). Representation of Multiple Body Parts in the Missing-Hand Territory of Congenital One-Handers. *Current Biology*, *27*(9), 1350–1355. https://doi.org/10.1016/j.cub.2017.03.053

Heuer, H., Hegele, M., & Sülzenbrück, S. (2011). Implicit and explicit adjustments to extrinsic visuo-motor transformations and their age-related changes. *Human Movement Science*, *30*(5), 916–930. https://doi.org/10.1016/j.humov.2010.07.004

Kao, P.-C., & Pierro, M. A. (2022). Motor adaptation to cognitive challenges and walking perturbations in healthy young adults. *Gait & Posture*, *92*, 167–175. https://doi.org/10.1016/j.gaitpost.2021.11.030

King, B. R., Kagerer, F. A., Contreras-Vidal, J. L., & Clark, J. E. (2009). Evidence for Multisensory Spatial-to-Motor Transformations in Aiming Movements of Children. *Journal of Neurophysiology*, *101*(1), 315–322. https://doi.org/10.1152/jn.90781.2008

Krakauer, J. W., & Mazzoni, P. (2011). Human sensorimotor learning: Adaptation, skill, and beyond. *Current Opinion in Neurobiology*, *21*(4), 636–644. https://doi.org/10.1016/j.conb.2011.06.012

Li, N., Chen, G., Xie, Y., & Chen, Z. (2021). Aging Effect on Visuomotor Adaptation: Mediated by Cognitive Decline. *Frontiers in Aging Neuroscience*, *13*. https://doi.org/10.3389/fnagi.2021.742928

Li, N., Liu, J., Xie, Y., Ji, W., & Chen, Z. (2023). Age-related decline of online visuomotor adaptation: A combined effect of deteriorations of motor anticipation and execution. *Frontiers in Aging Neuroscience*, *15*. https://doi.org/10.3389/fnagi.2023.1147079

Malone, L. A., Hill, N. M., Tripp, H., Zipunnikov, V., Wolpert, D. M., & Bastian, A. J. (2025). The control of movement gradually transitions from feedback control to feedforward adaptation throughout childhood. *Npj Science of Learning*, *10*(1), 13. https://doi.org/10.1038/s41539-025-00304-7

Maresch, J., Werner, S., & Donchin, O. (2021). Methods matter: Your measures of explicit and implicit processes in visuomotor adaptation affect your results. *European Journal of Neuroscience*, *53*(2), 504–518. https://doi.org/10.1111/ejn.14945

Rawlings, B., Flynn, E. G., & Kendal, R. L. (2022). Personality predicts innovation and social learning in children: Implications for cultural evolution. *Developmental Science*, *25*(1), e13153. https://doi.org/10.1111/desc.13153

Ruitenberg, M. F. L., Koppelmans, V., Seidler, R. D., & Schomaker, J. (2023). Developmental and age differences in visuomotor adaptation across the lifespan. *Psychological Research*, *87*(6), 1710–1717. https://doi.org/10.1007/s00426-022-01784-7

Tahej, P.-K., Ferrel-Chapus, C., Olivier, I., Ginhac, D., & Rolland, J.-P. (2012). Multiple representations and mechanisms for visuomotor adaptation in young children. *Human Movement Science*, *31*(6), 1425–1435. https://doi.org/10.1016/j.humov.2012.02.016

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *The Journal of Neuroscience*, *34*(8), 3023–3032. https://doi.org/10.1523/JNEUROSCI.3619-13.2014

Tsay, J. S., Kim, H. E., McDougle, S. D., Taylor, J. A., Haith, A., Avraham, G., Krakauer, J. W., Collins, A. G., & Ivry, R. B. (2024). Fundamental processes in sensorimotor learning: Reasoning, refinement, and retrieval. *eLife*, *13*, e91839. https://doi.org/10.7554/eLife.91839

Tsay, J. S., Schuck, L., & Ivry, R. B. (2023). Cerebellar Degeneration Impairs Strategy Discovery but Not Strategy Recall. *The Cerebellum*, *22*(6), 1223–1233. https://doi.org/10.1007/s12311-022-01500-6

Tucciarelli, R., Bird, L., Straka, Z., Szymanska, M., Kollamkulam, M., Sonar, H., Paik, J., Clode, D., Hoffmann, M., Cowie, D., & Makin, T. R. (2024). *Shaping the developing homunculus: The roles of deprivation and compensatory behaviour in sensory remapping* (p. 2024.11.26.624817). bioRxiv. https://doi.org/10.1101/2024.11.26.624817

Tzvi, E., Koeth, F., Karabanov, A. N., Siebner, H. R., & Krämer, U. M. (2020). Cerebellar – Premotor cortex interactions underlying visuomotor adaptation. *NeuroImage*, *220*, 117142. https://doi.org/10.1016/j.neuroimage.2020.117142

Vandevoorde, K., & Orban de Xivry, J.-J. (2020). Why is the explicit component of motor adaptation limited in elderly adults? *Journal of Neurophysiology*, *124*(1), 152–167. https://doi.org/10.1152/jn.00659.2019

von Hofsten, C., & Rönnqvist, L. (1988). Preparation for grasping an object: A developmental study. *Journal of Experimental Psychology: Human Perception and Performance*, *14*(4), 610–621. https://doi.org/10.1037/0096-1523.14.4.610

Wang, T., Avraham, G., Tsay, J. S., Thummala, T., & Ivry, R. B. (2022). *Advanced Feedback Enhances Sensorimotor Adaptation* (p. 2022.09.14.508027). bioRxiv. https://doi.org/10.1101/2022.09.14.508027

Wilterson, S. A., & Taylor, J. A. (2021). Implicit Visuomotor Adaptation Remains Limited after Several Days of Training. *eNeuro*, *8*(4). https://doi.org/10.1523/ENEURO.0312-20.2021

Wolpert, D. M., Diedrichsen, J., & Flanagan, J. R. (2011). Principles of sensorimotor learning. *Nature Reviews Neuroscience*, *12*(12), 739–751. https://doi.org/10.1038/nrn3112

Chapter 6: General discussion

This thesis explored how sensorimotor experience, and biomechanical constraints shape emerging motor skills, using congenital upper limb differences as a model. Across four studies, we explored: (1) the emergence of early gross motor milestones, (2) the development of compensatory motor strategies throughout childhood, (3) the interplay between imitation and self-guided motor exploration in supporting innovative problem-solving, and (4) the flexibility of internal motor models and the ability to flexibly adapt to new motor mappings. This speaks to the broad question of flexible motor development, which has been the focus of much recent discussion (Adolph et al., 2018; Adolph & Hoch, 2019).

This thesis makes several contributions to the field of motor development. First, it builds on previous findings (Tucciarelli et al., 2024) providing the most comprehensive account to date of early motor development in children with congenital upper limb differences, highlighting the flexibility of milestone acquisition amid structural variation. Second, it advances our knowledge of motor adaptation under biomechanical constraints by examining how compensatory motor strategies are acquired, refined, and applied across a range of contexts. This work also addresses the limitations in existing assessments of limb function, and for the first time explores the factors that drive adaptive behavioural choices. Third, our findings reveal a nuanced relationship between imitation and self-guided exploration in learning, offering new insights into embodied cognition and cognitive flexibility. Finally, this research presents the first visuomotor adaptation study to incorporate ballistic movements and abrupt perturbations in typically developing two-handed children, and the first to examine motor adaptation in children with congenital upper limb differences. Collectively, these studies provide new insights into how biomechanical constraints and sensorimotor experience interact to shape motor learning and problem-solving across development.

Summary of key findings

We found that while children with upper limb differences experienced modest but progressive delays in achieving certain gross motor milestones, particularly those requiring greater postural stability and balance demands, other milestones such as crawling emerged on a typical timeline. Notably, children developed a wide array of alternative crawling strategies, underscoring the capacity for early adaptation to structural variation. In later childhood, these children employed highly individualised and task-specific compensatory motor strategies to accomplish bimanual tasks. Unlike their two-handed peers, they engaged a greater variety of effectors, often coordinating up to three body parts in a single strategy. Strategy use evolved with age, shifting from broad exploration to a more refined and efficient repertoire. While anatomy and experience constrained what actions were possible, strategic flexibility was also shaped by subjective factors such as comfort and control, suggesting that compensatory behaviour is not solely outcome driven.

Having shown that that structural variation in the context of congenital upper limb differences significantly shapes the development of motor skills, from the timing of early motor milestones to the flexible compensatory strategies employed in everyday life, we shifted our focus to the mechanisms underpinning motor learning. In particular, we investigated both cognitive and implicit processes involved in the acquisition and refinement of adaptive behaviours. We found that children with limb differences performed comparably to their two-handed peers on a tool innovation task. However, the underlying processes differed. Two-handed children benefitted from high imitation fidelity, while children with limb differences performed best when they imitated less, suggesting a greater reliance on selective imitation of necessary steps and self-guided exploration. These results suggest that early motor challenges may foster cognitive flexibility and more efficient goal-directed learning. Finally, in a visuomotor adaptation task, both children with and without limb differences demonstrated successful adaptation. Among two-handed children, there was evidence of increasing reliance on explicit strategies to guide early adaptation by middle childhood. Although children with upper limb differences performed comparably to their two-handed peers, explicit strategy use was not measured in this population. Contrary to our expectations, children with upper limb differences did not outperform their peers, suggesting that increased sensorimotor variability does not necessarily translate to enhanced internal model updating.

Taken together, these studies contribute to our understanding of how motor development unfolds in the context of anatomical variability. They demonstrate that structural variation. in the form of congenital upper limb differences, gives rise to alternative developmental trajectories. This divergence from typical motor development should not be considered atypical, but rather a parallel pathway through which functional outcomes are achieved through a different means. These findings highlight the role of exploration, strategic flexibility, and embodied experience in shaping both functional outcomes and the cognitive processes that support them.

Theoretical contributions

Building on these findings, our work advances several important theoretical perspectives on motor development and learning. In particular, we highlight the dynamic interplay between biomechanical constraints and exploratory behaviour, supporting a more nuanced view of motor development as a flexible and adaptive system.

Dynamic systems theory of motor development

Our findings provide compelling evidence for the dynamic systems theory of motor development, which posits that motor skills emerge from the continuous and reciprocal interaction between the person, task, and environment (Adolph & Hoch, 2019; Thelen, 1995; Thelen & Smith, 1994). For example, motor behaviours are shaped by various factors such as clutter in the environment, carrying objects, and even clothes and footwear (Cole & Adolph, 2023). Infants walking in shoes, for instance, exhibit slower and wider steps than when barefoot (Cole et al., 2022).

This perspective challenges traditional maturational theories by emphasising the role of experience. It frames development as a fluid process, dynamically assembled through multiple subsystems and real-time interactions with the world (Adolph & Hoch, 2019; Thelen & Smith, 1994). By studying children with congenital upper limb differences, we were able to investigate how functional motor skills emerge in the absence of typical motor templates. Our findings showed that while anatomical constraints influenced the timing and sequencing of early gross motor milestones, evidenced by modest delays and reversed order milestones, they did not impede the development of functional motor skills. Instead, these children adopted alternative motor strategies, such as commando crawling or bum-shuffling in place of traditional hands-and-knees crawling, exemplifying the flexibility of the developing motor system. Here, children forge individualised pathways based on their structural constraints to achieve functional outcomes. Such pathways should not be interpreted as deficits, but rather as examples of divergence within an adaptive system.

This behavioural flexibility becomes even more apparent in later childhood. Consistent with the dynamic systems theory, children with congenital upper limb differences did not develop a single, fixed compensatory strategy to compensate for their missing hand functionality (Adolph et al., 2018). Instead, they developed a diverse repertoire of adaptive strategies that were shaped by the task demands, anatomical variation, and prior experience. Children selected different effectors in response to their optimal functional capacity, such as stability, precision, visibility, or force. The torso and legs, for example, were used more frequently for object stabilisation. We also found that anatomical factors played a key role in shaping compensatory strategies, such that children with longer residual limbs used their residual limb more frequently, likely due to the enhanced functionality of an elbow joint. Importantly, compensatory strategies were not solely driven by the task or body alone. Our findings suggest that children also considered subjective factors such as comfort, control, and social acceptability when choosing how to act. This may explain the variability in strategy use among children with identical limb differences. Our findings align with those of Mnif et al., (2024), who demonstrated that motor and emotional functioning are modulated by social contexts, particularly those involving cooperation or competition.

Together, these findings contribute to dynamic systems theory by illustrating how motor development reflects the integration of biological constraints, lived experience, and contextual variability. They support an embodied, multi-dimensional model of development in which compensatory motor strategies are not merely an outcome-driven, but emergent behaviours grounded in exploration, reflecting the child's physical, emotional, and social reality.

Embodied cognition and sensorimotor experience

Our findings also offer important insights into embodied cognition, which emphasises that cognitive and perceptual development are both enabled and constrained by the body (Wilson, 2002). From this perspective, cognitive development emerges through the interplay between the physical structure of the body and its sensorimotor engagement with the environment. Congenital limb differences offer a unique opportunity to understand how this interplay operates under morphological variability.

Children are inherently social learners, often relying on others to learn about the world (Csibra & Gergely, 2009; Tomasello, 1999). However, anatomical constraints can disrupt this process. For children with upper limb differences, directly imitating observed behaviours is often not possible. As a result, they must actively adapt the behaviours they see or forgo imitation altogether, shaping a developmental trajectory that relies more heavily on self-guided exploration and adaptive problem-solving. Our findings indicate that children with upper limb differences engage in an extended period of exploration in early childhood, systematically testing multiple strategies within a task to arrive at a functional solution. Cruicially, this exploratory behaviour goes beyond compensation, enhancing novel problem-solving skills. This idea is supported by previous work with two-handers suggesting that the process of self-generating strategies through trial, error, and refinement provides rich sensorimotor experiences that promote cognitive flexibility, creativity, and resilience (Kidd & Hayden, 2015; Sutton & Barto, 2018). In our imitation and innovation study, children with upper limb differences who imitated the least were predicted to outperform even the most successful two-handed children on tool innovation tasks.

Notably, overall levels of imitation did not differ between groups, but the relationship between imitation and innovation diverged significantly. In two-handed children, higher imitation fidelity was associated with greater innovation success, suggesting that imitation served as a proxy for instrumental learning. By contrast, in children with upper limb differences lower imitation fidelity predicted greater innovation success. This suggests imitation may serve a more social or affiliative role in this group, while instrumental learning and innovative problem-solving abilities are shaped by self-guided exploration and adaptive reasoning. These findings align with those of Allen et al., (2024) who identified distinct problem-solving styles among children and adults with congenital upper limb differences. While overall time to find a solution in an online problem-solving game did not differ between groups, compared to two-handed participants, individuals with limb differences spent more time thinking before acting, ultimately solving problems in fewer attempts. This suggests a more deliberate and reflective approach to problem-solving, one that may stem from the need to think flexibly and adapt their motor actions in daily life.

Together, this growing body of research supports a central claim of embodied cognition: that the structure and use of the body does not only shape how individuals act, but also how they think. For children with congenital upper limb differences, lifelong adaptation to a world designed for two hands appears to foster cognitive flexibility, strategic planning, and a reduced reliance on imitation-based learning. Through daily motor adaptations, these children develop problem-solving strategies grounded in sensorimotor experience, providing a powerful example of how structural variability gives rise to cognitive diversity.

Motor learning mechanisms: implicit vs explicit processes

Our visuomotor adaptation study advance the theoretical understanding of motor learning by uncovering important developmental nuances in feedforward control. To our knowledge, this is the first ballistic reaching task employing an abrupt perturbation that limits online feedback control, thereby isolating feedforward mechanisms. We found that children as young as 5 can update their internal forward models, challenging prior assumptions that predictive internal model updating emerges closer to 8 years (Contreras-Vidal et al., 2005). We argue that earlier studies, which allowed online feedback control, may have masked this capacity because younger children naturally prefer online feedback control strategies (Malone et al., 2025). By restricting this, our ballistic task revealed an earlier capacity for feedforward adaptation, suggesting that the developmental timeline for internal model updating may be earlier than previously thought, and highlighting the critical role of task constraints in engaging motor learning mechanisms.

The consistency of implicit adaptation across development suggests that implicit feedforward learning is a foundational and maturationally robust process. Notably, implicit learning emerged when children were forced to rely on feedforward mechanisms, whereas previous studies showed more variable results when no time limit was enforced allowing both feed forward and feedback control (Contreras-Vidal et al., 2005; Deng et al., 2019; Malone et al., 2025; Tahej et al., 2012). This supports models that conceptualise implicit adaptation as a stable scaffold for motor learning, upon which explicit processes build (Tsay et al., 2022, 2024).

In contrast, we observed a non-linear developmental trajectory in explicit strategy use, such that 8-9-year-olds exhibited a distinct peak in early explicit strategy engagement, an effect not seen in younger children or adults. These findings align with developmental theories of cognitive flexibility and tool innovation emerging around this age (Beck et al., 2011; Rawlings et al., 2022), suggesting a sensitive period in mid-childhood where children begin to more effectively incorporate external cues into strategic motor planning. Their performance contrasts with both younger children, who may lack the cognitive resources for such strategies; and with adults, who may adopt a more cautious approach, gathering information to guide strategic thinking.

Cruicially, contrary to predictions, children with congenital upper limb differences did not exhibit superior or accelerated feedforward adaptation compared to their two-handed peers. This finding implies that while daily reliance on self-guided motor exploration may shape compensatory motor behaviours and cognitive learning styles, the underlying implicit mechanisms for internal model updating remain comparable. This novel finding contributes to the theoretical landscape by highlighting that sensorimotor experience and anatomical variability do not enhance or indeed impede foundational implicit learning processes.

Practical implications

This thesis provides the first comprehensive developmental account of congenital upper limb differences, offering important insights for clinical practice, early intervention, and parental support. While these condition rarely require ongoing treatment, the clinical aim remains to optimise limb function in order to support independence and participation in daily life (Watson, 2000; World Health Organisation, 2001). Our findings demonstrate that motor development in children with upper limb differences follows a distinct yet functional trajectory, characterised by flexible motor adaptations, and individualised use of different body parts to support functional outcomes. These insights have several practical implications.

First, our research underscores the need for individualised assessments that acknowledge the diversity of compensatory strategies used by children with upper limb differences. The strategies we observed were highly variable, shaped by age, anatomical constraints, prior experience, and subjective features such as comfort or habit. Existing functional assessments primarily focus on ease of task completion, use of the affected limb, range of motion, grip strength, and dexterity (Bagley et al., 2006; Bagley & James, 2004; Buffart et al., 2006; Cordray et al., 2025; Ho & Clarke, 2005; Kelley et al., 2016; Krumlinde-Sundholm et al., 2007; Waljee et al., 2015). The Assisting Hand Assessment, for example, scores how effectively the residual limb is used in conjunction with the intact hand, while the Unilateral Below-Elbow test codes how the affected limb is used - whether the end of the residual limb is used to stabilise or manipulate, or whether stabilisation is achieved using the elbow or torso (Bagley et al., 2006; Krumlinde-Sundholm et al., 2007). While informative, both tools remain centred on residual limb use and may fail to capture the full scope of a child's functional capacity. Our data show, for example, that many young children spontaneously use their feet to stabilise objects during bimanual tasks, an adaptation that is not captured by the current assessments of function. More broadly, children coordinated multiple body parts within a single strategy. These behaviours fall outside the scope of traditional assessments, yet they represent meaningful and often efficient adaptations. Our findings therefore highlight a need to assess functional outcomes more holistically, considering how other body parts are recruited and coordinated, and how strategies change over time.

These findings have important implications not only for assessment, but also for the design of training protocols for enhancing functionality. Rather than focusing on use of the residual limb, as standardised assessments do, or on prosthetic training, therapeutic interventions could be broadened to support the development of full-body compensatory strategies, building on the strategies that children are already employing spontaneously. For example, interventions could instead support the cognitive aspects of adaptation by promoting self-guided exploration, trial-and-error learning, and flexible problem-solving strategies that mirror children's natural approaches. This would encourage coordinated use of alternative effectors in bimanual tasks, with a focus on comfort, control, and functional outcome. These strength-based, child-led approaches could not only enhance functional independence but also improve quality of life by validating diverse motor strategies and fostering autonomy in everyday tasks.

Second, our findings emphasise the importance of recognising individual variability in motor skill acquisition. Children in our study generally achieved their early gross motor milestones at the upper limit of the typical range or with modest delays (Who Multicentre Growth Reference Study & de Onis, 2006), often using alternative strategies such as novel crawling patterns. These strategies reflect a flexible but functional response to structural differences. We therefore propose that clinicians should adopt a strength-based perspective when assessing developmental trajectories in this population, rather than relying on normative benchmarks derived from two-handed children.

Finally, these results have important implications for parental reassurance and early guidance. Congenital upper limb differences are mostly identified at birth, leaving parents with limited information and support (Clelland et al., 2024; Mason, 1991; *NCARDRS Congenital Anomaly Statistics*, 2021). Our findings provide valuable insights into children's early gross motor development, later functional outcomes, and enhanced cognitive flexibility.

Communicating these insights to parents may offer much needed support, shifting the narrative from one of deficit and concern to one of adaptation and potential, offering valuable reassurance during high uncertainty.

Limitations and Future directions

While this thesis provides new insights into the developmental trajectories of children with congenital upper limb differences, several limitations should be acknowledged, and how they point towards opportunities for future investigation.

Longitudinal research

Our first two studies provide a snapshot of motor development in children with congenital upper limb differences, retrospectively mapping the emergence of gross motor milestones, and using a cross-sectional design to explore compensatory motor behaviours. Although these findings provided valuable insight into how functional motor skills emerge in this population, they are limited in their ability to capture changes within children over time. Longitudinal research would allow us to build on these findings by mapping the emergence of early motor milestones with greater temporal resolution, capturing skill acquisition in days rather than months, and by tracking the developmental progression of adaptive behaviours at the individual level. This would enable more precise analysis of how compensatory motor strategies evolve, including shifts in the number and types of body parts employed, diversity of combinations trialled prior to success, and the increasing efficiency of these strategies over time.

Structural variability

For the purposes of this thesis, we intentionally recruited a functionally homogenous sample of children with congenital upper limb differences. Specifically, participants in our study examining compensatory motor strategies were all born with one hand capable of performing a pincer grip between a thumb and any finger. This sampling constraint allowed us to isolate the effects of unilateral functional differences and draw clearer conclusions about compensatory behaviours. However, future research should broaden this scope to include children with bilateral limb differences resulting in no pincer-gripping hands, or those born with upper limb differences that do not impact the pincer grip. Expanding the range of structural presentations would enable comparisons across different anatomical profiles and provide a more comprehensive understanding of how limb anatomy influences motor adaptation.

Innovation and executive functioning

Several important questions remain regarding the cognitive mechanisms that support motor learning and problem-solving in this population. One area for further exploration is the nuanced relationship between imitation and innovation. While our tool innovation task revealed that children with upper limb differences performed comparably to two-handed children, they did so by relying less on imitation and more on self-guided exploration. Future studies should unpick this relationship further by assessing innovation using open-ended tasks without a single correct solution. Although such tasks do not reveal greater innovation in two-handed children (Carr et al., 2015), the predicted relationship between imitation and innovation showing that children with upper limb differences may outperform their two-handed peers when imitation fidelity is low, provides a promising avenue for investigating how structural variability and an extended period of exploration supports divergent thinking and exploratory problem-solving.

Relatedly, this extended period of exploration observed in children with congenital upper limb differences may foster enhanced cognitive flexibility or creativity. Investigating this possibility using standardised measures of executive functioning would shed light on the broader cognitive impact of structural differences and self-directed skill acquisition.

Conclusion

In conclusion, this thesis presents the first comprehensive developmental account of motor learning in children with congenital upper limb differences, offering new insights into how biomechanical variation shapes both functional and cognitive outcomes. Through a multi-method approach spanning early infancy to late childhood, we have shown that structural constraints give rise to alternative, yet functional developmental trajectories grounded in flexibility, exploration, and adaptation. While these children may reach milestones slightly later or in unique ways, they develop a diverse repertoire of compensatory strategies that evolve with age and experience. These adaptations demonstrate how multiple systems work together to solve problems creatively and effectively. Our findings highlight the powerful role of exploration and embodied experience in shaping development and provide critical evidence in support of dynamic systems-based theories of motor development. For both researchers and caregivers, this work offers a more inclusive perspective on child development, one that embraces differences as a source of adaptive potential and cognitive diversity.

References

Adkinson, J. M., Bickham, R. S., Chung, K. C., & Waljee, J. F. (2015). Do Patient- and Parent-reported Outcomes Measures for Children With Congenital Hand Differences Capture WHO-ICF Domains? *Clinical Orthopaedics and Related Research®*, *473*(11), 3549. https://doi.org/10.1007/s11999-015-4505-5

Adolph, K., & Hoch, J. (2019). Motor Development: Embodied, Embedded, Enculturated, and Enabling. *Annual Review of Psychology*, *70*(1), 141–164. https://doi.org/10.1146/annurev-psych-010418-102836

Adolph, K., Hoch, J., & Cole, W. (2018). Development (of Walking): 15 Suggestions. *Trends in Cognitive Sciences*, *22*(8), 699–711. https://doi.org/10.1016/j.tics.2018.05.010

Adolph, K., Joh, A. S., & Eppler, M. A. (2010). Infants' Perception of Affordances of Slopes Under High and Low Friction Conditions. *Journal of Experimental Psychology. Human Perception and Performance*, *36*(4), 797–811. https://doi.org/10.1037/a0017450

Adolph, K., Vereijken, B., & Shrout, P. E. (2003). What changes in infant walking and why. *Child Development*, *74*(2), 475–497. https://doi.org/10.1111/1467-8624.7402011

Allen, K. R., Smith, K. A., Bird, L.-A., Tenenbaum, J. B., Makin, T. R., & Cowie, D. (2024). Lifelong learning of cognitive styles for physical problem-solving: The effect of embodied experience. *Psychonomic Bulletin & Review*, *31*(3), 1364–1375. https://doi.org/10.3758/s13423-023-02400-4

Ardon, M. S., Janssen, W. G., Hovius, S. E., Stam, H. J., & Selles, R. W. (2012). Low Impact of Congenital Hand Differences on Health-Related Quality of Life. *Archives of Physical Medicine and Rehabilitation*, *93*(2), 351–357. https://doi.org/10.1016/j.apmr.2011.09.004

Ardon, M. S., Janssen, W. G. M., Hovius, S. E. R., Stam, H. J., Murawska, M., Roebroeck, M. E., & Selles, R. W. (2014). Relationships Among Manual Body Functions, Manual Capacity, and Bimanual Performance Using the Prosthetic Upper Extremity Functional Index in Children With Congenital Hand Differences. *Physical Therapy*, *94*(6), 767–775. https://doi.org/10.2522/ptj.20130209

Arnould, C., Penta, M., Renders, A., & Thonnard, J.-L. (2004). ABILHAND-Kids. *Neurology*, *63*(6), 1045–1052. https://doi.org/10.1212/01.WNL.0000138423.77640.37

Bae, D. S., Canizares, M. F., Miller, P. E., Waters, P. M., & Goldfarb, C. A. (2018). Functional Impact of Congenital Hand Differences: Early Results From the Congenital Upper Limb Differences (CoULD) Registry. *The Journal of Hand Surgery*, *43*(4), 321–330. https://doi.org/10.1016/j.jhsa.2017.10.006

Bagley, A. M., & James, M. (2004). The Unilateral Below Elbow Test. *Developmental Medicine and Child Neurology*, *46*, 33–34.

Bagley, A. M., Molitor, F., Wagner, L. V., Tomhave, W., & James, M. A. (2006). The Unilateral Below Elbow Test: A function test for children with unilateral congenital below elbow deficiency. *Developmental Medicine and Child Neurology*, *48*(7), 569–575. https://doi.org/10.1017/S0012162206001204

Bayley, N. (2006). *Bayley Scales of Infant and Toddler Development* (Third Edition). The Psychological Corporation.

Beck, S. R., Apperly, I. A., Chappell, J., Guthrie, C., & Cutting, N. (2011). Making tools isn't child's play. *Cognition*, *119*(2), 301–306. https://doi.org/10.1016/j.cognition.2011.01.003

Bonawitz, E., Shafto, P., Gweon, H., Goodman, N. D., Spelke, E., & Schulz, L. (2011). The double-edged sword of pedagogy: Instruction limits spontaneous exploration and discovery. *Cognition*, *120*(3), 322–330. https://doi.org/10.1016/j.cognition.2010.10.001

Bourgeois, K. S., Khawar, A. W., Neal, S. A., & Lockman, J. J. (2005). Infant Manual Exploration of Objects, Surfaces, and Their Interrelations. *Infancy*, *8*(3), 233–252. https://doi.org/10.1207/s15327078in0803_3

Buffart, L. M., Roebroeck, M. E., Pesch-Batenburg, J. M. F. B., Janssen, W. G. M., & Stam, H. J. (2006). Assessment of arm/hand functioning in children with a congenital transverse or longitudinal reduction deficiency of the upper limb. *Disability and Rehabilitation*, *28*(2), 85–95. https://doi.org/10.1080/09638280500158406

Carr, K., Kendal, R. L., & Flynn, E. G. (2015). Imitate or innovate? Children's innovation is influenced by the efficacy of observed behaviour. *Cognition*, *142*, 322–332. https://doi.org/10.1016/j.cognition.2015.05.005

Carson, V., Zhang, Z., Predy, M., Pritchard, L., & Hesketh, K. D. (2022). Longitudinal associations between infant movement behaviours and development. *International Journal of Behavioral Nutrition and Physical Activity*, *19*(1), 10. https://doi.org/10.1186/s12966-022-01248-6

Chan, C. C. H., Stirling, P. H. C., & Lam, W. L. (2022). The impact of socioeconomic deprivation on congenital hand differences: A retrospective cohort study. *Hand Surgery and Rehabilitation*, *41*(2), 265–269. https://doi.org/10.1016/j.hansur.2021.12.005

Claxton, L. J., Keen, R., & McCarty, M. E. (2003). Evidence of Motor Planning in Infant Reaching Behavior. *Psychological Science*, *14*(4), 354–356. https://doi.org/10.1111/1467-9280.24421

Clelland, A. D., Lester, R., Duncan, Ó., & Lam, W. L. (2024). Parental experience after diagnosis of a congenital upper limb difference: A national survey. *Journal of Hand Surgery (European Volume)*, *49*(11), 1327–1333. https://doi.org/10.1177/17531934241249014

Cole, W. G., & Adolph, K. (2023). Learning to Move in a Changing Body in a Changing World. *Integrative and Comparative Biology*, *63*(3), 653–663. https://doi.org/10.1093/icb/icad083

Cole, W. G., Hospodar, C., & Adolph, K. (2022). *Is Barefoot Really Best? Infants Walking Barefoot, in Bendy Shoes, and in Stiff Shoes*. International congress on infant studies, Ottawa, Canada.

Comalli, D. M., Keen, R., Abraham, E. S., Foo, V. J., Lee, M.-H., & Adolph, K. (2016). The development of tool use: Planning for end-state comfort. *Developmental Psychology*, *52*(11), 1878–1892. https://doi.org/10.1037/dev0000207

Contreras-Vidal, J. L., Bo, J., Boudreau, J. P., & Clark, J. E. (2005). Development of visuomotor representations for hand movement in young children. *Experimental Brain Research*, *162*(2), 155–164. https://doi.org/10.1007/s00221-004-2123-7

Corbetta, D., & and Bojczyk, K. E. (2002). Infants Return to Two-Handed Reaching When They Are Learning to Walk. *Journal of Motor Behavior*, *34*(1), 83–95. https://doi.org/10.1080/00222890209601933

Cordray, H., Fiandeiro, M., Banala, M., Vaile, J. R., Struble, S. L., Pehnke, M., Shah, A. S., & Mendenhall, S. D. (2025). Gamified assessments of pediatric upper extremity function: A systematic review and appraisal. *Journal of Hand Therapy*. https://doi.org/10.1016/j.jht.2025.02.003

Corriveau, K., & Harris, P. L. (2009). Choosing your informant: Weighing familiarity and recent accuracy. *Developmental Science*, *12*(3), 426–437. https://doi.org/10.1111/j.1467-7687.2008.00792.x

Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences*, *13*(4), 148–153. https://doi.org/10.1016/j.tics.2009.01.005

Cusack, R., Ranzato, M., & Charvet, C. J. (2024). Helpless infants are learning a foundation model. *Trends in Cognitive Sciences*, *28*(8), 726–738. https://doi.org/10.1016/j.tics.2024.05.001

Dall'Orso, S., Steinweg, J., Allievi, A. G., Edwards, A. D., Burdet, E., & Arichi, T. (2018). Somatotopic Mapping of the Developing Sensorimotor Cortex in the Preterm Human Brain. *Cerebral Cortex*, *28*(7), 2507–2515. https://doi.org/10.1093/cercor/bhy050

Davis, S., Rawlings, B., Clegg, J. M., Ikejimba, D., Watson-Jones, R. E., Whiten, A., & Legare, C. H. (2022). Cognitive flexibility supports the development of cumulative cultural learning in children. *Scientific Reports*, *12*(1), 14073. https://doi.org/10.1038/s41598-022-18231-7

Dempsey-Jones, H., Wesselink, D. B., Friedman, J., & Makin, T. R. (2019). Organized Toe Maps in Extreme Foot Users. *Cell Reports*, *28*(11), 2748-2756.e4. https://doi.org/10.1016/j.celrep.2019.08.027

Deng, K., Chan ,John S. Y., & and Yan, J. H. (2019). Explicit Aiming Strategy Decreases the Differences in Visuomotor Adaptation between Children and Young Adults. *Developmental Neuropsychology*, *44*(7), 495–512. https://doi.org/10.1080/87565641.2019.1675664

DiYanni, C., & Kelemen, D. (2008). Using a bad tool with good intention: Young children's imitation of adults' questionable choices. *Journal of Experimental Child Psychology*, *101*(4), 241–261. https://doi.org/10.1016/j.jecp.2008.05.002

Dominici, N., Ivanenko, Y. P., Cappellini, G., d'Avella, A., Mondì, V., Cicchese, M., Fabiano, A., Silei, T., Di Paolo, A., Giannini, C., Poppele, R. E., & Lacquaniti, F. (2011). Locomotor Primitives in Newborn Babies and Their Development. *Science*, *334*(6058), 997–999. https://doi.org/10.1126/science.1210617

Flynn, E., Turner, C., & Giraldeau, L.-A. (2016). Selectivity in social and asocial learning: Investigating the prevalence, effect and development of young children's learning preferences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1690), 20150189. https://doi.org/10.1098/rstb.2015.0189

Fooken, J., Baltaretu, B. R., Barany, D. A., Diaz, G., Semrau, J. A., Singh, T., & Crawford, J. D. (2023). Perceptual-Cognitive Integration for Goal-Directed Action in Naturalistic Environments. *Journal of Neuroscience*, *43*(45), 7511–7522. https://doi.org/10.1523/JNEUROSCI.1373-23.2023

Franchak, J. M., & Adolph, K. (2024). An update of the development of motor behavior. *WIREs Cognitive Science*, *15*(6), e1682. https://doi.org/10.1002/wcs.1682

Franzblau, L. E., Chung, K. C., Carlozzi, N., Chin, A. Y. T., Nellans, K. W., & Waljee, J. F. (2015). Coping with Congenital Hand Differences. *Plastic and Reconstructive Surgery*, *135*(4), 1067–1075. https://doi.org/10.1097/PRS.0000000000001047

Gesell, A. (1928). *Infancy and human growth* (pp. xvii, 418). MacMillan Co. https://doi.org/10.1037/14664-000

Gesell, A. (1946). The ontogenesis of infant behavior. In L. Carmichael (Ed.), *Manual of child psychology.* (pp. 295–331). John Wiley & Sons Inc. https://doi.org/10.1037/10756-006

Hahamy, A., Macdonald, S. N., van den Heiligenberg, F., Kieliba, P., Emir, U., Malach, R., Johansen-Berg, H., Brugger, P., Culham, J. C., & Makin, T. R. (2017). Representation of Multiple Body Parts in the Missing-Hand Territory of Congenital One-Handers. *Current Biology*, *27*(9), 1350–1355. https://doi.org/10.1016/j.cub.2017.03.053

Hahamy, A., & Makin, T. R. (2019). Remapping in Cerebral and Cerebellar Cortices Is Not Restricted by Somatotopy. *Journal of Neuroscience*, *39*(47), 9328–9342. https://doi.org/10.1523/JNEUROSCI.2599-18.2019

Haywood, K., & Getchell, N. (2024). *Life Span Motor Development*. Human Kinetics.

Ho, E. S., & Clarke, H. M. (2005). Upper Extremity Function in Children with Congenital Hand Anomalies. *Journal of Hand Therapy*, *18*(3), 352–364. https://doi.org/10.1197/j.jht.2005.04.005

Hopkins, B., & Westra, T. (1990). Motor development, maternal expectations, and the role of handling. *Infant Behavior & Development*, *13*(1), 117–122. https://doi.org/10.1016/0163-6383(90)90011-V

Iverson, J. M. (2021). Developmental Variability and Developmental Cascades: Lessons From Motor and Language Development in Infancy. *Current Directions in Psychological Science*, *30*(3), 228–235. https://doi.org/10.1177/0963721421993822

James, M. A., Bagley, A. M., Brasington, K., Lutz, C., McConnell, S., & Molitor, F. (2006). Impact of Prostheses on Function and Quality of Life for Children with Unilateral Congenital Below-the-Elbow Deficiency. *JBJS*, *88*(11), 2356. https://doi.org/10.2106/JBJS.E.01146

Karasik, L. B., Adolph, K., Fernandes, S. N., Robinson, S. R., & Tamis-LeMonda, C. S. (2023). Gahvora cradling in Tajikistan: Cultural practices and associations with motor development. *Child Development*, *94*(4), 1049–1067. https://doi.org/10.1111/cdev.13919

Karasik, L. B., Tamis-LeMonda, C. S., & Adolph, K. (2011). Transition From Crawling to Walking and Infants' Actions With Objects and People. *Child Development*, *82*(4), 1199–1209. https://doi.org/10.1111/j.1467-8624.2011.01595.x

Karasik, L. B., Tamis-LeMonda, C. S., Ossmy, O., & Adolph, K. (2018). The ties that bind: Cradling in Tajikistan. *PLOS ONE*, *13*(10), e0204428. https://doi.org/10.1371/journal.pone.0204428

Keen, R. (2011). The Development of Problem Solving in Young Children: A Critical Cognitive Skill. *Annual Review of Psychology*, *62*(1), 1–21. https://doi.org/10.1146/annurev.psych.031809.130730

Kelley, B. P., Franzblau, L. E., Chung, K. C., Carlozzi, N., & Waljee, J. F. (2016). Hand Function and Appearance following Reconstruction for Congenital Hand Differences: A Qualitative Analysis of Children and Parents. *Plastic and Reconstructive Surgery*, *138*(1), 73e–81e. https://doi.org/10.1097/PRS.0000000000002286

Kidd, C., & Hayden, B. Y. (2015). The Psychology and Neuroscience of Curiosity. *Neuron*, *88*(3), 449–460. https://doi.org/10.1016/j.neuron.2015.09.010

Krumlinde-Sundholm, L., Holmefur, M., Kottorp, A., & Eliasson, A.-C. (2007). The Assisting Hand Assessment: Current evidence of validity, reliability, and responsiveness to change. *Developmental Medicine & Child Neurology*, *49*(4), 259–264. https://doi.org/10.1111/j.1469-8749.2007.00259.x

Legare, C. H., & Nielsen, M. (2015). Imitation and Innovation: The Dual Engines of Cultural Learning. *Trends in Cognitive Sciences*, *19*(11), 688–699. https://doi.org/10.1016/j.tics.2015.08.005

Lerman, J. A., Sullivan, E., Barnes, D. A., & Haynes, R. J. (2005). The Pediatric Outcomes Data Collection Instrument (PODCI) and Functional Assessment of Patients With Unilateral Upper Extremity Deficiencies. *Journal of Pediatric Orthopaedics*, *25*(3), 405. https://doi.org/10.1097/01.bpo.0000149866.80894.70

Lyons, D. E., Young, A. G., & Keil, F. C. (2007). The hidden structure of overimitation. *Proceedings of the National Academy of Sciences*, *104*(50), 19751–19756. https://doi.org/10.1073/pnas.0704452104

Majnemer, A., & Barr, R. G. (2006). Association between sleep position and early motor Development. *The Journal of Pediatrics*, *149*(5), 623-629.e1. https://doi.org/10.1016/j.jpeds.2006.05.009

Makin, T. R., Cramer, A. O., Scholz, J., Hahamy, A., Henderson Slater, D., Tracey, I., & Johansen-Berg, H. (2013). Deprivation-related and use-dependent plasticity go hand in hand. *eLife*, *2*, e01273. https://doi.org/10.7554/eLife.01273

Malone, L. A., Hill, N. M., Tripp, H., Zipunnikov, V., Wolpert, D. M., & Bastian, A. J. (2025). The control of movement gradually transitions from feedback control to feedforward adaptation throughout childhood. *Npj Science of Learning*, *10*(1), 13. https://doi.org/10.1038/s41539-025-00304-7

Mano, H., Fujiwara, S., & Haga, N. (2018). Adaptive behaviour and motor skills in children with upper limb deficiency. *Prosthetics and Orthotics International*, *42*(2), 236–240. https://doi.org/10.1177/0309364617718411

Mano, H., Fujiwara, S., & Haga, N. (2020). Effect of prostheses on children with congenital upper limb deficiencies. *Pediatrics International*, *62*(9), 1039–1043. https://doi.org/10.1111/ped.14265

Marshall, P. J., & Meltzoff, A. N. (2020). Body maps in the infant brain: Implications for neurodevelopmental disabilities. *Developmental Medicine & Child Neurology*, *62*(7), 778–783. https://doi.org/10.1111/dmcn.14540

Mason, K. J. (1991). Congenital Orthopedic Anomalies and Their Impact on the Family. *Nursing Clinics of North America*, *26*(1), 1–16. https://doi.org/10.1016/S0029-6465(22)03001-8

McCarty, M. E., Clifton, R. K., Ashmead, D. H., Lee, P., & Goubet, N. (2001). How Infants Use Vision for Grasping Objects. *Child Development*, *72*(4), 973–987. https://doi.org/10.1111/1467-8624.00329

McDougall, L., Kennedy, J., Coombs, C., & Penington, A. (2021). The psychosocial impact of congenital hand and upper limb differences on children: A qualitative study. *Journal of Hand Surgery (European Volume)*, *46*(4), 391–397. https://doi.org/10.1177/1753193420967527

McGraw, M. B. (1932). From Reflex to Muscular Control in the Assumption of an Erect Posture and Ambulation in the Human Infant. *Child Development*, *3*(4), 291–297. https://doi.org/10.2307/1125356

McGraw, M. B. (1935). *Growth: A study of Johnny and Jimmy (Preface by F. Tilney; introduction by J. Dewey.)* (p. 319). Appleton-Century.

McGraw, M. B. (1943). *The neuromuscular maturation of the human infant* (p. 140). Columbia University Press.

Mei, J. (1994). The northern Chinese custom of rearing babies in sandbags: Implications for motor and intellectual development. In *Motor development: Aspects of normal and delayed development* (pp. 41–48). VU Uitgeverij.

Meltzoff, A. N., Saby, J., N., & Marshall, P. J. (2019). *Neural representations of the body in 60‐day‐old human infants*. *22*(1), e12698.

Mnif, M., Chikh, S., Watelain, E., Ben Aissa, M., Rebhi, M., Guelmami, N., Dergaa, I., & Jarraya, M. (2024). The Impact of Social Context on Motor, Cognitive, and Affective Behaviors: A Pilot Study Among Physical Education Students. *Annals of Applied Sport Science*, *12*(Spring Supplementary), 0–0. https://doi.org/10.61186/aassjournal.1239

Muret, D., & Makin, T. R. (2021). The homeostatic homunculus: Rethinking deprivation-triggered reorganisation. *Current Opinion in Neurobiology*, *67*, 115–122. https://doi.org/10.1016/j.conb.2020.08.008

NCARDRS congenital anomaly statistics: Annual data. (2021, September 29). GOV.UK. https://www.gov.uk/government/publications/ncardrs-congenital-anomaly-annual-data

Ossmy, O., Han, D., Cheng, M., Bianco, C., Kaplan, B., & Adolph, K. (2022). *First "Where" and then "How": Developmental Processes in Exploring Solutions to Problems with Hidden Demands*. OSF. https://doi.org/10.31234/osf.io/m7tcr

Palmer, C. F. (1989). The discriminating nature of infants' exploratory actions. *Developmental Psychology*, *25*(6), 885–893. https://doi.org/10.1037/0012-1649.25.6.885

Payne, V. G., & Isaacs, L. D. (2024). *Human Motor Development: A Lifespan Approach* (11th ed.). Routledge. https://doi.org/10.4324/9781032697147

Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*, *60*(4), 389–443. https://doi.org/10.1093/brain/60.4.389

Piaget. (1945). *Play, Dreams And Imitation In Childhood*. Norton Library.

Rawlings, B. (2022). After a decade of tool innovation, what comes next? *Child Development Perspectives*, *16*(2), 118–124. https://doi.org/10.1111/cdep.12451

Rawlings, B., Flynn, E. G., & Kendal, R. L. (2022). Personality predicts innovation and social learning in children: Implications for cultural evolution. *Developmental Science*, *25*(1), e13153. https://doi.org/10.1111/desc.13153

Rigato, S., Begum Ali, J., van Velzen, J., & Bremner, A. J. (2014). The Neural Basis of Somatosensory Remapping Develops in Human Infancy. *Current Biology*, *24*(11), 1222–1226. https://doi.org/10.1016/j.cub.2014.04.004

Robert, M. T., Guberek, R., Sveistrup, H., & Levin, M. F. (2013). Motor learning in children with hemiplegic cerebral palsy and the role of sensation in short-term motor training of goal-directed reaching. *Developmental Medicine & Child Neurology*, *55*(12), 1121–1128. https://doi.org/10.1111/dmcn.12219

Rochat, P. (1989). Object manipulation and exploration in 2- to 5-month-old infants. *Developmental Psychology*, *25*(6), 871–884. https://doi.org/10.1037/0012-1649.25.6.871

Root, V., Muret, D., Arribas, M., Amoruso, E., Thornton, J., Tarall-Jozwiak, A., Tracey, I., & Makin, T. R. (2022). Complex pattern of facial remapping in somatosensory cortex following congenital but not acquired hand loss. *eLife*, *11*, e76158. https://doi.org/10.7554/eLife.76158

Rosenbaum, D. A., Marchk, F., Barnes, H. J., Vaughan, J., Slotta, J. D., & Jorgensen, M. J. (1990). Constraints for Action Selection: Overhand Versus Underhand Grips. In *Attention and Performance Xiii*. Psychology Press.

Sheffler, L. C., Hanley, C., Bagley, A., Molitor, F., & James, M. A. (2009). Comparison of Self-Reports and Parent Proxy-Reports of Function and Quality of Life of Children with Below-the-Elbow Deficiency. *JBJS*, *91*(12), 2852. https://doi.org/10.2106/JBJS.H.01108

Snapp-Childs, W., & Corbetta, D. (2009). Evidence of Early Strategies in Learning to Walk. *Infancy*, *14*(1), 101–116. https://doi.org/10.1080/15250000802569835

Squires, J., & Bricker, D. D. (2009). *Ages & Stages Questionnaires, Third Edition (ASQ-3): A Parent-completed Child Monitroing System*. Paul H. Brookes Publishing.

Stadskleiv, K. (2020). Cognitive functioning in children with cerebral palsy. *Developmental Medicine & Child Neurology*, *62*(3), 283–289. https://doi.org/10.1111/dmcn.14463

Stoeckel, M. C., Seitz, R. J., & Buetefisch, C. M. (2009). Congenitally altered motor experience alters somatotopic organization of human primary motor cortex. *Proceedings of the National Academy of Sciences*, *106*(7), 2395–2400. https://doi.org/10.1073/pnas.0803733106

Striem-Amit, E., Vannuscorps, G., & Caramazza, A. (2018). Plasticity based on compensatory effector use in the association but not primary sensorimotor cortex of people born without hands. *Proceedings of the National Academy of Sciences*, *115*(30), 7801–7806. https://doi.org/10.1073/pnas.1803926115

Sutton, R. S., & Barto, A. G. (2018). *Reinforcement Learning, second edition: An Introduction*. MIT Press.

Tahej, P.-K., Ferrel-Chapus, C., Olivier, I., Ginhac, D., & Rolland, J.-P. (2012). Multiple representations and mechanisms for visuomotor adaptation in young children. *Human Movement Science*, *31*(6), 1425–1435. https://doi.org/10.1016/j.humov.2012.02.016

Thelen, E. (1995). Motor development: A new synthesis. *American Psychologist*, *50*(2), 79–95. https://doi.org/10.1037/0003-066X.50.2.79

Thelen, E., & Smith, L. B. (1994). *A dynamic systems approach to the development of cognition and action* (pp. xxiii, 376). The MIT Press.

Tomasello, M. (1999). *The Cultural Origins of Human Cognition*. Harvard University Press.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, *28*(5), 675–691. https://doi.org/10.1017/S0140525X05000129

Tonkin, M. A. (2017). Classification of congenital anomalies of the hand and upper limb. *Journal of Hand Surgery (European Volume)*, *42*(5), 448–456. https://doi.org/10.1177/1753193417690965

Tsay, J. S., Kim, H. E., McDougle, S. D., Taylor, J. A., Haith, A., Avraham, G., Krakauer, J. W., Collins, A. G., & Ivry, R. B. (2024). Fundamental processes in sensorimotor learning: Reasoning, refinement, and retrieval. *eLife*, *13*, e91839. https://doi.org/10.7554/eLife.91839

Tsay, J. S., Kim, H., Haith, A. M., & Ivry, R. B. (2022). Understanding implicit sensorimotor adaptation as a process of proprioceptive re-alignment. *eLife*, *11*, e76639. https://doi.org/10.7554/eLife.76639

Tucciarelli, R., Bird, L., Straka, Z., Szymanska, M., Kollamkulam, M., Sonar, H., Paik, J., Clode, D., Hoffmann, M., Cowie, D., & Makin, T. R. (2024). *Shaping the developing homunculus: The roles of deprivation and compensatory behaviour in sensory remapping* (p. 2024.11.26.624817). bioRxiv. https://doi.org/10.1101/2024.11.26.624817

Virginia Wright, F., Hubbard, S., Jutai, J., & Naumann, S. (2001). The prosthetic upper extremity functional index: Development and reliability testing of a new functional status questionnaire for children who use upper extremity prostheses. *Journal of Hand Therapy*, *14*(2), 91–104. https://doi.org/10.1016/S0894-1130(01)80039-9

von Hofsten, C. (1980). Predictive reaching for moving objects by human infants. *Journal of Experimental Child Psychology*, *30*(3), 369–382. https://doi.org/10.1016/0022-0965(80)90043-0

Waljee, J. F., Carlozzi, N., Franzblau, L. E., Zhong, L., & Chung, K. C. (2015). Applying the Patient-Reported Outcomes Measurement Information System to Assess Upper Extremity Function among Children with Congenital Hand Differences. *Plastic and Reconstructive Surgery*, *136*(2), 200e. https://doi.org/10.1097/PRS.0000000000001444

Want, S. C., & Harris, P. L. (2001). Learning from Other People’s Mistakes: Causal Understanding in Learning to Use a Tool. *Child Development*, *72*(2), 431–443. https://doi.org/10.1111/1467-8624.00288

Watson, S. (2000). The principles of management of congenital anomalies of the upper limb. *Archives of Disease in Childhood*, *83*(1), 10–17. https://doi.org/10.1136/adc.83.1.10

Who Multicentre Growth Reference Study, & de Onis, M. (2006a). Assessment of sex differences and heterogeneity in motor milestone attainment among populations in the WHO Multicentre Growth Reference Study. *Acta Paediatrica*, *95*(S450), 66–75. https://doi.org/10.1111/j.1651-2227.2006.tb02377.x

Who Multicentre Growth Reference Study, & de Onis, M. (2006b). WHO Motor Development Study: Windows of achievement for six gross motor development milestones. *Acta Paediatrica*, *95*(S450), 86–95. https://doi.org/10.1111/j.1651-2227.2006.tb02379.x

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review*, *9*(4), 625–636. https://doi.org/10.3758/BF03196322

World Health Organisation. (2001). *International Classification of Functioning Disability and Health (ICF)*. World Health Organization.

Wright, F. V., Hubbard, S., Naumann, S., & Jutai, J. (2003). Evaluation of the validity of the prosthetic upper extremity functional index for children. *Archives of Physical Medicine and Rehabilitation*, *84*(4), 518–527. https://doi.org/10.1053/apmr.2003.50127