Specialization of the motor system in typically developing infants and infants with Down syndrome

Hana Kyjonková

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I, Hana Kyjonková, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Signed: Date:

For Dean

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Abstract

A growing body of evidence suggests that, compared to later in development, the infant brain starts out less specialized, producing more widespread activation in response to stimuli. Such theorizing has hitherto been mainly applied to perceptual and socio-cognitive development. In this thesis, I investigate whether a similar process of gradual specialization operates in motor development in infancy. I examine whether purposeful actions are initially 'broadly tuned' and widespread across limbs by measuring developmental changes in *extraneous movements* (movements in the other limbs that accompany the movement of a limb engaged in goal-directed action). In Study 1, I found a decrease in extraneous movements between 9- and 12-months of age in typically developing infants. I showed that this decrease is related to improvements in selective attention and amount of motor experience. In Study 2, I demonstrated that spatiotemporal coupling of both arms is a general characteristic of motor functioning in early infancy, and that this coupling declines between 9- and 12-months of age. Furthermore, I observed increased coupling with speed. In Study 3, I showed that extraneous movements are linked to, and likely limit, functional behaviour (in this case, intermanual coordination). Based on this series of studies with typically developing infants, I concluded that infant motor activity starts out broadly tuned and becomes progressively specialized over development. I subsequently extended my investigation to include atypically developing infants and toddlers (with Down syndrome). In Study 4, I showed that motor specialization in Down syndrome was more delayed than expected for children at their developmental level. Taken together with evidence that motor difficulties often appear before the onset of other behavioural symptomatology in disorders of unclear aetiology (e.g., ASD, ADHD), this opens up an important line of research in the possibility of using extraneous movements as an early marker of neurodevelopmental difficulties.

Keywords: progressive specialization, motor development, extraneous movements, motor overflow, reaching, infancy, Down syndrome

List of abbreviations

ADHD = attention-deficit/hyperactivity disorders

ASD = autism spectrum disorder

CA = chronological age

CC = corpus callosum

CNS = central nervous system

DCD = developmental coordination disorder

DS = Down syndrome

DTI = diffusion tensor imaging

EEG = electroencephalography

EMG = electromyography

fMRI = functional magnetic resonance imaging

fNIRS = functional near-infrared spectroscopy

IMC = intermanual coordination

MA = mental age

MRI = magnetic resonance imaging

MSEL = Mullen Scales of Early Learning

SICI = short-latency intracortical inhibition

TD = typically developing

TMS = transcranial magnetic stimulation

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CHAPTER 1

INTRODUCTION

Motor development is prolonged in human infants relative to other species. Many mammals can walk within minutes or hours of birth, yet in human infants it takes around a year before independent walking emerges (Garwicz, Christensson, & Psouni, 2009). This makes young humans particularly vulnerable and dependent on others around them. However, it may also allow for greater developmental plasticity, providing an opportunity for the infant to gradually specialize in interaction with the environment, allowing for greater adaptability (Gould, 1977).

How does specialization of the motor system occur over development? I propose that control over the body is initially 'broadly tuned' and becomes more specialized over time. More specifically, I propose here a scenario in which motor activation is widespread early in development leading to goal-directed motor action being accompanied by *extraneous movements*. These are movements that occur in the limbs that are not directly engaged in the action, but which accompany the movement of the acting limb (Addamo, Farrow, Hoy, Bradshaw, & Georgiou-Karistianis, 2007; Soska, Galeon, & Adolph, 2012). For example, when a child reaches for an object with her right hand, if her left hand also moves, then according to the definition above, the movement of the left hand would be classified as an extraneous movement. I hypothesize in this thesis that over the course of development, motor activation becomes more specialized and refined so that only the body parts that are needed for any given action are activated.

In this thesis, I examine developmental changes in extraneous movements in infancy (Study 1 and Study 2). I also investigate the relationship between extraneous movements and two factors that I predict are associated with developmental changes in extraneous movements: motor experience and attention (Study 1). Furthermore, I examine the link between extraneous movements and the ability to coordinate two hands to produce intermanual action (Study 3). Moreover, I address the question of whether extraneous movements and intermanual coordination differ between typically developing (TD) children and children with Down syndrome (DS) (Study 4). This line of research contributes to our understanding of motor specialization and the role of experience and attention in this process. It also examines the link between motor specialization and a functional behaviour—intermanual coordination. Finally, applying the methods developed with typically developing infants to an atypical population could open a new area of research into extraneous movements as a predictor of neurodevelopmental disorders.

In this introduction, I first outline the main theoretical approaches to motor development (the neuromaturationist approach, constructivism, developmental approaches). Secondly, I discuss the development of voluntary movements in infancy, with a particular focus on reaching. I show that while many studies have described developmental changes within a limb (e.g., how coordination between muscles within one limb changes over development), very few have examined developmental changes across the limbs (e.g., how infants develop control of one limb independently from the other limbs). In relation to this, I will also introduce the concept of extraneous movements. Finally, I put forward a set of hypotheses which I test in the experimental part of this thesis, and I explain the rationale behind them.

1.1. Theoretical approaches to motor development

1.1.1. The neuromaturationist approach

A large amount of descriptive data focusing on motor development was generated by Gesell and McGraw in the first half of the 20th century. These researchers carefully monitored the ages at which various motor skills, such as grasping, rolling, crawling, and walking, appeared (Gesell, 1928; Gesell, 1933; McGraw, 1943; see also Thelen & Adolph, 1992). The rich descriptions that they provided laid down the basis for a variety of standardized tests and norms of motor development (e.g., the Bayley Scales of Infant Development, the Denver Developmental Screening Test, the Mullen Scales of Early Learning). Furthermore, they provided an important stepping stone for further investigations into motor development.

McGraw and Gesell applied a maturationist approach to development. According to this framework, structure precedes function. In other words, maturation of the central nervous system (CNS) drives motor development. As the CNS matures, new motor abilities come online in the infants' repertoire. According to McGraw (1943), the CNS is divided into the 'lower' levels of the CNS and the ‘higher-level’ cerebral cortex. At birth, the cerebral cortex was considered not to be functioning; movements were thought to originate from the lower centres of the CNS and be reflexive. According to this approach, as the cortex develops, it inhibits the automatic activity of the lower levels of the CNS and is responsible for generating voluntary movements. Thus, researchers who take this maturational stance pay scant attention to *how* infants learn new behaviours (such as reaching or walking), because they place more emphasis on the timetable for neuromuscular connections to mature and come under cortical control (see discussion in Thelen, 1995; Thelen & Adolph, 1992; Williams, Corbetta, & Guan, 2015). Thus, from this neuromaturationist perspective, changes in the child’s motor ability have no effect on the brain processes involved in motor development. In other words, changes in motor behaviour occur only as the result of maturational changes in the brain.

Similarly to McGraw, Gesell (1928, 1933) proposed that motor development was the direct result of changes in the CNS. According to Gesell, development progresses through a particular sequence that is fixed across individuals. He argued that the rate of developmental progression is ultimately controlled by the child’s hereditary background (the principle of *individuating maturation*). Thus, he recognized that a new skill might appear at different ages in different individuals. However, the rate of development was, for Gesell, not under the influence of any external variable (e.g., parenting practices); rather he considered it to be internally driven by maturational changes in the CNS. In other words, experience itself does not play a role; different behaviours come online simply as a function of the development of the underlying substrates.

How would the neuromaturationist approach account for cultural variation in the onset of motor milestones such as sitting and walking (Adolph, Karasik, & Tamis-LeMonda, 2009)? One potential interpretation is that genes vary across cultural groups, and that this explains why infants from different cultures reach milestones at different time points (following Gesell’s principle of individuating maturation). However, there is evidence against this explanation. One example comes from Jamaican families. Jamaican infants sit and walk early relative to British infants. According to Hopkins and Westra (1988), the reason for this is that being able to sit and walk early on is more important to Jamaican than British mothers. Jamaican mothers selectively facilitate the development of these two abilities (sitting, walking) through practices termed *formal handling*. These practices include passive stretching and massaging which start shortly after birth, as well as involve active movements (such as stepping) around two to three months of age. These practices are widespread in many non-Western cultures, particularly in cultures of African origin (see Hopkins & Westra, 1988, for more details). Hopkins and Westra (1990) monitored the cultural practices of Jamaican families who moved to the UK. All infants who took part in their study were born in the same hospital in a large British city. However, there were large individual differences in the use of the formal handling practices described above. The Jamaican mothers who used child-handling practices were shown to also expect their infants to be able to sit and walk independently earlier than the Jamaican mothers who used the handling routines only partly or not at all. In line with this, the infants from the first group of mothers sat and, to a lesser extent, walked earlier (Hopkins & Westra, 1988, 1990). This study, and many others (see Adolph et al., 2009, for review), have highlighted the importance of experience for motor development, and thus provide evidence against the neuromaturationist approach.

Although many aspects of the neuromaturationist approach to development have not stood the test of time, some of the themes are still relevant to developmental science today, such as the notion of development as *differentiation*. This mechanism, studied by embryologist Coghill (1929), was an inspiration to both McGraw and Gesell. According to Coghill, mature behaviour develops through a process of increasing specificity. The developing organism starts as a whole, not a collection of parts that needs to be orchestrated to work together. "*Specific functions are carved out and not glued together*" (Thelen & Adolph, 1992, p. 372). This process is analogous to the single cell at the beginning of embryonic development which gives rise—through differentiation—to the human body with many different cell types (Hauf, Waizenegger, & Peters, 2001). Coghill argued that all neural and behavioural development is a result of differentiation. This idea has long been present in developmental theorizing (e.g., the ecological approach, Gibson & Pick, 2000; the dynamic systems approach, Thelen & Smith, 1994; for an overview see Gibson & Pick, 2000; see also Section 1.1.3 of this chapter).

1.1.2. The constructivist approach

Differentiation as a developmental process inspired a large number of theoretical approaches (as discussed in Section 1.1.1 above, see also Section 1.1.3). An alternative set of influential theories is built on the developmental process of *enrichment* (e.g., the constructivist approach, Piaget, 1952, 1954; the nativist approach, Chomsky, 1965; Spelke, 1990). These approaches share the view that the organism is impoverished at the beginning of development and has to be supplemented by stimulation from the environment. The most influential developmental theory building on the mechanism of enrichment was the constructivist theory formulated by Piaget (1954). This theory aims to explain the process of learning and developmental change. Although Piaget was primarily interested in cognitive, rather than motor, development, action-exploration and interaction with environment is at the core of his theory.

According to Piaget, the infant starts out with relatively simple reflexive actions from which complex mental representations develop over time (*schemas*; Bartlett, 1932; Vernon, 1954). Piaget argued that infants have no intentions during the first few months of life, and that early movements, which we perceive as intentional, are merely coincidental. Through repetition of activity (*circular reactions*), infants learn about the consequences of their actions. For example, an infant may kick her crib – and thereby create a sound. By repeating this action, the infant learns about the effects of their actions and constructs sensorimotor schemas. Thus, representations of action-perception relationships are, for Piaget, outcomes of an *enrichment* process. Piaget calls this initial phase of development the s*ensorimotor stage*, which lasts roughly from birth to one year of age. The schemas formed during this stage of development serve as a basis for the development of higher cognitive functions. Thus, in Piagetian theory, cognition originates in sensorimotor activities. Although cognition and motor are tightly connected early on, according to Piaget's theory they become separated over developmental time.

Piaget's constructivism is one of the most influential accounts of early cognitive development, which stimulated a large body of infant research. However, not all aspects of Piaget's theory have been supported by the empirical evidence (Bahrick & Lickliter, 2000; Clifton, Muir, Ashmead, & Clarkson, 1993; McCarty, Clifton, Ashmead, Lee, & Goubet, 2001; Slater, Quinn, Brown, & Hayes, 1999; Streri & Gentaz, 2004). Nevertheless, Piaget's notion that self-generated activity drives the emergence of goal-directed action was revolutionary to the field of motor development, as I show in the following section.

1.1.3. Contemporary accounts of motor development

A number of developmental approaches have emerged over the last several decades, including the developmental systems approach (Adolph & Robinson, 2008; Oyama, Griffiths, & Gray, 2001; Spencer et al., 2009), ecological psychology (e.g., Adolph, 1997; Gibson & Pick, 2000; Turvey, 1990), dynamic systems approach (Thelen & Smith, 1994), dynamic field theory (Schöner & Spencer, 2016), connectionism (e.g., Bates & Elman, 1993; Elman, 1990; Rumelhart & McClelland, 1986), neuroconstructivism (Karmiloff-Smith, 1998, 2006, 2009; Mareschal et al., 2007), and the theory of neuronal group selection (Edelman, 1987). Originating from different disciplines, these approaches often use different terminology to describe development, which makes it challenging to assess the extent to which these theories differ from each other (for comparisons see Spencer, Thomas, & McClelland, 2009; Thelen & Smith, 1994). However, core principles can be identified across these approaches. Contrary to the neuromaturationist perspective, all these developmental approaches share the view that development is a process of self-organization that results from interactions between multiple interdependent subsystems within an environment. Intrinsic factors (e.g., physiological, psychological, neural) as well as extrinsic factors (e.g., informational cues, surface, social context) contribute to the developmental outcome.

The developmental approach that has been most often applied to motor development is the *dynamic systems approach* (Spencer, Perone, & Buss, 2011). This theory derives from a field of mathematics that uses equations to describe the behaviour of complex dynamical systems (which in turn has its origins in Newtonian mechanics; Gleick, 1996; Smith & Thelen, 2003). Initially, the approach was applied by Kelso, Kugler, and Turvey to the domains of perception and action (Kelso, 1995; Kelso, Holt, Kugler, & Turvey, 1980; Kugler & Turvey, 1987). But then Thelen, Smith, Goldfield and others extended the approach to developmental science, mainly to address theoretical and empirical issues in motor development (Goldfield, 1995; Newell, Liu, & Mayer-Kress, 2001, 2003; Thelen & Smith, 1994; Thelen & Ulrich, 1991). McGraw's and Gesell's view of development as differentiation and Piaget's emphasis on self-generated activity are consistent with this approach. Similarly to the other current developmental approaches, a core part of the dynamic systems approach is the multi-causal view where interactions between the body, nervous system, and environment drive developmental change (Chiel & Beer, 1997; D. Corbetta, 2009; Gottlieb et al., 1998; Spencer, Thomas, et al., 2009; Thelen, 1992). Novel behaviours self-organize through these probabilistic interactions, without any predetermined rules present in the system *a priori* (Thelen, 1989, 1992, 1995). This is dramatically different from the neuromaturationist view where the system is assumed to contain an innate set of rules that determines how the system's development will unfold.

According to the dynamic systems approach, in order for goal-directed activity such as reaching to emerge, the infant needs to assemble a large number of elements. For example, infants need to locate a target in space, be motivated to reach for the target, assess whether it is close enough to reach for, control the arm muscles to lift the arm against gravity, and modulate the speed of their movement while controlling posture (Clearfield & Thelen, 2001). How is it possible that infants as young as 3 months of age pull these elements together and reach for objects successfully? It is not an easy task for infants and it requires a lot of practice. From birth, infants have been learning to control their body and act on their environment through spontaneous movements as well as movement attempts directed at objects (D. Corbetta & Thelen, 1999; Thelen et al., 1993). Some suggest that this practice starts even earlier—in utero (de Vries, Visser, & Prechtl, 1982, 1985; Sparling, Van Tol, & Chescheir, 1999).

Learning occurs through perception-action cycles (Edelman, 1987; Gibson, 1988). During the early stages of learning, the organism acts on the environment by producing various movements and perceives the effects of the action (*variability*). Through repetition of these cycles, the individual discovers the most adaptive forms of motor patterns (*selection*). These selected patterns become relatively stable over time yet retain some flexibility in order to adapt to various task demands. So the fit between action and environment progressively increases over developmental time (Adolph, 1997; Angulo-Kinzler, 2001; Thelen et al., 1993; von Hofsten & Lindhagen, 1979).

The dynamic systems account uses a specific set of concepts and terminology to describe development (see Spencer, Thomas, & McClelland, 2009; Thelen & Smith, 1994; Thelen & Ulrich, 1991). For the purpose of this thesis, I will focus on one concept that is central to the dynamic systems account: the *attractor*. According to the dynamic systems account, complex systems "*autonomously prefer certain patterns of behavior strictly as a result of the cooperativeness of the participating elements in a particular context*" (Thelen & Ulrich, 1991, p. 10). An attractor is a state of the system which is neither prescribed nor innate. It is an emergent phenomenon. The system shifts between qualitatively different attractor states. These *phase shifts* are the result of *control parameters*. A control parameter can be any organic or environmental variable that moves the system into a new attractor state. The terminology can be illustrated with an example of gait changes in quadrupeds. Most horses, for example, possess four natural gaits: walk, trot, canter, and gallop. When horses increase the speed of their locomotion from one gait (e.g., walk) to another (e.g., gallop), we observe a shift from one pattern (or attractor) to another. In this case, the speed of locomotion is a control parameter which causes a phase shift from walking, an attractor stable at a slower speed, to galloping, an attractor stable at a faster speed. Although attractors are not hard wired or predetermined, the system seems to 'prefer' certain attractors (walk, trot, canter, gallop) over others (e.g., a hypothetical attractor between walk and trot). This may arise from intrinsic (e.g., morphology) or extrinsic factors (e.g., task, environmental context) or a combination of both. Development can be viewed as a process of transitions between attractor states (Newell, Liu, & Mayer-Kress, 2003; Thelen & Ulrich, 1991).

While the dynamic systems account *describes* developmental changes as a result of self-organization when the system enters new attractor states, it does not always *explain* how transitions between attractor states occur developmentally and why certain developmental paths are taken. *Reinforcement learning models* have been instrumental in elucidating mechanisms of developmental change (e.g., the development of reaching; Berthier, Rosenstein, & Barto, 2005; see also Barto, 2002; Sutton & Barto, 1998). Reinforcement learning models rely on a signal that evaluates the learner's performance without specifying the target output. The signal can be an external agent (e.g., a parent) but is more likely to have an intrinsic origin. In the case of reaching, it may be information about whether the reach was successful, accomplished with relative ease, etc. This signal has a learning value because it can discriminate between the movements that were more efficient in achieving the goal and those which were less efficient. Because the system does not receive target outputs directly from a teacher, the way the system learns is by actively trying alternatives, evaluating the outcome, and using previous experience to select the most successful solution.

As a theoretical approach to explain development, the dynamic systems account is predominantly employed for motor development, mostly focusing on change at the level of behaviour. Although the dynamic systems account views the brain as an important subsystem that contributes to the emergence of behaviour, the dynamic systems account itself does not make many specific predictions about neural processes. Researchers in the dynamic systems account often use Edelman's *neuronal group selection theory* (Edelman, 1987; Sporns & Edelman, 1993). This developmental theory emphasizes the structural variability of brain circuits. According to Edelman, the infant brain does not start out with precisely wired circuits, but repertoires of variant circuits that form neuronal groups consisting of strongly interconnected neurons. These neuronal groups compete against each other over the processing of different stimuli. The neuronal groups whose activation in a given context matches the environmental and internal constraints better than the other groups gradually become selected through the mechanism of synaptic change.

The neuronal group selection theory makes very similar predictions to those of other theories working with the principle of selection, such as *neuroconstructivism* (M. H. Johnson, 2011b; Karmiloff-Smith, 2006; Mareschal et al., 2007). These approaches point out that while the adult brain shows relatively stable patterns of activation that are often specific to particular stimuli (e.g., the fusiform face area activates when an adult sees a face; Kanwisher, McDermott, & Chun, 1997), the infant brain does not start out that way. Early in development, the brain is characterized by overproduction of unspecified synaptic connections (Bourgeois, 2001; Greenough, Black, & Wallace, 1987). Thus patterns of activation in the infant brain are more diffuse than those in the adult brain. Brain activation becomes increasingly specialized over developmental time through interactions between various brain regions and the environment (Elman et al., 1996; Fair et al., 2007; M. H. Johnson, 2001b, 2011b). Scant specialization and high plasticity in the infant brain is reflected in the differential impact of brain injury over development: brain injury is more likely to cause a specific deficit in the highly specialized adult brain than in the less specialized (and somewhat more plastic) infant brain (M. H. Johnson, 2011b; Mareschal et al., 2007; Stiles & Jernigan, 2010).

Evidence of specialization and increasing selectivity of brain responses has been found across various cognitive domains – for example in studies examining face perception (Aylward et al., 2005; de Haan, Humphreys, & Johnson, 2002; Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Golarai et al., 2007; Joseph, Gathers, & Bhatt, 2011; Passarotti, Smith, DeLano, & Huang, 2007; Scherf, Behrmann, Humphreys, & Luna, 2007), social cognition (Blakemore, Den Ouden, Choudhury, & Frith, 2007; Carter & Pelphrey, 2006; Kobayashi, Glover, & Temple, 2007; Pfeifer, Lieberman, & Dapretto, 2007; A. T. Wang, Lee, Sigman, & Dapretto, 2006), learning to read (Brem et al., 2010; Schlaggar & McCandliss, 2007), executive function (Casey et al., 1997; Durston, Davidson, et al., 2006; K. M. Thomas et al., 1999) and verbal fluency (Gaillard et al., 2000; Holland et al., 2001).

There is currently very limited empirical evidence for early brain changes related to motor activity in human infants. However, it is likely that early on, due to the large number of unspecified synaptic connections, motor activity is broadly tuned to its environment (Huttenlocher, 2002; Passingham, 1993). Therefore, motor activity is unlikely to be specific to any particular context in early development. How does this broadly-tuned motor activity become increasingly specialized? Because motor activity is variable, some actions will initially by chance be more successful in accomplishing a goal than others. For example, early in reaching, certain movements will lead to successful contact with a toy or a close approach to the toy. This particular pattern of neuronal activation will be facilitated and stabilized through Hebbian learning (Munakata & Pfaffly, 2004). Through this mechanism, the connections for this particular pattern are strengthened and this pattern is more likely to be selected in future. Through repetition of this cycle, certain synaptic connections become stabilized and the brain specializes to perform certain actions (Edelman, 1987; Hollerbach, 1982; Schöner & Thelen, 2006; Sporns & Edelman, 1993).

The selection of successful goal-oriented movements occurs through exploration (Thelen, 1995; Thelen & Corbetta, 1994). This enables the system to develop actions adaptive to their environment. Thus, experience with various motor skills is likely to play an important role in shaping the brain. Although data from human infants that would confirm this assumption are not hitherto available (for first attempts, see Bell & Fox, 1996; D. Corbetta, Friedman, & Bell, 2014; Rigato, Begum Ali, van Velzen, & Bremner, 2014), data from older children and adults indeed show that motor experience shapes the brain (e.g., Andres et al., 1999; Karni et al., 1998; Luft et al., 2004; McCombe Waller & Whitall, 2005; Petersen, van Mier, Fiez, & Raichle, 1998). More specifically, the studies with older children and adults provide evidence that the brain changes when the individual learns a new motor skill. Could this evidence be generalized to infants learning fundamental motor skills? In my view, motor skill acquisition in infants is dramatically different from those in older children and adults. While the latter two groups have a repertoire of proficient basic motor skills (e.g., walking, reaching, jumping, balancing, sitting) which can be built upon when a new skill is learned (e.g., playing the piano), infants are faced with the problem of how to establish basic skills in the first place. Although evidence is not currently available in the human infant case, in the animal literature results consistently show how important early motor experiences are for developing a motor system (Dorris, Paré, & Munoz, 2000; Greenough, Larson, & Withers, 1985; Kleim, Barbay, & Nudo, 1998; J. H. Martin, 2004, 2005; J. H. Martin, Friel, Salimi, & Chakrabarty, 2007; Nudo, Milliken, Jenkins, & Merzenich, 1996). But the mechanisms that give rise to the development of certain behaviours in animal models may not be the same as those that give rise to human behaviour (Konopka et al., 2012).

1.2. Motor development as specialization

If the relationship between neural structures and motor behaviour is bidirectional (Kleim, Jones, & Schallert, 2003), then interactions between motor behaviour and the environment shape neural structures but at the same time neural substrates affect behaviour. Thus, if it is a general principle that neural activity is 'broadly-tuned' at the beginning of development (M. H. Johnson, 2011b), then it follows, in my view, that motor activity should also be broadly tuned. My proposal is that across development both functional brain and functional motor activity are being sculpted in interaction with each other and with the environment, leading to the development of both specialized neural substrates and a repertoire of motor activity which is adaptive for a range of environmental circumstances.

The developmental process of selection of successful goal-directed movements has often been studied within one limb (see Section 1.2.1 below). However, little attention has been given to the selection processes that determine which of the limbs could successfully perform a given action. This is illustrated with the following example: Berthier, Clifton, McCall, and Robin (1999) identified two significant problems that infants face when learning to reach for an object. Firstly, they must move their hand close to the object. Secondly, they must adjust the hand itself to perform a grasp. In this thesis, I will argue that both of these problems are linked to the specialization of a *single* limb and that there is at least one additional problem that infants are required to solve when learning to reach: *Infants need to select an appropriate limb with which to perform the action*. In the following paragraphs, I review what is known about specialization within a limb and also highlight how relatively little is known about limb selection.

1.2.1. Specialization within a limb

One of the most frequently studied goal-directed activities in infancy is the ability to reach for an object. When adults reach for an object, their arm shows stereotyped kinematic patterns: typically, a straight hand path with a bell-shaped velocity profile (e.g., Morasso, 1983). A number of studies have demonstrated that these stereotyped arm kinematics are not inborn motor patterns (e.g., Konczak & Dichgans, 1997; Thelen et al., 1993; Thelen, Corbetta, & Spencer, 1996; von Hofsten, 1991a). Rather, as I outline below, they result from learning in interaction with the environment.

The ability to reach emerges from around 3-5 months of age (Lee, Liu, & Newell, 2006; Thelen et al., 1993; von Hofsten & Lindhagen, 1979). Before this age, infants show poor motor control of their arms. Although they are able to move their arms (Thelen et al., 1993; van der Meer, van der Weel, & Lee, 1995), they are unable to intentionally contact and grasp an object. However, the swiping movements they produce sometimes lead to contact with an object by chance. These pre-reaching movements show poor differentiation in control between arm and finger segments of the upper limb—when the arm extends, the fingers also extend. No flexion of the hand or zooming in on the target is yet present (Hofsten, 1993). Also, coupling or coactivation of antagonist muscles within arm during arm movement has also been detected using electromyography (EMG; Hadders-Algra, Van Eykern, Klip-Van den Nieuwendijk, & Prechtl, 1992). This coactivation is present until three months of age when a substantial change occurs: a decrease in the co-contraction of antagonist muscle groups and an increase in their reciprocal activation (as one muscle contracts, another one is elongated; Hadders-Algra et al., 1992). Thus, control over the arm becomes gradually specialized: from controlling the arm and hand as one unit of co-contracting muscles to the emergence of reciprocal activation. Around the same time, the first successful purposeful reaches occur (von Hofsten & Lindhagen, 1979).

Early successful reaches appear jerky, being comprised of multiple accelerations and decelerations (Fetters & Todd, 1987; Mathew & Cook, 1990; von Hofsten, 1991; von Hofsten & Lindhagen, 1979). These jerky movements have been named by von Hofsten and Lindgahen (1979) as *multiple movement units*. Over development, the infant's reaching movements become straighter and more directly aimed towards the target and the number of movement units that comprise a reach decreases. As reaches become more proficient, the first movement unit (one acceleration and deceleration) involves a larger proportion of the reach. This brings the hand close to the target. This may be followed by a small correction (Halverson, 1931; von Hofsten & Lindhagen, 1979).

Reaching ability continues to improve over the second half of the first year of life, with grasps becoming differentiated and adjusted to the size of the object (Lee et al., 2006; Newell, Scully, McDonald, & Baillargeon, 1989; von Hofsten & Rönnqvist, 1988). Around 6 months of age, infants do not adjust grasp configuration to object size and instead perform whole hand grasps with poor coordination between the palm and fingers. By 9-10 months, control over the hand becomes more differentiated with the ability to grasp using the forefinger depending on the object size. Infants can also adjust their hand opening (aperture) according to the size of the object. Nine-month-olds also coordinate reaching and grasping into one continuous movement. They are also able to correct their hand trajectory to a moving object even after initiating the reaching movement (Angulo-Barroso & Tiernan, 2008).

There is high variability in early reaches not only across individuals but also within individual infants. Over development, the infant systematically reduces between-trial variability by selecting the most successful trajectories as predicted by reinforcement learning models (Section 1.1.3 of this chapter). However, this is a very challenging process because of *motor redundancy* – there are multiple ways for an organism to perform a movement in order to achieve a particular goal (Bernstein, 1967; Sporns & Edelman, 1993). As Bernstein (1967) states, "*It is clear that the basic difficulties for co-ordination consist precisely in the extreme abundance of* *degrees of freedom, with which the [nervous] centre is not at first in a position to deal*" (p. 107). In this context, a *degree of freedom* refers to a feature of motor activity that can be controlled. It can be either a mechanical (e.g., a possible rotation of a joint or direction of movement) or physiological quantity (e.g., the firing of a motor neuron controlling the muscles of a particular joint). Bernstein (1967) proposed that the complexity of degrees of freedom (the *degrees-of-freedom problem*) is solved by the developed system by employing *synergies*, or functional patterns of control, instead of controlling every single degree of freedom separately. For example, in reaching for an object, an individual controls the activity of certain muscles together to produce a particular synergy rather than sending specific signals to each muscle separately (e.g., Bekoff, Kauer, Fulstone, & Summers, 1989). This is offered as an explanation of why adults can produce movement trajectories with relatively small variability between trials (e.g., Morasso, 1983).

An ability to employ movement synergies is not something we are born with. We need to learn this skill through practice. How do we manage to control the large number of degrees of freedom when learning a new skill? Bernstein (1967) proposed that during the acquisition of a new motor skill, the individual restricts or 'freezes' some points of articulation, effectively reducing the number of degrees of freedom in order to simplify the control of acting limbs. Restricted degrees of freedom become released as the individual gains more proficiency, and attempts more precise and complex skilled movements. The proposal about 'freezing' degrees of freedom during the initial stages of learning has also been applied to motor development in infancy (Konczak & Dichgans, 1997; Sporns & Edelman, 1993). The infant was proposed to initially have control over a limited number of degrees of freedom, but the number of degrees of freedom that the infant can control increases over developmental time with the progressive specialization of the system. This is consistent with the proposal that infants initially possess a small number of synergies that are applied across various contexts (Kato, Hirashima, Oohashi, Watanabe, & Taga, 2014); these synergies then become differentiated over developmental time (see Section 1.2.2).

The dynamic systems approach describes reaching as an emergent skill which results from the interaction of subsystems (e.g., movement direction, forces generated during a reach) within a particular context. As I mentioned above, adults are able to produce straight, smooth reaching trajectories over many different contexts (e.g., the trajectory is straight if the adult is reaching straight ahead or if the adult is crossing the midline). Thus, adults show a stable spatiotemporal topography of reaching. The dynamic systems approach considers the spatiotemporal topography of adult reaching to be an *attractor state*, "*pulling together many components (e.g., joints, motor neurons) into a coherent pattern of coordination*" (Thelen & Spencer, 1998, p. 508). Thus, the dynamic systems approach would label the emergence of stable reaching in infancy as the emergence of an attractor.

To sum up, a large body of literature shows that, across development, control over the components of movement in a reaching limb becomes more differentiated, beginning with newborns controlling the hand and arm together as a single unit, with co-contracting muscles, through to the appearance of reciprocal activation and the differentiation of digits to produce finer grips (e.g., Angulo-Barroso & Tiernan, 2008; Hadders-Algra et al., 1992; von Hofsten & Lindhagen, 1979). Reaching trajectories also become smoother and less variable (e.g., Konczak & Dichgans, 1997), which the dynamic systems approach would describe as the emergence of a stable attractor for reaching (Thelen & Spencer, 1998). According to the account developed in this thesis (and elaborated further below), this is the result of gradual fine-tuning of the selection of particular features of motor control to action goals. The developmental specialisation of movement synergies offers a way of describing the form that these features would take.

1.2.2. Specialization across limbs

As mentioned earlier, although there is ample research considering the development of specialization of movements within one limb, the developmental specialization of movements across different limbs has received relatively little attention. Although many studies, as I show below in more detail, collect data from more than one limb, they subsequently focus their analysis on only one limb –

understandably so, since the research questions posed have usually been about specialization within a limb (e.g., Galloway & Thelen, 2004). Thus, a typical approach has been to collapse analyses across limbs. This approach is also reflected in the way many computational modelling studies address the problem of how reaching emerges: such models often comprise a single arm (e.g., Berthier et al., 2005; Schlesinger, Parisi, & Langer, 2000; Sporns & Edelman, 1993). This is clearly not a true representation of the human body. The challenge of reaching is not only a problem of controlling the arm as it reaches towards a target. It is also a problem of how to select a particular limb from all the limbs available to perform the action. Although limb selection might seem facile to older children and adults, I suggest here that it may not be so for the developing infant.

1.2.2.1. Developmental transition from bimanual to unimanual reaching

The studies that monitor more than one limb during a goal-directed action mostly focus on the infants' arms, reporting whether the infants produce unimanual or bimanual reaching. Interestingly, D. Corbetta and Thelen (1994) observed early reaches to be bimanual, even though some objects were small and could easily have been grasped by a single hand. The bimanual tendency was present for several weeks after reaching onset, despite the fact that infants did have repeated experience with the objects (D. Corbetta & Thelen, 1994). The unimanual preference for reaching for small objects seems only to emerge at around 8 months of age (D. Corbetta & Thelen, 1994, 1996; Thelen et al., 1996), although other studies have reported an earlier change: at around 5-6 months of age (Bresson, Maury, Pieraut-Le Bonniec, & de Schonen, 1977; Fagard, 2000; Gesell & Ames, 1947; Ramsay & Willis, 1984; Rochat, 1992).

The shift from bimanual to unimanual reaching for small objects is a consistent finding across many different infant studies (D. Corbetta & Thelen, 1996; Fagard, 2000; Fagard & Jacquet, 1996; Fagard & Pezé, 1997; Flament, 1974, 1975; Gesell & Ames, 1947; Newell et al., 1989; White, Castle, & Held, 1964). This has led to the proposal that initially young infants have difficulty controlling their arms independently (Diamond, 1991; Fagard & Jacquet, 1989; Fagard & Lockman, 2005;

Fagard & Marks, 2000; Ramsay & Weber, 1986) and that control over the arms is symmetrical early in development (Dennis, 1976; Diamond, 1991; Duque et al., 2007; Goldfield & Michel, 1986b; Meyer, Röricht, von Einsiedel, Kruggel, & Weindl, 1995; Swinnen & Carson, 2002).

How would the transition from bimanual to unimanual reaching emerge? I believe that a clue is provided in the observation by Flament (1974, 1975) that, during early reaches, infants often extend both hands/arms towards an object even though only one of the hands grasped the object. Therefore, early in development, reaching is bimanual irrespective of the size of the object. However, infants receive different feedback from different sized objects. For example, if an object is large and the infant approaches it bimanually, then it is quite likely that both hands will make contact with the object. However, if the object is very small and the infant approaches it bimanually, then there is more chance that only one hand will ultimately make contact with the object (i.e., if the object is too small to place both hands on it). Thus, compared to reaching for a large object when both hands receive the same feedback, during reaching for a small object, the hand that makes contact with the object will receive different feedback from the hand that fails to make contact. I propose that this differential feedback between hands may be one of the factors that, over developmental time, leads to the emergence of unimanual reaching for small objects. Put another way, it may be that infants early on operate a motor synergy that includes both limbs moving in symmetry, i.e., they do not manipulate the degree of freedom of movement between the arms. A synergy for unimanual reaching emerges later on through interaction with the environment.

1.2.3. Is motor action in early development characterized by activation of all four limbs?

Infants rarely have only two limbs; they typically have four. Perhaps inter-limb synergy does not initially include only two arms but also the legs? In other words, do young infants activate all their limbs when interacting with the environment?

1.2.3.1. Infants reaching with their feet

Although the research question on whether early motor action involves the activation of all four limbs has not been addressed directly, Galloway and Thelen (2004) examined the ability of infants to reach for a toy using their feet. In this study, 2- to 3-month-olds were provided with an opportunity to reach for toys with their hands or feet. The authors were interested in whether infants can control their early leg movements with precision. This was an important question considering the once-dominant view that motor development progresses in cephalocaudal fashion (from head to toe) as a result of increasing cortical control over spinal and brainstem circuits (McGraw, 1943). Thus, the legs were believed to be developmentally out of the infant's control for a longer time than the arms. To test this neuromaturationist hypothesis, Galloway and Thelen (2004) presented infants with a toy either at a position where it was easily accessible to the infants' hands or at a position where it was easily accessible to their feet. The study showed that infants contacted the toy with their feet a month or more earlier than with their hands. This was an important result which contradicted the neuromaturationist view that motor skills are acquired in a cephalocaudal direction (McGraw, 1943).

However, it remains unclear whether the infants in Galloway and Thelen's (2004) study attempted to reach for the toy with all four limbs (arms and legs), irrespective of whether only some of the limbs contacted the object. If this was the case, it would provide support for the proposal made earlier in this chapter that control over the body is broadly tuned early in development, with an initial synergy including all four limbs. It is impossible to answer this question from the data reported by Galloway and Thelen (2004). The authors only coded for 'contact' with the toy and information about the actual attempts at contact were not reported. Thus, even if the infant attempted to reach with their arms for the toy that was presented at the location of their feet, then the toy would be so far from the infant that it would be highly unlikely that the infant would be able to actually contact the toy with their hand; this information would not have been captured in the authors' coding scheme. Also, to truly test whether an infant would reach for a toy with all four limbs, the toy would have to be presented at a ‘limb neutral’ location; yet it is debatable whether such a location even exists!

The only information from the Results section of the Galloway and Thelen (2004) paper that could shed light on what other parts of the body were activated during the reaching movements is the durations for which each infant spent handling the toy when it was presented at the location of the feet, and the duration each toy was in contact with the infant’s feet when the toy was presented at the location of the infant’s hands. From the onset of grasp with the hands, infants spent around 50% of the 15-second trial touching the toy with their hands—when the toy was presented in the hand location. Interestingly, infants also spent around 35% of the time touching the toy with their feet when it was presented in the hand location. In other words, although the toy was presented at the location of the hands, infants spent a substantial amount of time touching it with their feet. However, a crucial piece of information is missing here: when the infants touched the toy with their feet, did they approach or contact it with their hands *at the same time*? If so, then this would support my proposal that activity is initially broadly-tuned and that infants would thus reach for the toy with all their limbs (i.e., using a synergy involving all four limbs). If one only monitors the activity of the upper limbs during a reaching task, then this synergy for all four limbs would look like a synergy for bimanual reaching. However, just because what the feet were are doing is not measured, does not mean that they are not moving in an attempt to reach for the object.

1.2.3.2. The conjugate reinforcement mobile paradigm

There is another line of research that could provide insight into whether there is an early synergy for performing actions with all four limbs. Piaget’s (1952) observation that a young infant can repeat a leg kick that happens to shake a toy attached to the infant’s crib inspired the *conjugate reinforcement mobile* procedure (Rovee & Rovee, 1969; for a review see Rovee-Collier, Hayne, & Colombo, 2001; Rovee-Collier & Gekoski, 1979). In this procedure, as infants from 1- to 6-months lie in a crib, a ribbon is used to attach their ankle to an overhead mobile. When the infant spontaneously moves, the mobile moves. Infants quickly learn about the correspondence between their own movement and the subsequent movement of the mobile. They learn that they can increase the movement of the mobile by increasing their own leg movements (e.g., Angulo-Kinzler, 2001; Rovee-Collier & Gekoski, 1979). The feedback in this procedure is called *conjugate reinforcement* because the amount of movement of the mobile (reinforcement) received by the infants is directly proportional (conjugate) to the duration and amplitude of their own movements.

The conjugate reinforcement mobile paradigm is traditionally used to investigate memory in infants and also to examine developmental changes within a limb (Angulo-Kinzler & Horn, 2001; Angulo-Kinzler, Ulrich, & Thelen, 2002; Chen, Fetters, Holt, & Saltzman, 2002; Heathcock, Bhat, Lobo, & Galloway, 2004; Rovee & Rovee, 1969; Thelen, 1994). Most studies that employ this paradigm focus on the difference between the movement of a limb when it has not been attached to the mobile versus when it has been attached to the mobile. Thus, like those studies described in Section 1.2.1, these studies mostly focus on changes in a single limb (the one attached to the mobile), describing increasing differentiation of control within that limb. What would we observe if we were to examine what is happening in the other three limbs when one of them is attached to a mobile? How much differentiation of limbs would the infants display?

The answers to these questions were indirectly provided by Watanabe and Taga (2006). Like many other studies that have used the conjugate reinforcement mobile paradigm, the purpose of this particular study was to investigate the development of memory in infancy. The researchers examined developmental changes in the motor activity of 2-, 3-, and 4-month-olds when one of the infants' arms was attached to a baby cot mobile. However, unlike traditional conjugate reinforcement mobile analyses, these authors provided data for all four limbs. Although infants across all three age groups made more movements in general when a limb was attached to the mobile (producing *extraneous movements*, i.e., movements in the limbs not attached to a mobile), the specificity of the limbs they activated increased with age (i.e., extraneous movements decreased). While the 2-month-olds increased movements in all their limbs, the 3-month-olds did so only in both arms (i.e., even though only one arm was connected to the mobile). At 4 months of age, the infants selectively increased movements solely in the arm that was attached to the mobile. Thus, this study provided evidence in support of a synergy for initial action with all four limbs. However, although the 4-month-olds showed significantly more motor activity of the limb that was necessary and sufficient for the action compared to activity of the other limbs, there was still activity present in the other limbs (see also Watanabe & Taga, 2009, for a similar result). Because—as with the other studies described above—Watanabe and Taga's (2006) research question was not about the origins of the motor system, they did not provide details of any data that could give us insight into these extraneous movements. For example, the authors did not measure the onset times of any specific movement. Hence, we are unable to draw any firm conclusions about whether the onset of extraneous movements was tightly linked to the movements of the arm attached to mobile (*motor overflow*; Addamo et al., 2007). Furthermore, the mechanisms behind the increase in specificity of motor activation remain unknown.

1.2.3.3. Extraneous movements, motor overflow, and mirror movements in infants

The ability to activate only specific limbs for unimanual actions has been further investigated in older infants (4.5- to 7-month-olds) by Soska and colleagues (2012). These authors focused on two types of extraneous movements—*motor overflow* and *mirror movements*. *Motor overflow* refers to extraneous movements that begin with the onset of goal-directed movement (e.g., if fingers on the left hand start moving at the moment the right hand starts reaching for an object). Overflow movements that are symmetrical to the movements of the acting limb along the body midline are called mirror movements (Addamo et al., 2007). Soska et al. (2012) found that a high proportion of unimanual exploration in 4.5- to 7-month-olds was accompanied by motor overflow (around 75% in the non-acting hand/arm; 50% in the feet/legs) and by mirror movements (20%). Although these authors did not find any developmental change in extraneous movements, in my view, they captured the *emergence* of a synergy for using a single limb for unimanual action. Why were these extraneous movements not captured in any of the previous studies examining the transition from bimanual to unimanual reaching? It is probable that previous coding schemes were not sufficiently sensitive to capture this information.

No information exists about what happens with extraneous movements later on in infancy. However, we do know that it is possible to elicit motor overflow and mirror movements in older children and adults (e.g., Abercrombie, Lindon, & Tyson, 2008; Baliz et al., 2005; Bodwell, Mahurin, Waddle, Price, & Cramer, 2003; Cohen, Taft, Mahadeviah, & Birch, 1967; Lazarus & Todor, 1987; Mayston, Harrison, & Stephens, 1999; Shinohara, Keenan, & Enoka, 2003). Because of their tight temporal synchrony to the onset of the movement of the acting limb, it has been suggested that motor overflow and mirror movements reflect motor commands that leak from one body part to others (Addamo et al., 2007). The commonly proposed neural structure underpinning motor overflow and mirror movements is the corpus callosum (Koerte et al., 2009; Lazarus & Todor, 1987; Mayston et al., 1999; Mayston, 1997; Qiu et al., 2011). In adults, when a unilateral motor command is generated in one hemisphere, the interhemispheric connections of the corpus callosum usually inhibit the corresponding area in the other hemisphere (Grefkes, Eickhoff, Nowak, Dafotakis, & Fink, 2008). However, this inhibition is difficult to sustain when the system is exposed to challenging motor tasks, such as finger tapping, squeezing, or applying force, which leads to production of extraneous movement (e.g., Addamo et al., 2007; Armatas, Summers, & Bradshaw, 1996). Development of the corpus callosum coincides with changes in extraneous movements in children (J. A. Lazarus & Todor, 1987; Todor & Lazarus, 1986). However, there is evidence that brain activation remains to some extent symmetrical, even in older children when the overt action is unimanual (Huo et al., 2011). Thus, findings from older children and adults indicate that the synergy for unimanual action is stable, until the system is put under pressure when it returns to its ontogenetically older synergy for bimanual action (and possibly, hypothetically, if more pressure is exerted, to an even older attractor for activating all four limbs).

As I have shown this section, the infant motor system seems to start as symmetrical and broadly tuned to its environment. There is some evidence suggesting that infants initially act on the environment by employing symmetrical synergies involving multiple limbs (Soska et al., 2012; Watanabe & Taga, 2006, 2009). Their motor system becomes gradually specialized (fine-tuned) for unimanual action. However, little is known about how this happens.

1.3. Rationale for this thesis

This thesis addresses a gap in our knowledge concerning how infants progressively specialize their motor system in order to perform unimanual action by focusing on developmental changes in extraneous movements across limbs. In the first three studies, I consider factors that could be related to the development of motor specialization (motor experience, attention, intermanual activity). For Study 4, I also examine motor specialization in infants and toddlers with a neuro-developmental disorder (Down syndrome). Here, I delineate a range of hypotheses arising from the literature, providing a rationale for each of them.

1.3.1. Developmental changes in extraneous movements in infancy (Study 1; Hypothesis 1)

Although infants can perform an action with a single limb within the first year of life, extraneous movements in other limbs accompany these actions (Soska et al., 2012). Older children and adults only tend to show extraneous movements under strenuous conditions (Addamo et al, 2007). No developmental decreases in extraneous movements have yet been observed in early development (see Section 1.2.3.3). In this thesis, I investigate developmental change in extraneous movements towards the end of the first year of life. During this period, infants acquire a number of motor skills that are indicative of improving motor control. Firstly, at around 12 months of age, infants begin to coordinate the actions of both arms (D. Corbetta & Thelen, 1996; Goldfield & Michel, 1986b; see also *Hypothesis 5* in Section 1.3.3 below). Secondly, gross motor development involving the independent and coordinated control of upper and lower limbs occurs rapidly between 9 and 12 months of age (e.g., crawling, standing alone; Wijnhoven et al., 2004). These improvements in motor control are hypothesized to be associated with an increase in the specificity of motor activation for unimanual action (see *Hypothesis 5* in Section 1.3.3 below). I predict that 9-month-olds will produce more extraneous movements than 12-month-olds (*Hypothesis 1*).

1.3.2. Spatiotemporal congruency of extraneous movements and the effect of speed over development (Study 2; Hypotheses 2, 3, & 4)

The shift from bimanual to unimanual reaching for small objects observed in infancy (D. Corbetta & Thelen, 1996; Fagard, 2000; Fagard & Jacquet, 1996; Fagard & Pezé, 1997; Flament, 1974, 1975; Gesell & Ames, 1947; Newell et al., 1989; White et al., 1964) led to the proposal that young infants have difficulty controlling their arms independently (e.g., Diamond, 1991; Fagard & Jacquet, 1989; Fagard & Lockman, 2005; Fagard & Marks, 2000; Ramsay & Weber, 1986) and that control over the arms is symmetrical early in development (Dennis, 1976; Diamond, 1991; Duque et al., 2007; Goldfield & Michel, 1986b; Meyer et al., 1995; Swinnen & Carson, 2002). The initial symmetry needs to be modified over development in order to control the body efficiently in a unilateral manner.

The proposal explored in this thesis is that the bilateral activation observed early in development is the initial state of the motor system, which contributes to early bimanual reaches. However, it seems reasonable to propose that through experience with the environment, infants gradually develop the ability to inhibit one of the hemispheres, which is associated with the emergence of a synergy for unimanual action. I propose that extraneous movements observed during infancy are indicative of such a process. Studies with adults show that inhibiting unimanual actions is difficult to sustain when the effort required for a motor response is increased (Perez & Cohen, 2008; Tinazzi & Zanette, 1998), leading to bilateral activation. To investigate the relationship between effort and extraneous movements in infancy, I examine changes in the symmetricity of extraneous movements both over development and with increasing speed. I expect that 9-month-olds will show more spatiotemporal congruency in extraneous movements than older infants (*Hypothesis 2*). Furthermore, I hypothesize that increasing speed is associated with greater spatiotemporal congruency (*Hypothesis 3*) and also that this relationship is stronger for younger infants (*Hypothesis 4*).

1.3.3. Motor experience and extraneous movements (Study 1; Hypothesis 5)

Infants accumulate a lot of experience with their emerging motor skills. By 3.5 months, they experience 3-6 million eye movements (S. P. Johnson, Amso, & Slemmer, 2003). Indeed, around the first year of life, infants spend about half of their day manipulating objects (Karasik, Tamis-LeMonda, & Adolph, 2011). Between 12-19 months, toddlers produce over 14,000 steps per day (in terms of distance, this is equivalent to walking 45 football fields), and they fall around 100 times per day (Adolph et al., 2012). It is known that experience shapes both brain development (Dorris et al., 2000; Greenough et al., 1985; Kleim et al., 1998; J. H. Martin, 2004, 2005; J. H. Martin et al., 2007; Nudo et al., 1996) and motor function (Adolph et al., 2009; Adolph, Vereijken, & Denny, 1998; Adolph, Vereijken, & Shrout, 2003; D. Corbetta & Bojczyk, 2002; Fogel, 1992; Fogel, Dedo, & McEwen, 1992; Libertus & Needham, 2010; Lobo & Galloway, 2008). I examine whether motor experience is associated with extraneous movements.

Major motor milestones have been found to be associated with changes in manual control. For example, it has been shown that decoupling in hand use is associated with the onset of crawling (e.g., D. Corbetta & Thelen, 2002; Goldfield, 1993). Goldfield (1993) proposed that a decrease in the symmetry of the manual motor system actually facilitates crawling. More specifically, he proposed that infants with a well-defined hand preference are more likely to start reaching for a toy when they are in the crawling posture. This would throw them off balance and initiate crawling (cf. Babik, Campbell, & Michel, 2014). However, in my view, it is also possible that the more experience with various motor skills, such as crawling, infants have, the more specialized their body movements are in a reaching task (i.e., the less they activate their lower limbs when it is not goal-appropriate). In this thesis I test the prediction that infants' motor experience is positively correlated with the specificity of their limb activation (i.e., negatively correlated with the prevalence of extraneous movements; *Hypothesis 5*).

1.3.4. Attention and extraneous movements (Study 1; Hypothesis 6)

The ability to visually select stimuli in the environment (*selective attention*) is closely linked to motor processes in adult humans and non-human animals (Allport, 1989; Astafiev et al., 2003; M. Corbetta et al., 1998; Perry & Zeki, 2000; Rizzolatti, 1983; Rizzolatti & Camarda, 1987). Selective attention has also been implicated in the modulation of extraneous movements (for review see Addamo et al., 2007). For example, children who are more easily distracted produce more extraneous movements (Waber, Mann, & Merola, 2008). Furthermore, extraneous movements in adults increase when their attention is diverted (Baliz et al., 2005). A relationship between attention and extraneous movements has also been found in infants by Soska et al. (2012). In that study, infants who looked more at objects during unimanual exploration exhibited fewer extraneous movements.

A tight coupling between attention and motor development in infancy has been found in several studies (e.g., Bacher & Robertson, 2001; Robertson & Johnson, 2009). This relationship was suggested to be underpinned by corticobasal ganglia network (Atkinson, Hood, Wattam-Bell, & Braddick, 1992; Dalton & Bergenn, 2007; Hood & Atkinson, 1993; M. H. Johnson, 2011a; Rothbart, Posner, & Rosicky, 1994). The basal ganglia were proposed to broadly inhibit all movements, while the frontal cortex selectively disinhibits the desired movement patterns (Alexander & Crutcher, 1990; Kostović & Jovanov-Milošević, 2006; Mink, 1996, 2003; Watanabe, Homae, & Taga, 2011). In relation to this thesis, it is possible that the development of the frontal lobe is linked to the ability to selectively disinhibit desired movements, which could be related to the more specific activation of a limb (more specificity, less extraneous movements) as well as better attentional abilities (in the form of improved disengagement). Therefore, my prediction is that infants with better selective attention will also be better at producing more specific movements that are tailored to the goal of the action (*Hypothesis 6*).

1.3.5. Intermanual coordination and extraneous movements (Study 3; Hypothesis 7)

If a decrease in extraneous movements over developmental time reflects the gradual specialization of the motor system, then I predict that infants who are better at producing unimanual reaches with fewer extraneous movements will also be better at intermanual coordination (*Hypothesis 7*). Intermanual coordination (also called *role-differentiated bimanual manipulation*; Kimmerle, Mick, & Michel, 1995; or *bimanual coordination*; Fagard & Jacquet, 1989) refers to activity in which the two hands perform different, but complementary movements (Bruner, 1970; Connolly & Dalgleish, 1989). An example is opening a drawer while retrieving a pen inside. This ability has been proposed to reflect collaboration between the two hemispheres (Fagard, Hardy-Léger, Kervella, & Marks, 2001; Ramsay, Campos, & Fenson, 1979).

Intermanual coordination emerges towards the end of the first year of life (Birtles et al., 2011; Bruner, 1970; Cornwell, Harris, & Fitzgerald, 1991; Diamond, 1991; Fagard, 1994; Fagard & Marks, 2000; Fagard & Pezé, 1997; Goldfield, 1983; Goldfield & Michel, 1986a; Kimmerle et al., 1995; Michel, Ovrut, & Harkins, 1985; Ramsay et al., 1979; Ramsay & Weber, 1986). Large individual differences have been reported for this ability. Studies show that only around half of all infants can perform intermanual actions by around 12 months of age, while the majority of them are able to perform such actions by around 18 months of age (Birtles et al., 2011; Fagard & Lockman, 2005; Kimmerle, Ferre, Kotwica, & Michel, 2010; Kimmerle et al., 1995; Michel et al., 1985; Ramsay, 1980; Ramsay et al., 1979; Ramsay & Weber, 1986). This suggests that intermanual actions are challenging for infants. I use these large individual differences to my advantage in Study 3, where I focus on the relationship between the ability to produce unimanual reaches without extraneous movements and intermanual coordination in 12-month-olds. I propose that the specialization of motor abilities to perform unimanual action without extraneous movements is related to the development of intermanual coordination abilities (*Hypothesis 7*). The brain has to have control over both hands independently if it is to perform unimanual reaches without extraneous movements and also engage in intermanual coordination.[1]

1.3.6. Motor specialization and atypical development (Study 4; Hypotheses 8, 9, & 10)

Aggravated extraneous movements have been described in various clinical populations including children with ADHD (attention-deficit/hyperactivity disorder; e.g., Gilbert, Isaacs, Augusta, MacNeil, & Mostofsky, 2011; MacNeil et al., 2011; Mostofsky et al., 2006; Mostofsky, Newschaffer, & Denckla, 2003) or ASD (autism spectrum disorder; e.g., Jansiewicz et al., 2006). Importantly, problems in the motor domain are often observed in these children before the emergence of cognitive and neurophysiological prodromal symptoms (e.g., ADHD; Kroes et al., 2007; ASD; Leonard, Elsabbagh, & Hill, 2013). Thus, extraneous movements might well be used as an early marker of developmental difficulties.

It has been impossible to find any previous study that has investigated the development of extraneous movements in infants and toddlers with a neurodevelopmental disorder. In this thesis I focus on extraneous movements in infants and toddlers with Down syndrome (DS). Because this disorder is usually diagnosed early in development, it presents an opportunity to study extraneous movements in atypically developing infants and toddlers. Considering the presence of motor delays in children with DS, I expect them to show more extraneous movements than TD children (*Hypothesis 8*) and also more difficulties with intermanual coordination (*Hypothesis 9*). Following from *Hypothesis 7* with a TD population (Section 1.3.5 above), I also expect links between extraneous movements and intermanual coordination to be present in infants and toddlers with DS (less extraneous movements associated with better intermanual coordination; *Hypothesis 10*). By testing these hypotheses, this thesis provides an important first step towards

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[1] Experience in coordinating the limbs is also likely to contribute to the development of the brain.

using extraneous movements as a possible predictor of neurodevelopmental disorders that do not have a clearly identified genetic origin and thus are not as easy nor as early to diagnose as DS.

CHAPTER 2

DEVELOPMENTAL DECREASE IN EXTRANEOUS MOVEMENTS DURING REACHING AND ITS RELATIONSHP WITH MOTOR EXPERIENCE AND SELECTIVE ATTENTION (STUDY 1)

Towards the end of the first year of life there are marked improvements in the ways in which infants use their limbs to act on the world across a range of behaviours, including manual exploration, reaching, intermanual coordination, and locomotion (e.g., Adolph & Berger, 2011; Fagard, 2000; Kimmerle, Ferre, Kotwica, & Michel, 2010; von Hofsten, 2007). Developmental theorists generally agree that such developments involve the increasing specificity and differentiation of the motor system during infancy (e.g., Gesell, 1933; Gibson & Pick, 2000; Sporns & Edelman, 1993; Thelen, 1985; see also Section 1.1). The development of an ability to select efficient goal-directed movements has often been studied during reaching, focusing particularly on changes in the characteristics of movements within limbs (e.g., Bhat & Galloway, 2007; Hofsten, 1991; Konczak & Dichgans, 1997; Thelen et al., 1993; see also Section 1.2.1). Yet, less attention has been paid to more broad-scale changes in action across the body, i.e., the transition from a less specialized state of motor selection in which multiple limbs are activated, to one in which only relevant limbs are selectively activated in the service of a goal (Soska et al., 2012). In this chapter, I focus on the development of limb selection during purposeful action; specifically, I examine for the progressive development of an ability to select only a single hand/arm during unimanual actions.

A growing body of evidence suggests that, early in development, the brain is 'broadly tuned' to the environment (M. H. Johnson, 2011b; see also Section 1.1.3). In other words, it starts out functionally diffuse, with the response properties of neural regions being less selective to particular stimuli (i.e., less specialized). Thus, patterns of activation in the adult brain are more localised than those in the infant brain. Brain activation becomes increasingly specialized over developmental time through interactions between various brain regions and the environment (Edelman, 1987; Elman et al., 1996; Fair et al., 2007; M. H. Johnson, 2011b; Supekar, Musen, & Menon, 2009). It is likely that motor development is yoked to brain development and follows a similar trajectory, with motor ability being initially 'broadly tuned' and becoming specialized over time. This gradual specialization likely happens in interaction with the environment through perception-action cycles (Gibson & Pick, 2000; Sporns & Edelman, 1993), leading to a better fit between action and environment.

Previous work has shown that, in infants of 4.5-7.5 months of age (with no observed developmental changes across this period), actions with one hand are often accompanied by goal-irrelevant movements in other limbs, such as clenching, splaying, or wiggling of the fingers and toes (Soska et al., 2012). The production of these extraneous movements in the first months of life contrasts with the skilled purposeful movements of adults and even young children (Addamo et al., 2007). However, developmental changes in extraneous movements in infancy remain undocumented and poorly understood. Thus, my investigation began with the hypothesis that the large prevalence of extraneous movements observed in young infants (Soska et al., 2012) may reflect a lack of specificity of the motor system, and that developmental decreases in such extraneous movements will signify the increasing specialization of the infant motor system. More specifically, I hypothesize that specialization (and thus reduction of extraneous movements) would occur particularly at the end of the first year of life, as part of the major developments in reaching, intermanual coordination, and locomotion seen at that time (e.g., Adolph & Berger, 2011; Fagard, 2000; Kimmerle et al., 2010; von Hofsten, 2007).

In this study, I began by measuring extraneous movements in non-acting limbs during unimanual reaching, predicting a developmental decrease in such movements between 9 and 12 months of age. This study also investigated two factors that I expected would be related to the ability to select appropriate movements in infancy: individual differences in (1) motor experience, and (2) selective attention. As described above, I was expecting decreases in extraneous movements to be specifically linked to the emergence of motor skills in which the use of the limbs is differentiated, such as walking with assistance. Therefore, I asked parents to report on their child's motor experience. I predicted that infants' motor experience would correlate negatively with extraneous movements in task irrelevant limbs.

The ability to visually select stimuli in the environment (visual selective attention) is closely linked to motor processes in adult humans and non-human animals, with overlapping brain areas involved in attention shifts and movement preparation (Allport, 1989; Astafiev et al., 2003; M. Corbetta et al., 1998; Perry & Zeki, 2000; Rizzolatti, 1983; Rizzolatti & Camarda, 1987). Attention has also been implicated in the modulation of extraneous movements across the lifespan (Addamo et al., 2007). For example, children who are more easily distracted also produce more extraneous movements (Waber et al., 2008). Furthermore, extraneous movements in adults increase when their attention is diverted (Baliz et al., 2005). A relationship between attention and extraneous movements has also been found in infants: looking more at an object during unimanual exploration was associated with fewer extraneous movements (Soska et al., 2012).

To explore the relationship between attention and extraneous movements in more depth, I administered a well-established attention task (Gap-Overlap) to assess the selection of visual information (Elsabbagh et al., 2013; Hood & Atkinson, 1993; M. H. Johnson, Posner, & Rothbart, 1991; Wass, Porayska-Pomsta, & Johnson, 2011). My prediction is that infants with better selective attention will also be better at controlling their extraneous movements and will produce more specific movements that are tailored to the goal of the action. A tight coupling between attention and motor development in infancy has been found in several studies (e.g., Bacher & Robertson, 2001; Robertson & Johnson, 2009). At around 3 months of age, attention also undergoes major transformation when it is temporarily described as ‘obligatory’ or ‘sticky’ because infants have difficulty disengaging their attention from a fixated stimulus as measured by the Gap-Overlap task (Atkinson et al., 1992; Rothbart et al., 1994). At the same time, the motor system undergoes a transition in the domain of spontaneously produced general movements (Einspieler, Prechtl, Bos, Ferrari, & Cioni, 2005; Prechtl, 1997; Prechtl & Hopkins, 1986). Both of these changes have been proposed to be a consequence of a developing corticobasal ganglia network (Atkinson et al., 1992; Dalton & Bergenn, 2007; Hood & Atkinson, 1993; M. H. Johnson, 2011a; Rothbart et al., 1994). The basal ganglia were proposed to broadly inhibit all movements, while the frontal cortex selectively disinhibits the desired movement patterns (Alexander & Crutcher, 1990; Kostović & Jovanov-Milošević, 2006; Mink, 1996, 2003; Watanabe et al., 2011). The proposal that a developing corticobasal ganglia network underlies the tight relationship between attention and movement has received empirical support from MRI studies of infants with perinatal brain damage where lesions to the basal ganglia have been associated with difficulty in disengaging from a stimulus as well as other neuromotor difficulties (Mercuri et al., 1997, 2004). Therefore, I predict that greater difficulty with visual selection in the Gap-Overlap task will be associated with a higher prevalence of extraneous movements.

In summary, this study focuses on extraneous movements in non-acting limbs while infants were reaching with one hand (i.e., unimanually) for a ball. Measures of the proportion of unimanual reaches accompanied by extraneous movements were taken: (1) across the entire duration of the reach, and (2) within +/- 100 ms of the onset of the unimanual reach to the ball, comparing groups of 9- and 12-month-old infants. Extraneous movements were also analysed in relation to infants' motor experience measured by parental report (how long infants had been sitting without support, crawling, standing with assistance, and walking with assistance), and infants' visual attention as measured by the Gap-Overlap task.

2.1. Methods

2.1.1. Participants

Two age groups, 9- and 12- month-olds, were tested in this study. The final sample sizes for each age group and other characteristics are presented in Table 2.1. Six additional infants were tested but excluded from analysis due to: (1) experimenter error (one 12-month-old), (2) producing fewer than four unimanual reaches (three 9-month-olds, one 12-month-old), and (3) not reaching for objects at all (one 9-month-old). The sample size in this study was consistent with sample sizes used in other comparable studies (e.g., Adolph, 2000; Bhat & Galloway, 2007). The infants were recruited via a database of parents who expressed an interest in participating in developmental studies. Ethical approval was gained from the Goldsmiths Research Ethics Committee. Prior to testing, informed consent was obtained from all parents. Testing only took place if the infant was awake and alert.

The participants were given a small gift (e.g., a T-shirt) in return for their participation.

Table 2.1

Participant characteristics in Study 1

Age group	*n*	Sex	*M* age (months)	*SD* age (months)
9-month-olds	18	9f, 9m	8.88	0.30
12-month-olds	20	8f, 12m	12.14	0.32

2.1.2. Procedure and materials

2.1.2.1. The reaching task

The infant was placed in an infant seat (Bébépod Flex, Prince Lionheart Inc., Santa Maria, CA, USA), and secured into place with adjustable straps around the waist so that movement of the trunk was restricted. There were 12 reaching trials in total. On each trial, the infant was presented with a 3.5 cm-diameter ball at the body midline, and at arm's length (calibrated for each infant) so that the infant could just grasp it without leaning forwards. The above measures were taken to prevent any potential compensatory movements in non-acting limbs resulting from changes in posture. The size of the ball was selected to induce unimanual reaching (see, e.g., Fagard, 2000). The ball's colour (white, orange, blue, green) was varied in a pseudorandom order (the same colour presented no more than twice in a row) between trials in order to maintain the infants' interest. Two video cameras operating at 100 Hz were used to record the infants' movements, each facing the infant either side of the midline. The movements were then coded offline.

For the purpose of the current study, only unimanual reaches were analysed. Unimanual reaches were selected using the following discrimination criteria from D. Corbetta and Thelen (1996). Unimanual reaches had to comprise a unilateral extension of one arm (the acting arm) towards the target which was followed by contact with the target. To be counted as a unimanual reach, the other non-reaching arm was required to either remain still or produce non-target-oriented movements which remained at least a fist size away from the ball. On average, each 9-month-old contributed 8.3 unimanual reaches (*SD* = 2.7). Each 12-month-old contributed on average 9.8 unimanual reaches (*SD* = 2.1).

For each unimanual reach, the coder identified the timings of: (1) *the onset of the reach* (i.e., the moment when any part of the acting hand and/or arm from the fingertips to the shoulder started a continuous trajectory which ended in target contact), and (2) *contact* (i.e., the moment when the hand touched the target for the first time in the trial). Next, the coder identified for each unimanual reach, whether any extraneous movement occurred. For the purpose of this study, an extraneous movement in the hand/arm was any non-target oriented movement of the non-acting hand and/or arm (from the fingertips to the shoulder) which did not come within one fist size of the target ball. Most of these movements included one or more of the following: clenching, lifting, splaying, or wiggling of the fingers, twisting of the wrist, twisting or jerking of the arms. An extraneous movement in the feet/legs was any movement in a foot and/or leg (from the toes to the hips). Most of these movements included one or more of the following: clenching, lifting, splaying, or wiggling of the toes, flexion, extension, or rotation at the ankles, rotation at the knee, jerking of the leg (Soska et al., 2012). The feet/legs never touched the target or came within one fist's size of it. If there was an extraneous movement during the reach, then it was coded whether it was tightly linked to the onset of movement in the acting limb (starting +/- 100 ms around the onset of the reach of the acting hand/arm). To compute inter-rater reliability, a second coder independently scored whether the reach was unimanual in 20% of all the reaches. Subsequently, the second coder scored for the presence of movement in the limbs not involved in the unimanual reach and whether they were tightly linked to the onset of the reach in 20% of the data. Inter-rater reliability was over 90%.

The proportion of unimanual reaches accompanied by extraneous movement was calculated for each infant. The measure was computed separately for the non-acting hand/arm and (the average across both) feet/legs. Furthermore, I calculated a proportion of reaches in which extraneous movement onset was tightly linked to the onset of movement in the acting limb (+/- 100 ms around the onset of the reach in the acting hand/arm). The proportion of unimanual reaches accompanied by these reach-onset-locked extraneous movements was computed separately for the non-acting hand/arm and (the average across both) feet/legs. Since these data were proportional, they were arcsine transformed prior to inferential analyses. Raw data are presented in the figures.

2.1.2.2. The Gap-Overlap task

The infant was placed on his or her parent's lap approximately 65 cm from a 20" screen. The experimenter monitored and recorded the infant's looking behaviour from an adjacent room, via a video camera operating at 25 Hz. Eye movements were then manually coded offline. Before each trial, an attractive centrally-located stimulus (an 'attention-getter') was displayed on the screen to attract the infant's attention. This was a square of black and white geometrical shapes changing in size (zooming in and out) accompanied by an interesting sound. Once the infant was looking at the attention-getter, the experimenter manually initiated a trial. On each trial, the attention-getter first disappeared and was replaced by a central fixation stimulus. After 800 ms, a peripheral target appeared on the left or right side of the screen and remained displayed for 1200 ms. In the Gap trials, the central fixation stimulus disappeared 200 ms prior to the onset of the peripheral target, thus leaving the screen blank for 200 ms before the appearance of the target. This normally has a facilitating effect in speeding eye movements to the peripheral stimulus. In the Overlap trials, the peripheral target appeared while the central fixation stimulus remained onscreen, leading to an overlap in time between these two stimuli. This normally results in slower response times to the peripheral stimulus. The central fixation and peripheral target stimuli were selected from a pool of four stimuli (pictures of balls visually matched on colour, attractiveness, and size [5.3 x 5.3 cm]). The pairs of pictures were presented to the infants in a pseudorandom order. Throughout the study, each stimulus was used an equal number of times as a central fixation and a peripheral target. The central fixation and the peripheral target were never the same stimuli within any given trial.

The Gap-Overlap task consisted of 3 blocks. In each block, 8 Gap and 8 Overlap trials were presented, thus 16 trials in each block, and 48 trials in total. The order of presentation of the Gap and Overlap trials was randomized within each block. Trials were considered invalid if: (1) the infant did not look at the central stimulus immediately before the presentation of the peripheral target; and/or (2) the infant did not look at the peripheral target within the duration of the trial. Inter-rater reliability calculated over 20% of the data was 98% for the validity of trials and 92% for saccadic reaction times. In accordance with previous studies, exclusion criteria were set *a priori*: any reaction times under 150 ms or over 1200 ms were excluded (e.g., see Csibra, Tucker, & Johnson, 1998; Wass et al., 2011).

Nine-month-olds contributed an average of 14.2 valid Gap trials (*SD* = 4.7) and 13.4 valid Overlap trials (*SD* = 4.7). Twelve-month-olds contributed on average 15 valid Gap trials (*SD* = 4.9) and 14.1 valid Overlap trials (*SD* = 4.4). The 'Gap effect' (the difference in reaction times between Gap and Overlap trials) was computed for each infant as a measure of efficiency of disengaging from a central visual stimulus to orient to a peripheral one. Outliers below and above 2 *SD* were excluded from the data set. The Gap effect was 86 ms (*SD* = 39 ms) for 9-month-olds and 81 ms (*SD* = 30 ms) for 12-month-olds.

2.1.2.3. Motor experience scoring

The amount of experience with motor skills was reported by parents in a custom interview (reporting on sitting without support, crawling, standing with assistance, walking with assistance, standing alone, walking alone; Wijnhoven et al., 2004). Parents were encouraged to use baby books, calendars, pictures, and videos to facilitate their memories (Adolph, 2002). An experimenter also confirmed that the infants could perform the motor skills listed above. A motor experience score was computed based on experience with a range of skills which were present in more than half of the infants tested in each age group. The resultant skills which were included in this measure were: sitting without support, crawling, standing with assistance, walking with assistance. The number of months' experience with each of these skills was summed for each infant to yield a 'motor experience score'. Outliers below and above 2 *SD* were excluded from the data set. On average, the motor experience score was 7.1 (*SD* = 4.5) for 9-month-olds and 12.1 (*SD* = 4.6) for 12-month-olds.

2.2. Results

2.2.1. The reaching task

Throughout the reach, significantly more extraneous movements in the non-acting hand/arm during unimanual reaching were present in 9-month-olds compared to 12-month-olds, $t(36) = 3.27$, $p = .002$, $d = 1.09$ (Figure 2.1a). Nine-month-olds also moved their feet/legs during a greater proportion of unimanual reaches than 12-month-olds, $t(36) = 2.78$, $p = .009$, $d = 0.93$ (Figure 2.1b).

Traces of motor activity in extraneous limbs which are closely linked to the onset of purposeful movement have been observed in children and adults (Addamo et al., 2007; H. J. Cohen et al., 1967; Koerte et al., 2010). Such movements have been characterized as reflecting a motor command which overflows from one limb to others (Addamo et al., 2007; H. J. Cohen et al., 1967). This ‘motor overflow’ in children and adults is typically observed during difficult motor tasks, and very much smaller in amplitude than the extraneous movements in infants documented here and elsewhere (Soska et al., 2012). In order to investigate the presence of motor overflow, I examined the extent to which the onsets of infants’ extraneous movements were tightly linked to reach onsets by reporting extraneous movements with an onset within a window of +/- 100 ms around reach onset (henceforth, ‘tightly linked extraneous movements’). Within this window, 9-month-olds continued to show a higher proportion of unimanual reaches accompanied by the onset of extraneous movements in the non-acting hand/arm than 12-month-olds, $t(36) = 5.36$, $p < .001$, $d = 1.79$ (Figure 2.1a). A trend in the same direction was also observed with tightly linked extraneous movements in feet/legs, $t(36) = 1.81$, $p = .078$, $d = 0.61$ (Figure 2.1b).

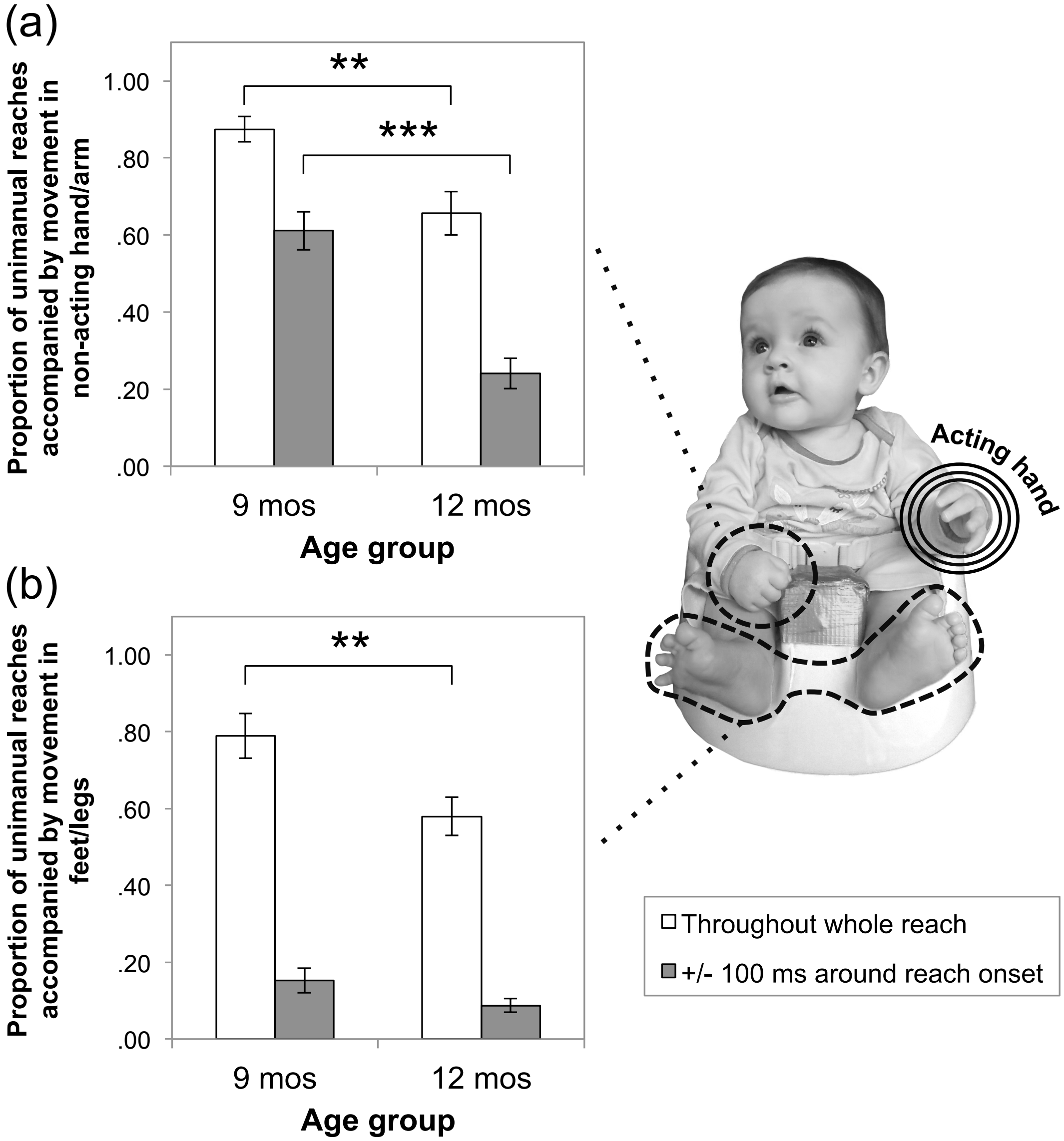

Figure 2.1. Proportion of unimanual reaches accompanied by movements in non-reaching limbs, for 9- and 12-month-olds. (a) Overall movements observed in the non-acting hand/arm throughout the reach, and movements in the non-acting hand/arm with an onset that is tightly linked to the onset of the reach (+/- 100 ms). (b) Overall movements in the feet/legs throughout the reach, and movements in the feet/legs with an onset that is tightly linked to the onset of the reach (+/- 100 ms). Error bars show +/- 1 *SE*; **p* < .050, ***p* < .010, ****p* < .001.

2.2.2. Extraneous movements, selective attention, and motor experience

A multiple regression analysis was conducted to evaluate whether age, selective attention, and/or motor experience predicted extraneous movements in the non-acting hand/arm. Using the Enter method, it was found that the linear combination of all three predictors explained a significant amount of the variance in both overall and tightly linked extraneous movements in the non-acting hand/arm, overall: $R^2 = .52$, $F(3, 29) = 10.33$, $p < .001$; tightly linked: $R^2 = .61$, $F(3, 28) = 14.60$, $p < .001$. Age and selective attention made a significant contribution to the prediction equation, while motor experience did not, for overall extraneous movements in the non-acting hand/arm (age: $t(29) = -3.81$, $p < .001$; selective attention: $t(29) = 3.48$, $p = .002$; motor experience: $t(29) = 0.72$, $p = .479$), and also for tightly linked extraneous movements in the non-acting hand/arm (age: $t(28) = -5.21$, $p < .001$; selective attention: $t(28) = 2.98$, $p = .006$; motor experience: $t(28) = 1.09$, $p = .283$). To confirm that selective attention explained a unique proportion of variance, I conducted a hierarchical regression that initially only included age as a predictor. The addition of selective attention as a predictor led to a significant increase in the proportion of variance explained, overall: change in $R^2 = .24$, $F(1,30) = 14.47$, $p < .001$, Table 2.2a; tightly linked: change in $R^2 = .16$, $F(1,29) = 11.14$, $p = .002$, Table 2.2b. Thus, the greater the Gap effect (i.e., the more difficulty infants had with visual selection), the more extraneous movements (overall, as well as tightly linked to movement onset) they produced in their non-acting hand/arm.

A multiple regression analysis was conducted to evaluate whether age, selective attention, and/or motor experience predicted extraneous movements in feet/legs. Using the Enter method, it was found that the linear combination of all three predictors explained a significant amount of the variance in overall extraneous movements in the feet/legs, but this time not in extraneous movements which were tightly linked to movement onset, overall: $R^2 = .40$, $F(3, 29) = 6.47$, $p = .002$; tightly linked: $R^2 = .18$, $F(3, 29) = 2.14$, $p = .117$. For overall extraneous movements in feet/legs, only motor experience made a significant contribution to the prediction equation, while age and selective attention did not, motor experience: $t(29) = -3.00$, $p = .005$; age: $t(29) = -1.31$, $p = .202$; selective attention: $t(29) = 1.36$, $p = .185$; see

Table 2.2

Hierarchical regression analysis (Enter method) for variables predicting (a) overall movements observed in the non-acting hand/arm during the reach, and (b) movements in the non-acting hand/arm with an onset that is tightly linked to the onset of the reach (+/- 100 ms)

(a)

	B	*SE B*	β
Model 1			
Constant	2.419	0.433	
Age	-0.138	0.041	-.520**
Model 2			
Constant	1.869	0.390	
Age	-0.136	0.034	-.511***
Selective attention	0.006	0.002	.487***

Note. R^2 = .27 for Model 1 (p < .01); ΔR^2 = .24 for Model 2 (p < .001).
*p < .050, **p < .010, ***p < .001.

(b)

	B	*SE B*	β
Model 1			
Constant	1.727	0.272	
Age	-0.123	0.025	-.661***
Model 2			
Constant	1.431	0.251	
Age	-0.122	0.022	-.658***
Selective attention	0.003	0.001	.395**

Note. R^2 = .44 for Model 1 (p < .001); ΔR^2 = .16 for Model 2 (p < .01).
*p < .050, **p < .010, ***p < .001.

Table 2.3. Thus, the more experience infants had with motor skills, the fewer overall extraneous movements in feet/legs they produced.

To disentangle which type of motor experience (out of: sitting without support, crawling, standing with assistance, and walking with assistance) predicts overall extraneous movements in feet/legs, I carried out additional multiple regression analyses. Using the Enter method, it was found that the linear combination of all four predictors explained a significant amount of the variance in overall extraneous movements in feet/legs, $R^2 = .50$, $F(4, 26) = 6.57$, $p < .001$. Crawling and walking with assistance made a significant contribution to the prediction equation, while sitting without support and standing with assistance did not, crawling: $t(26) = -2.24$, $p = .034$; walking with assistance: $t(26) = -2.15$, $p = .041$; sitting without support: $t(26) = -0.10$, $p = .923$; standing with assistance: $t(26) = 1.77$, $p = .089$; see Table 2.4a. This therefore suggests that locomotor experience is predictive of the decrease of extraneous movements in feet/legs but not, as shown earlier, in the hands/arms. A stepwise regression revealed that crawling and walking with assistance do not contribute a unique proportion of variance, with crawling being a significant predictor in this entry method, $R^2 = .42$, $F(1, 31) = 22.62$, $p < .001$, $t(31) = -4.76$, $p < .001$, see Table 2.4b.

Table 2.3

Multiple regression analysis (Enter method) for variables predicting overall movements in the feet/legs during the reach

	B	*SE B*	β
Constant	1.697	0.473	
Age	-0.059	0.046	-.214
Selective attention	0.003	0.002	.201
Motor experience	-0.045	0.015	-.504**

Note. $R^2 = .40$ ($p < .01$); *$p < .050$, **$p < .010$, ***$p < .001$.

Table 2.4

Multiple regression analysis for motor experience variables predicting overall movements in the feet/legs during the reach: (a) Enter method; and (b) Stepwise method

(a)

	B	*SE B*	β
Constant	1.060	0.182	
Sitting without support	-0.004	0.042	-.019
Crawling	-0.099	0.044	-.439*
Standing with assistance	0.069	0.039	.275
Walking with assistance	-0.182	0.084	-.378*

Note. R^2 *= .50 (p < .001);* **p* < .050, ***p* < .010, ****p* < .001.

(b)

	B	*SE B*	β
Constant	1.215	0.099	
Crawling	-0.149	0.031	-.650***

Note. R^2 *= .42 (p < .001);* **p* < .050, ***p* < .010, ****p* < .001.

2.3. Discussion

Study 1 documented for the first time a substantial decrease in extraneous movements accompanying unimanual object-directed reaching between 9- and 12-months of age. In my view, this finding reflects a wider developmental process of gradual motor specialization over the first year of life, in which infants' motor responses to action goals become increasingly tailored to their purpose, resembling the developmental processes of specialization seen in other domains including language and face processing (Gervain & Mehler, 2010; Lewkowicz & Ghazanfar, 2009; Maurer & Werker, 2014; Pascalis et al., 2005; Scott & Monesson, 2010; Werker & Tees, 1984).

The 'broad tuning' of the motor system early in development is likely shaped through interactions with the environment (Gibson & Pick, 2000; Sporns & Edelman, 1993). For example, in this study, 9-month-olds activated multiple limbs even though only one of the hands successfully retrieved the object. It is likely that feedback about which limb was successful at retrieval over many repetitions gives rise to the ability to retrieve an object unimanually without activating any other limb. This would lead to a decrease in extraneous movements by 12 months of age. However, the current study focused specifically on arm movements in reaching. Future research should explore the emergence of specialization in different motor sub-domains, which may differ in developmental timing.

In adults, the brain areas involved in movement preparation overlap substantially with those implicated in selective attention (Astafiev et al., 2003; M. Corbetta et al., 1998; Perry & Zeki, 2000; see also Rizzolatti & Camarda, 1987). Here, I found that infants with a greater ability to disengage from a familiar visual stimulus and shift attention to a new event were better able to produce movements more specifically tailored to their action goals (i.e., fewer extraneous movements), indicating an overlap in early life between processes of selective attention and movement (Bacher & Robertson, 2001; Robertson & Johnson, 2009). The emerging ability to shift attention between sensory stimuli which occurs during the first months of life (Colombo, 2001; Richards & Casey, 1992) likely provides the crucial foundation for the selective processes required in motor skills, which continue to be perfected well beyond infancy (Addamo et al., 2007; Koerte et al., 2010).

Furthermore, the finding of a link between greater motor experience and fewer extraneous movements in the feet/legs suggests that motor specialization (as with specialization in other domains; Curtin & Werker, 2007; Gervain & Mehler, 2010; M. H. Johnson, 2011b; Pascalis et al., 2005; Scott & Monesson, 2010; Werker & Tees, 1984) is an experience-dependent process. It is interesting to note that the locomotor skills were the most related to a reduction in extraneous movements in feet/legs. Given that the acquisition of locomotor skills places a particular burden on learning to move the feet/legs independently, the particular coupling between motor skills and extraneous movements of the feet/legs reinforces the view that motor learning is specific to the mode of action (Adolph, 2000). Further research will be needed to determine how motor experience interacts with the neural mechanisms described above and which, I suggest, underlie the development of motor specialization. A better understanding of the developmental processes underlying motor specialization has great clinical significance since aggravated extraneous movements have been described in various clinical populations including children with attention-deficit/hyperactivity disorder (D’Agati, Casarelli, Pitzianti, & Pasini, 2010; MacNeil et al., 2011) and autism (Jansiewicz et al., 2006).

What developmental processes underlie this motor specialization? Some have suggested (e.g., Fagard, 1998; Goldfield & Michel, 1986; Goldfield & Wolff, 2004) that symmetrical activation of the hands is a general principle of action in early infancy which over development is surmounted via inhibitory processes (Dennis, 1976; Duque, Murase, & Celnik, 2007). If this is the case, the extraneous movements of younger infants should be more synchronized with the movement of the acting limb than those of older infants. This hypothesis is supported by the finding of the current study that younger infants produce more extraneous movements which start at the same time as the movement of the acting arm (synchronized in time), than older infants. However, the current study cannot reveal whether these movements actually look similar to each other (synchronized in space), which would be expected if the activation of the hands were symmetrical, potentially originating from the same motor command (Addamo et al., 2007). Thus, the following study (Chapter 3) focuses on the spatiotemporal congruency between acting and non-acting hands. If symmetrical activation of the hands is a general principle of action in early infancy, then younger infants should show more spatiotemporal congruency between acting and non-acting arms compared to older infants.

CHAPTER 3

DEVELOPMENTAL DECREASE IN SPATIOTEMPORAL CONGRUENCY DURING SHAKING (STUDY 2)

Study 1 revealed a developmental decrease in extraneous movements during reaching between 9 and 12 months of age. I also observed that a large proportion of 9-month-olds' unimanual reaches were accompanied, at their onset (+/- 100 ms), by extraneous movements in the non-acting hand/arm. These onset-locked movements are likely the developmental precursor of the extraneous movements seen in older children and adults during demanding actions (Addamo et al., 2007).

In older children and adults, activation in the motor cortex of one hemisphere initially activates homologous cortical regions in the other hemisphere via the corpus callosum. But this activity is often inhibited, allowing them to perform efficient unimanual movements (Grefkes et al., 2008). However, if the activation continues to increase, for example from forceful or effortful voluntary movements, then interhemispheric inhibition is replaced with secondary activation, leading again to extraneous movements (Addamo et al., 2007; Bodwell et al., 2003; Hoy, Fitzgerald, Bradshaw, Armatas, & Georgiou-Karistianis, 2004; Meyer et al., 1995; Morrison, Hong, & Newell, 2011; Muellbacher, Facchini, Boroojerdi, & Hallett, 2000). Thus, it has been argued that the default symmetrical control of the two hands is surmounted via inhibitory processes in older children and adults (Dennis, 1976; Duque et al., 2007). However, inhibitory processes are limited in infancy and some have suggested (e.g., Fagard, 1998; Goldfield & Michel, 1986; Goldfield & Wolff, 2004) that symmetrical activation of the hands is a general principle of action in early infancy.

If symmetrical activation of the hands is indeed a general principle of action in early infancy, then younger infants should show more symmetrical spatiotemporal congruency between acting and non-acting arms than older infants. The current study tested this hypothesis by examining the spatiotemporal congruency between the acting and non-acting hands/arms. Using motion capture, I measured in fine detail the spatiotemporal coupling between movements in acting and non-acting hands/arms during the action of shaking a rattle with a single hand in 9- and 12-month-olds. I predicted the presence of spatiotemporal coupling (symmetrical about the body midline) in 9-month-olds, which would be significantly reduced in 12-month-olds. A key advantage of the rattling action is that it allows greater confidence that any extraneous movements are an unintended outcome of the action. Many studies of reaching behaviour (including Study 1 in this thesis) have to make assumptions about whether the infants actually intended to reach towards the objects with one or two hands (see Fagard & Pezé, 1997). With unimanual rattle shaking, an intention to act bimanually is extremely unlikely.

As mentioned above, in adults and older children, the interhemispheric inhibition responsible for suppressing bilateral motor activation is down-regulated as the effort required for a motor response increases (Perez & Cohen, 2008; Tinazzi & Zanette, 1998). For example, Perez and Cohen (2008) investigated changes in interhemispheric inhibition during a hand motor task with various levels of effort (represented by force in their particular study). As the effort increased, interhemisperic inhibition decreased, which suggests that interhemispheric inhibition was more difficult to sustain with increasing task demands. Furthermore, Morrison and colleagues (2011) also examined the effect of effort on the motor response. In their study, they investigated the effect of increasing movement frequency in a unilateral hand-clapping task on the hand that is not performing the task. As the speed of the unilateral clapping increased, overflow muscle activity emerged in the hand that was not performing the action. Therefore, I decided to investigate the effect of effort (speed of shaking) on spatiotemporal congruency during rattle shaking in the infants. If increased speed of shaking is related to increases in between-arm congruency in infants, this would suggest that the developmental suppression of extraneous movements in infancy is driven at least in part by inhibitory processes.

3.1. Methods

3.1.1. Participants

The 9- and 12-month-olds recruited for Study 1 were also asked to participate in Study 2. The final sample sizes for each age group and other characteristics are presented in Table 3.1. Ten additional infants were tested but excluded from analysis because: (1) they produced fewer than four shaking sequences (six 9-month-olds, two 12-month-olds) and (2) due to equipment failure (one 9-month-old, one 12-month-old). The sample size in this study was consistent with sample sizes used in other comparable studies (e.g., Adolph, 2000; Bhat & Galloway, 2007; Study 1 of this thesis). The infants were recruited via a database of parents who expressed an interest in participating in developmental studies. Ethical approval was gained from the Goldsmiths Research Ethics Committee. Prior to testing, informed consent was obtained from all parents. Testing only took place if the infant was awake and alert. The participants were given a small gift (e.g., a T-shirt) in return for their participation.

Table 3.1

Participant characteristics in Study 2

Age group	*n*	Sex	*M* age (months)	*SD* age (months)
9-month-olds	14	8f, 6m	8.90	0.31
12-month-olds	19	7f, 12m	12.19	0.28

3.1.2. Procedure and materials

The infant was placed in the same infant seat as used in the previous study (Study 1, Chapter 2), and secured with adjustable straps around the waist so that movement of the trunk was restricted. The rattle (which was 19 cm in length and 6.7 cm in diameter at its widest point) was presented to the infant. Following extensive piloting with several types of rattle, this particular rattle was selected as being the one which produced the greatest amount of unimanual shaking in infants. The procedure alternated between giving the infants either an opaque or a transparent version of two otherwise identical rattles, in order to maintain their engagement in the task. At the beginning of each trial, the experimenter demonstrated the shaking of a rattle and placed the rattle in the infant's left or right hand to facilitate unimanual shaking. The side of presentation was presented in a novel pseudorandom order for each participant (with the constraint that the rattle could not be placed in the same hand more than twice consecutively). There were 6 shaking trials in total, each lasting 30 seconds.

Movement of the arms during shaking was recorded using an eight-camera OptiTrack motion capture system operating at 100 Hz (NaturalPoint, Inc., Corvallis, OR, USA). Six of the cameras recorded position-time data from both arms while two cameras served as video cameras (100 Hz). This made it possible to obtain motion capture data synchronized with video footage. Cameras were placed surrounding the infant. The reference frame of the system was set relative to the infant, such that the *x*-axis (horizontal) corresponded to the left-right axis of the body (left shoulder to right shoulder). Very little trunk rotation was observed, which might otherwise have misaligned the body left-right axis with the reference *x*-axis. Likewise, the *y*-axis (vertical) corresponded to the vertical axis of the body, and very little forward trunk sway was observed which might otherwise have misaligned the body and room vertical axes.

To capture the position of the arms, two custom-made rigid bodies were constructed. Each was made up of an array of four reflective markers (each 15.88 mm in diameter) placed in fixed positions on a small non-reflective plastic board (550 x 550 mm). The rigid bodies were each mounted on a velcro strap which was used to secure them to the infants' forearms (one on each arm).

From the video recording, the coder selected unimanual shaking sequences which were at least 2 seconds long, when one hand was shaking the rattle on one side of the body while the other hand was not touching the rattle and was free to move on the other side of the body. The motion capture data were analysed offline. At each frame the 3D positions of the centre of each of the rigid bodies were calculated using the system's analysis software (Tracking Tools, NaturalPoint Inc., Corvallis, OR, USA). Further analyses were performed with customized Matlab routines (Mathworks Inc., Natick, MA, USA). For each shaking sequence, the position of the centre of the rigid body on the *x*-, *y*-, and *z*-axis was plotted and then visually inspected to identify shaking sequences which did not contain sufficient data for further analysis (e.g., due to occlusion of motion capture markers). Segments of data with significant artefacts (e.g., spikes) were detected visually and deleted. Next, the data were interpolated using a cubic spline function and filtered using a second-order low pass Butterworth filter operating at 8 Hz.

As a measure of spatiotemporal congruency between the arms, the correlation at each time point between the positions of the acting and non-acting arms on the horizontal (*x*) and vertical (*y*) axes for every shaking sequence (following Fagard & Pezé, 1997) was calculated. I focused on the *x*- and *y*-axes, because shaking did not typically involve significant movement in depth (the *z*-axis). On the vertical (*y*) axis, a higher positive correlation indicates greater spatiotemporal congruency (e.g., as one arm moves up, the other also moves up, see Figure 3.1a). On the horizontal (*x*) axis, negative correlations indicate greater spatiotemporal symmetry about the body midline (e.g., as one arm moves right, the other moves left, see Figure 3.1b). Outliers above and below 2 *SD* were excluded from the dataset. Because the data were bounded between -1 and 1, they were arcsine transformed. The raw data are presented in the figures. The average speed of the shaking arm was also computed for each shaking sequence. In order to examine the role of shaking speed in spatiotemporal coupling between acting and non-acting arm movements, a median split (*Mdn* = 287 mm/sec) was performed on speed of the shaking arm to divide shaking sequences into a slower half (*M* = 187 mm/sec, *SD* = 64 mm/sec; henceforth 'slow') and a faster half (*M* = 431 mm/sec, *SD* = 120 mm/sec; henceforth 'fast').

Correlations in the vertical and horizontal axes for every sequence were used in the statistical analyses. In total, 242 unimanual shaking sequences were available for the analyses (9-month-olds: 126 shaking sequences; 12-month-olds: 116 shaking sequences). On average, each 9-month-old contributed 9 shaking sequences (*SD* = 5.9). Each 12-month-old contributed on average 6.1 shaking sequences (*SD* = 4.9).

3.2. Results

3.2.1. Vertical axis

The shaking sequences were entered into a 2 x 2 analysis of variance (ANOVA) examining the effect of Age (9- versus 12-month-olds) and Speed (of the acting arm; slow versus fast) on correlation scores in the vertical axis. The ANOVA revealed a main effect of Age, indicating more positive correlation scores in the

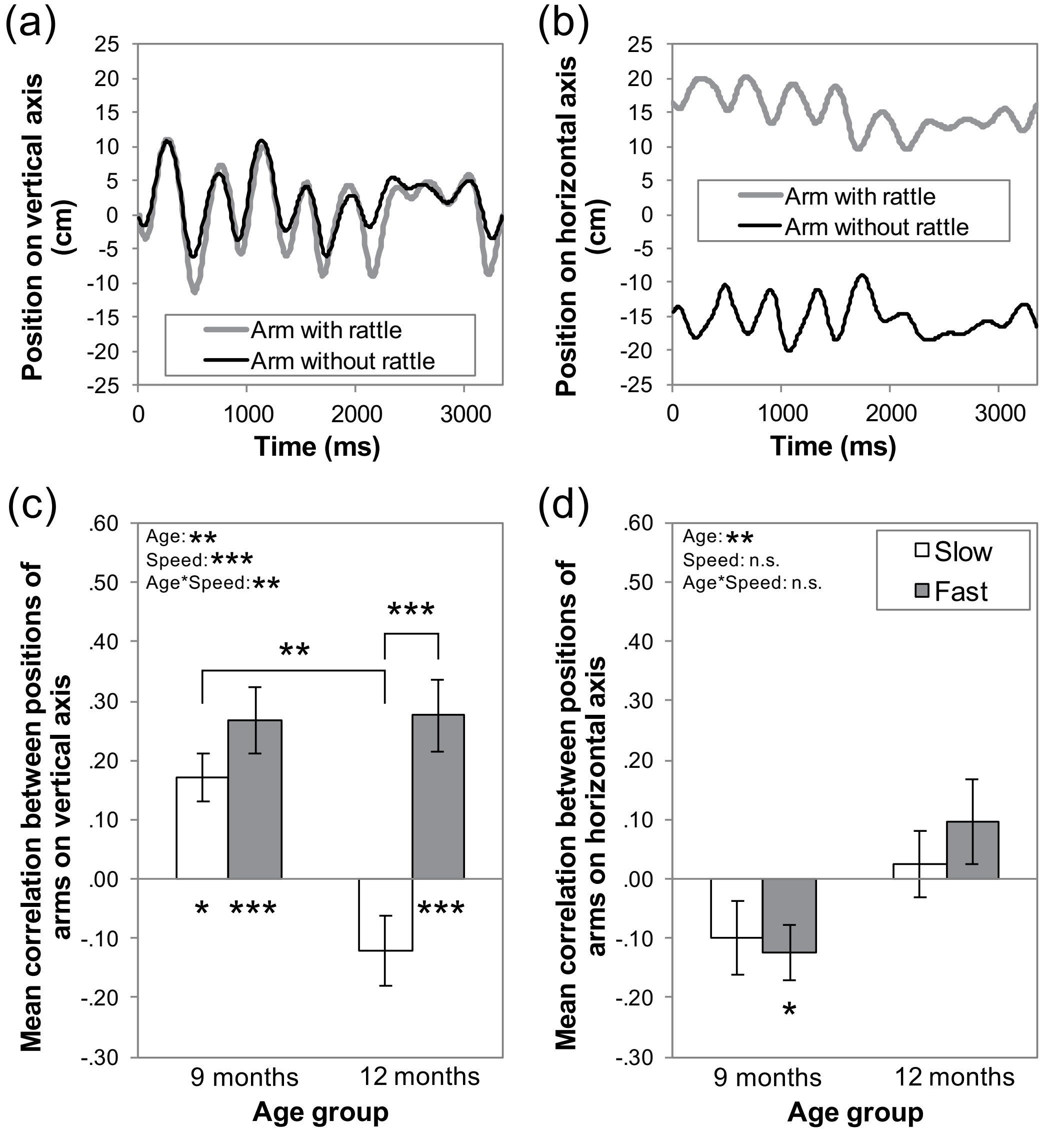

Figure 3.1. Correlation scores for unimanual rattle-shaking movements. (a) An example of a rattle-shaking sequence where acting and non-acting arms show large positive correlation on the vertical (*y*) axis indicating that they were moving up and down in synchrony (the correlation between positions of the arms is .92). (b) An example of a rattle-shaking sequence where acting and non-acting arms show moderate negative correlation on the horizontal (*x*) axis indicating that they were moving in symmetry about the midline (the correlation between positions of the arms is -.39). (c) Correlation scores on the vertical axis during shaking in 9- and 12-month-olds for slow speed and fast speed of shaking. (d) Correlation scores on the horizontal axis during shaking in 9- and 12-month-olds for slow speed and fast speed of shaking. Error bars show +/- 1 *SE*; *p < .050, **p < .010, ***p < .001.

shaking sequences of 9-month-olds than those of 12-month-olds, $F(1, 238) = 6.90$, $p = .009$, $\eta_p^2 = .03$. Furthermore, there was a main effect of Speed indicating that correlation scores were more positive with speed, $F(1, 238) = 20.51$, $p < .001$, $\eta_p^2 = .08$. There was also an interaction between Age and Speed, $F(1, 238) = 8.07$, $p = .005$, $\eta_p^2 = .03$. At a slow speed, 9-month-old's shaking sequences showed more positive correlation scores than those of the 12-month-olds, $t(119) = 3.57$, $p = .002$, $d = 0.66$ (p-value Bonferroni corrected) (see Figure 3.1c). But there was no significant difference between Ages for fast speed. While 9-month-olds did not show a difference in correlation scores between slow and fast speed movements, correlation scores at 12 months were significantly more positive for fast speed compared to slow speed movements, $t(114) = 4.56$, $p < .001$, $d = 0.87$ (p-value Bonferroni corrected) (see Figure 3.1c).

One-sample *t*-tests of correlation scores against zero (i.e., no correlation; see Figure 3.1c) revealed that correlation scores were significantly more positive than zero for both slow and fast speeds in 9-month-olds, $t(51) = 3.17$, $p = .012$, $d = 0.44$; $t(73) = 6.52$, $p < .001$, $d = 0.76$ (p-values Bonferroni corrected). This was also true for 12-month-olds, but only for fast speed movements, $t(46) = 4.58$, $p < .001$, $d = 0.67$ (p-value Bonferroni corrected).

3.2.2. Horizontal axis

The shaking sequences were entered into a 2 x 2 ANOVA examining the effect of Age (9- versus 12-month-olds) and Speed (of the acting arm; slow versus fast) on correlation scores in the horizontal axis. The ANOVA revealed a main effect of Age, indicating more negative correlation scores in the shaking sequences of 9-month-olds than those of 12-month-olds, $F(1, 238) = 9.01$, $p = .003$, $\eta_p^2 = .04$. There was no main effect of speed or interaction between Age and Speed.

One-sample *t*-tests of correlation scores against zero (i.e., no correlation; see Figure 3.1d) revealed that correlation scores were significantly negative with respect to zero for fast speed movements in 9-month-olds, $t(73) = -2.72$, $p = .032$, $d = 0.32$ (p-value Bonferroni corrected). But slow movements in 9-month-olds and both slow and fast movements in 12-month-olds were not significantly different from zero.

3.3. Discussion

The developmental decrease in extraneous movements reported in Study 1 (Chapter 2) is reflected in a decrease in the spatiotemporal congruency of movements between the arms during unimanual shaking in the current study. The present study provides further insight into the developmental processes that underlie gradual motor specialization. Study 1 (Chapter 2) showed that extraneous movements decrease over development during unimanual reaching. The current study validates and extends these findings with the same age groups but different unimanual activity, i.e., shaking. In my view, the advantage of unimanual shaking is that it gives us greater confidence that any extraneous movements are an unintended outcome of the unimanual action compared to unimanual reaching when one has to make assumptions about whether the infants had intended to reach for the object with one or two hands. Therefore, I believe that the convergence of results from the reaching and shaking studies are an important step in understanding motor specialization.

The current study showed that movements of hands in unilateral shaking sequences were more correlated in 9-month-olds than 12-month-olds. The younger infants showed a stronger positive correlation between hands on the vertical axis (e.g., when the hand holding the rattle was raised, so was the hand without a rattle) and a stronger negative correlation on the horizontal axis (e.g., as the hand holding the rattle moved out of the midline, so did the hand without a rattle) than 12-month-olds. This means that the movements of the acting and non-acting hands were more symmetrical along the midline in the younger infants than the older infants. These findings support the proposal that symmetrical activation of the hands is a general principle of action in early infancy (e.g., Fagard, 1998; Goldfield & Michel, 1986a; Goldfield & Wolff, 2004).

The increases in inter-limb congruency with speed, which were observed in this study, point to a role for inhibition in the modulation of extraneous movements (Addamo et al., 2007; Perez & Cohen, 2008). The main brain structure responsible for interhemispheric inhibition is the corpus callosum, and this develops progressively across early life, reaching its adult size and full myelination in later adolescence when extraneous movements typically decline to the adult level (Addamo et al., 2007; Giedd et al., 1999; Hasan et al., 2008; Keshavan et al., 2002; Wahl et al., 2007). The corpus callosum plays a central role in the production of extraneous movements in older children and adults. When a unilateral motor command is generated in one hemisphere, it leads to activation, via the corpus callosum, of homologous cortical regions in the other hemisphere. In older children and adults, the corpus callosum usually inhibits the corresponding area in the other hemisphere (Grefkes et al., 2008; Tamè, Pavani, Papadelis, Farnè, & Braun, 2015). However, this inhibition can be reduced by effortful or forceful movements such as finger tapping, squeezing, or applying force, which lead to motor overflow and mirror movements (Addamo et al., 2007; Armatas et al., 1996; Bodwell et al., 2003; Hoy, Fitzgerald, Bradshaw, Armatas, et al., 2004; Meyer et al., 1995; Morrison et al., 2011; Muellbacher et al., 2000). Causal evidence in support of corpus callosum's role in the production of extraneous movements has been provided by studies using transcranial magnetic stimulation (TMS). The studies demonstrate that the interhemispheric inhibition responsible for suppressing bilateral motor activation is indeed down-regulated when effort required for a motor response is increased (Perez & Cohen, 2008; Tinazzi & Zanette, 1998).

This current study is the first to show that a higher speed of movement during purposeful action is associated with greater spatiotemporal congruency between the arms during unimanual shaking towards the end of the first year of life. It also provides evidence consistent with age-related increases in the ability to inhibit extraneous movements. Nine-month-olds showed significant spatiotemporal congruency between arms at both slow and fast speeds of shaking. However, 12-month-olds were able to inhibit extraneous movements at a slow speed. Yet, at a faster speed, the spatiotemporal congruency of the 12-month-olds was as great as that of the 9-month-olds at the faster speed. Thus, it is likely that the ability to produce unimanual action is an emergent phenomenon that at least partly arises from the inhibitory capacity of the system.

As has been mentioned above, the main brain structure proposed to be responsible for interhemispheric inhibition is the corpus callosum. Corpus callosum has also been implicated in the development of a range of motor behaviours including the ability to perform coordinated complimentary actions with both hands (*intermanual coordination*). The next study (Chapter 4) will examine the relationship between the developmental decrease in extraneous movements and the development of intermanual coordination abilities (Muetzel et al., 2008). In my view, the more specialized infants are in their ability to control their hands separately, the better they will be at coordinating their hands to perform coordinated actions.

CHAPTER 4

THE RELATIONSHIP BETWEEN EXTRANEOUS MOVEMENTS AND INTERMANUAL COORDINATION

(STUDY 3)

Intermanual coordination (also referred to as *role-differentiated bimanual manipulation*, Kimmerle et al., 1995; or *bimanual coordination*, Fagard & Jacquet, 1989) is manual activity in which the two hands perform different but complementary movements, such as opening a drawer with one hand while retrieving a pen inside with the other. Intermanual coordination is important for adaptive behaviour across many different everyday life situations (e.g., opening a bottle, tying shoelaces, or buttoning a shirt). On average, intermanual coordination emerges towards the end of the first year of life (Birtles et al., 2011; Bruner, 1970; Cornwell et al., 1991; Diamond, 1991; Fagard, 1994; Fagard & Marks, 2000; Fagard & Pezé, 1997; Goldfield, 1983; Goldfield & Michel, 1986a; Kimmerle et al., 1995; Michel et al., 1985; Ramsay et al., 1979; Ramsay & Weber, 1986). However, large individual differences in the development of intermanual coordination have been described in typically developing children. Around half of the infants were found to perform intermanual actions by around 12 months of age, while most performed them by around 18 months of age (Birtles et al., 2011; Fagard & Lockman, 2005; Kimmerle et al., 2010, 1995; Michel et al., 1985; Ramsay, 1980; Ramsay et al., 1979; Ramsay & Weber, 1986). The current study investigates whether individual differences in intermanual coordination are associated with motor specialization in 12-month-olds.

The current study examines the proposal that intermanual coordination becomes possible due to a gradual decrease in intermanual coupling (Diamond, 1991; Fagard & Pezé, 1997; Goldfield & Michel, 1986a). Fagard and colleagues (2001) hypothesized that intermanual hand coordination is enabled by interhemispheric communication subserved by the corpus callosum (see also Diamond, 1991; Jeeves, Silver, & Milne, 1988; Trevarthen, 1978). In other words, Fagard and colleagues (2001) proposed that developmental changes in the corpus callosum contribute to the functional specialization of the upper limbs. Evidence that the corpus callosum plays, at least partially, a role in the performance of intermanual coordination, comes from a number of studies with nonhuman primates with split brain (Mark & Sperry, 1968) as well as from human infants with agenesis of the corpus callosum (Sacco, Moutard, & Fagard, 2006) and older children and adults with split brain or who were born without a corpus callosum (Dennis, 1976; Eliassen, Baynes, & Gazzaniga, 1999; Jeeves, 1969; Jeeves et al., 1988; Lassonde, Sauerwein, Geoffroy, & Décarie, 1986; Lassonde, Sauerwein, McCabe, Laurencelle, & Geoffroy, 1988; Preilowski, 1972, 1975, 1977, 1990).

Apart from transferring information from one hemisphere to the other, the corpus callosum also enables activity in one hemisphere to inhibit the activity of homologous areas in the other hemisphere (Cook, 1986; Meyer et al., 1995; Schnitzler, Kessler, & Benecke, 1996). Thus, the development of the corpus callosum is likely to be linked to the specialization of the motor system to perform unimanual actions. In turn, the ability to produce specialized movements with one limb may be linked to the development of intermanual coordination. In other words, the brain may need to have control over both hands independently if it is to perform unimanual reaches and also to engage in coordination of the two hands.

However, the studies that explored the relationship between reaching and intermanual coordination did not find a strong link between these two variables (Bojczyk & Corbetta, 2004; Fagard & Pezé, 1997). Fagard and Pezé (1997) followed infants longitudinally from 6 to 12 months of age. The infants were presented with large and small objects to reach for. At the same time, they were given three tasks measuring intermanual coordination (e.g., retrieving an object from a box with a hinged lid). The authors investigated whether a preference for a unimanual reaching strategy over a bimanual reaching strategy (suggestive of decoupling of limbs) is linked to intermanual coordination. Furthermore, they examined whether there is a relationship between spatiotemporal coupling of the arms during reaching and intermanual coordination. While Fagard and Pezé (1997) did not find any systematic relationship between intermanual coordination and reaching, they reported that infants made fewer bimanual reaches developmentally just before they demonstrated success on the intermanual task. However, there was no developmental decrease from 6 to 12 months of age in the spatiotemporal coupling between the two hands during reaching. The lack of developmental change in spatiotemporal coupling reported by Fagard and Pezé (1997) contrasts with findings from Goldfield and Michel (1986a) who reported a weakening of the spatiotemporal correlation between the arms in bimanual reaching between 7 and 11 months of age. But consider the reaching task used by Goldfield and Michel (1986a): Infants were presented with a transparent box with a hinged top, inside of which was a toy. Thus, the optimal strategy for retrieving the toy necessarily required intermanual coordination, not simple reaching. Thus, in my view, the disparity in the findings from Fagard and Pezé (1997) and Goldfield and Michel (1986a) is attributable to differences in task demands.

In another study which investigated the link between reaching and intermanual coordination, Bojczyk and Corbetta (2004) trained infants on an object retrieval task from 6.5 months of age until they were able to retrieve the toy from a box with a hinged lid using the most efficient intermanual strategy. Although the authors found that the training led to earlier emergence of intermanual coordination, they failed to find a relationship between intermanual coordination and bimanual reaching.

Although it seems reasonable to propose a link between reaching and intermanual coordination, neither Fagard and Pezé (1997) nor Bojczyk and Corbetta (2004) found robust evidence to support this link. I would like to suggest that this may be because the authors focused on the relationship between intermanual coordination and the proportion of *bimanual* reaches between the arms. While this type of reaching measure can inform us about the difficulty of decoupling arms in very young infants, the infants in Fagard and Pezé (1997) and Bojczyk and Corbetta (2004) were older than 6 months and thus would have been able to adapt their reaching to the size of the object (D. Corbetta & Thelen, 1996; Fagard, 2000; Fagard & Jacquet, 1996; Fagard & Pezé, 1997; Flament, 1974, 1975; Gesell & Ames, 1947; Newell et al., 1989; White et al., 1964). Therefore, the bimanual reaches that the infants produced in these two studies were likely to be *purposefully* bimanual and symmetrical, telling us little about the difficulty of decoupling arms, or, using the framework developed in this thesis, specialization of the motor system.

I would like to argue that in order to examine the relationship between intermanual coordination and reaching towards the first year of life, it is necessary to implement a reaching measure that is sensitive to the specialization of the motor system at the developmental stage when intermanual coordination appears. Extraneous movements in the non-acting hand/arm during unimanual reaching are likely to be such a measure (Study 1 of this thesis). Although infants are good at adapting their reaching strategies to the size of the object by the time they are able to perform intermanual coordination (i.e., towards the end of the first year of life), they still show extraneous movements (Study 1 and Study 2 of this thesis). Therefore, towards the end of the first year of life, I believe that extraneous movements in unimanual reaching are a more sensitive measure of the process of decoupling between arms (extraneous movements are likely to be *non-purposeful*) than a measure of bimanual reaching which is more likely to involve the *purposeful* activation of both limbs.

In the current study, I investigated the link between intermanual coordination and extraneous movements in 12-month-olds. To measure extraneous movements, I employed the same reaching task as the one I developed for Study 1 of this thesis (Chapter 2). Furthermore, to measure intermanual coordination, I presented infants with a box with a hinged lid with an object hidden inside. This task is commonly used to measure intermanual coordination in infants (Birtles et al., 2011; Bruner, 1970; Fagard & Pezé, 1997; Ramsay & Weber, 1986). I propose that infants who show less extraneous movements in the non-acting hand/arm during unimanual reaching will use a more differentiated intermanual coordination strategy. I also assessed the general developmental level of infants using a standardized developmental scale (the Mullen Scales of Early Learning) to show that the relationship between extraneous movements and intermanual coordination is specific to these two variables and is not a result of the overall developmental level of the child.

4.1. Methods

4.1.1. Participants

Twenty-two 12-month-olds (*M* = 12.14 months, *SD* = 0.24 months; 10 females) participated in this study. The sample size in this study was consistent with sample sizes used in previous comparable studies (e.g., Adolph, 2000; Bhat &

Galloway, 2007; Study 1 and Study 2 of this thesis). The infants were recruited via a database of parents who expressed an interest in participating in developmental studies. Ethical approval was gained from the Goldsmiths Research Ethics Committee. Prior to testing, informed consent was obtained from all parents. Testing only took place if the infant was awake and alert. The participants were given a small gift (e.g., a T-shirt) in return for their participation.

4.1.2. Procedure and materials

4.1.2.1. The Mullen Scales of Early Learning

The Mullen Scales of Early Learning (Mullen, 1995) comprises five subscales: (1) *Gross motor* (central motor control and mobility in supine, prone, sitting, and fully upright positions); (2) *Fine motor* (visually-directed motor planning, object manipulation, visual discrimination, and motor control); (3) *Visual reception* (visual perceptual ability, spatial awareness, and visual memory); (4) *Receptive language* (auditory comprehension, auditory memory, and the ability to process linguistic input); and (5) *Expressive language* (the ability to use sounds and language productively). These yield scores for each domain. Mental age was then computed as an average of Fine motor, Visual reception, Receptive language, and Expressive language scores (D'Souza, D'Souza, Johnson, & Karmiloff-Smith, 2015; Mullen, 1995). This standardized test has high internal consistency and test-retest reliability (Mullen, 1995; see also Bishop, Guthrie, Coffing, & Lord, 2011, for estimates of convergent validity).

4.1.2.2. The reaching task

The same reaching task used in Study 1 (Chapter 2, Section 2.1.2.1) was also used here. For each unimanual reach, the coder identified the timings of: (1) *the onset of the reach* (i.e., the moment when any part of the acting hand and/or arm from the fingertips to the shoulder started a continuous trajectory which ended in target contact), and (2) *contact* (i.e., the moment when the hand touched the target for the first time in the trial). Next, the coder identified for each unimanual reach, whether any extraneous movement occurred in the non-acting hand/arm. If there was an extraneous movement during the reach, then the coder identified whether it was tightly linked to the onset of movement in the acting limb (starting +/- 100 ms around the onset of the reach of the acting hand).

The proportion of unimanual reaches accompanied by extraneous movement in the non-acting hand/arm was calculated for each infant. Furthermore, the proportion of reaches in which extraneous movement onset in the non-acting hand/arm was tightly linked to the onset of movement in the acting limb (+/- 100 ms around the onset of the reach in the acting hand) was calculated for each infant.

4.1.2.3. The intermanual coordination task

This task followed the reaching task. Infants were seated in an infant seat (Bébépod Flex, Prince Lionheart Inc., Santa Maria, CA, USA) and secured into place with adjustable straps around the waist so that movement of the trunk was restricted. There were two intermanual coordination trials in total. In each trial, the experimenter first presented a semi-transparent plastic box (16 x 7 x 8 cm, width x height x depth) out of the infant's reach. The lid of the box was hinged so the lid would fall back on the top of the box if not held (adapted from Birtles et al., 2011; Bruner, 1970; Fagard & Pezé, 1997; Ramsay & Weber, 1986). A small red and navy blue ball with a jingle bell inside (4 cm in diameter) was placed inside the box and produced a ringing bell sound as it moved around. To retrieve the ball, the infant had to raise the lid and hold it open with one hand while retrieving the toy with the other hand. Retrieval with only one hand was almost, but not entirely, prevented by the hinged lid (following Fagard & Pezé, 1997). The experimenter demonstrated to the infant how to retrieve the ball. The ball was subsequently placed inside the box, and the box was positioned at the body midline and at arm's length (calibrated for each infant) so that the infant could interact with the box without leaning forwards. Infants were encouraged to retrieve the ball. The trial terminated after 60 seconds. Once the infant had retrieved the ball, he/she was allowed to play with it briefly and then it was taken away. Two digital video cameras (operating at a 100 Hz frame rate) were used to record the infant's movements, each facing the infant either side of the midline. The movements were then coded offline.

The retrieval strategy was classified into four categories of intermanual coordination (adapted from Birtles et al., 2011; Fagard & Pezé, 1997; Ramsay & Weber, 1986): (1) *Failure*: The toy was not retrieved. The infant may have banged on the lid or outside of the box, touched the box, or lifted the lid but did not retrieve the toy (score of 0); (2) *No differentiation*: The infant did not present any intermanual coordination. One hand raised the lid and retrieved the toy from underneath. The other hand was not engaged in the task (score of 1); (3) *Incomplete differentiation*: The differentiation presented by the infant was incomplete. Two possible strategies belong to this category. In the first, the infant raised the lid with the leading hand and then swapped the leading hand for the other hand in holding the lid while the leading hand was retrieving the ball. In the second strategy in this category, the infant raised the lid with both hands, then one of the hands held the lid while the other retrieved the ball (score of 2); (4) *Complete differentiation*: One hand was raising the lid, the other reached for the object inside (score of 3). To compute inter-rater reliability, a second coder independently scored all trials. Inter-rater reliability was 85%. For each child, an average score was computed. The highest score obtainable on this task was 3, which would indicate that the infant used a complete differentiation retrieval strategy on both trials. If the infant did not engage with the task in a particular trial, the trial was not counted.

4.2. Results

4.2.1. The reaching task

The majority of the 12-month-olds' reaches were unimanual (*M* = 81%; *SD* = 25%). On average, 61% of unimanual reaches (*SD* = 29%) were accompanied by extraneous movements in the other arm. On average, 29% of unimanual reaches (*SD* = 23%) were accompanied by extraneous movements with an onset that was tightly linked to the onset of the reach. The prevalence of extraneous movements during unimanual reaching in 12-month-olds is comparable to the results of Study 1 (Chapter 2) of this thesis.

4.2.2. The intermanual coordination task

Figure 4.1 illustrates the intermanual scores of the infants. Most infants (around 60%) scored two points on this task. In over half of the trials, the infants used an incomplete differentiation retrieval strategy (64%).

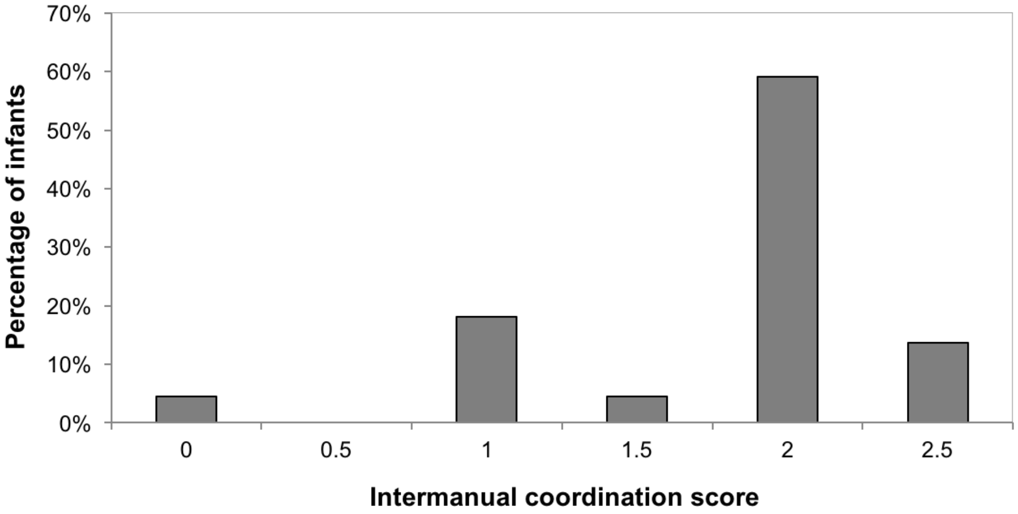

Figure 4.1. Distribution of intermanual coordination scores achieved by the infants.

4.2.3. Extraneous movements and intermanual coordination

Because intermanual coordination score is an ordinal variable, Spearman's rank correlations were performed in order to analyse the association of intermanual coordination with variables derived from the Mullen Scales of Early Learning and three measures of reaching (see Table 4.1). The only significant relationship was a negative correlation between extraneous movements tightly linked to the onset of the reach and intermanual coordination, $r_s(22) = -.55$, $p = .008$.

An ordinal regression using the Probit function was employed in order to investigate whether tightly linked extraneous movements in the hand/arm predicted intermanual coordination score. Including tightly linked extraneous movements to the baseline ('Intercept Only') model significantly improved the fit to the data, $\chi^2 = 6.00$, $p = .014$. The tightly linked extraneous movements explained 26% of the variation (as indicated by Nagelkerke pseudo R^2) in intermanual coordination scores in the infants.

Table 4.1.

Spearman's rank correlations of intermanual coordination with the Mullen Scales of Early Learning and three reaching measures

	Intermanual coordination
Mullen Scales of Early Learning	
Overall mental age	.07
Gross motor scale	-.07
Visual reception scale	.06
Fine motor scale	-.12
Receptive language scale	-.09
Expressive language scale	.18
Reaching measures	
Bimanual reaches	-.03
Overall extraneous hand/arm movements	-.23
Tightly extraneous hand/arm movements	-.55**

Note. ***p* < .010.

4.3. Discussion

This study provides a link between extraneous movements and a manual skill that is important for adaptive behaviour: intermanual coordination. In other words, the ability to select one hand for an action was found to be associated with the ability to control both hands separately but in a coordinated manner. The range of retrieval strategies presented in this study for intermanual activity is in line with other studies suggesting that 12 months of age might be considered a transitional stage in motor development for proficient intermanual coordination for this particular task (Birtles et al., 2011; Ramsay & Weber, 1986). The current study provides evidence that this transition is associated with the ability to produce unimanual reaching without extraneous movements. It can be concluded that although all the infants in the current study were of the same chronological age (12 months), individual differences indicated that they were at different stages of motor specialization. Future training studies could shed light on the exact nature of the relationship between extraneous movements and intermanual activity. It is known that experience constrains both reaching (e.g., Needham, Barrett, & Peterman, 2002; Williams et al., 2015) and intermanual coordination (Bojczyk & Corbetta, 2004).

Importantly, none of the variables from the Mullen Scales of Early Learning correlated with intermanual coordination. Therefore, changes in intermanual coordination are not due to changes in general developmental abilities (as indicated by mental age) or motor abilities (the Fine or Gross motor scale of the Mullen Scales of Early Learning). It is also important to note that, as predicted, the proportion of bimanual reaching was not related to intermanual coordination in the current study. This is consistent with the findings from the two previous studies which failed to detect a reliable relationship between reaching and intermanual coordination (Bojczyk & Corbetta, 2004; Fagard & Pezé, 1997). Adding an analysis of extraneous movements into the picture provides some explanation of why the reaching measures used in previous studies had not been found to be linked to intermanual coordination. The current study focused on 12-month-olds. It is known from other studies that children at that age can adapt their reaching actions (bimanual vs. unimanual) to the size of the target object (e.g., Fagard, 2000). Thus, 12-month-olds would often reach for a *small* object with one hand. Interestingly, in a small proportion of trials, infants in the current study produced seemingly unnecessary bimanual reaches towards a small object (also found in other studies, Bojczyk & Corbetta, 2004; Fagard & Pezé, 1997). I propose that these bimanual reaches might in fact have been *intentionally* bimanual rather than the result of symmetrical (mandatory) activation. Hence, because the bimanual reaching measure does not reflect the level of motor specialization in this age group, it is unlikely to be linked to intermanual coordination. Therefore, as this study shows, extraneous movements may be a more sensitive indicator of the level of motor specialization of the system.

Surprisingly, the extraneous movements that significantly correlated with intermanual coordination were those that were tightly linked to the onset of the reach but not overall extraneous movements (though the correlation was in the expected direction, it did not reach significance). This is somewhat puzzling because I expected both tightly linked and overall extraneous movements to be related to intermanual coordination. It is possible however, that tightly linked extraneous movements are a better indicator of difficulty with decoupling arm movements. Tightly linked 'onset-locked' movements are likely to be a developmental precursor of the motor overflow seen in older children and adults during demanding actions (Addamo et al., 2007), and so the association of these movements with intermanual coordination supports the proposals that, as discussed in detail in Study 2 (Chapter 3): (1) control over hands is symmetrical, and (2) this symmetricity is surmounted via inhibitory processes, which were suggested to be subserved by the corpus callosum. Developmental changes in these inhibitory processes are likely to contribute to both the developmental decrease in onset-linked extraneous movements and the emergence of intermanual coordination skills.

CHAPTER 5

MOTOR SPECIALIZATION AS AN EARLY MARKER OF NEURODEVELOPMENTAL DIFFICULTIES

Up until this point, this thesis has focused on the development of motor specialization in typically developing infants. In the remainder of this thesis I focus on motor specialization as a possible early marker of neurodevelopmental difficulties. In this chapter, I first outline why examining the process of specialization could provide insight into atypical development. I then focus on the distinction between syndrome-specific and syndrome-general markers of developmental difficulties. I then explain why I believe that *motor* specialization is of particular interest when looking for early markers of neurodevelopmental disorders. Finally, I introduce a neurodevelopmental disorder which can serve as an useful model of atypical motor development—*Down syndrome* (DS). DS is a disorder of known genetic origin, one that emerges early during ontogenesis, and is often diagnosed prenatally. This early diagnosis is key for this thesis because it allows us to examine children at an age at which most of the other disorders, especially the ones of unclear genetic origins, would not be diagnosed (e.g., ADHD, ASD, cerebral palsy). Therefore, DS presents a useful case for taking the initial steps in exploring the possibility that motor specialization, as indicated by extraneous movements, could serve as an early predictor of neurodevelopmental difficulties of unclear aetiology.

5.1. Progressive specialization

The protracted period of brain development observed in human infants allow late-generated structures such as neocortex to emerge (Clancy, Darlington, & Finlay, 2001). It also provides time for the infant brain to calibrate or adjust its internal operations (connectivity and computations) to the spatial and temporal metrics of the external world (Buzsáki, 2006). In other words, it is advantageous to have neural circuits gradually develop over time to ensure that circuitry is appropriately shaped by the specifics of the relevant input (Bates & Elman, 1993; D'Souza & Karmiloff-Smith, 2011; Elman et al., 1996; Greenough et al., 1987; M. H. Johnson, 2011b; Karmiloff-Smith, 1992; Stiles, 2008). The process of gradual, progressive *specialization* over developmental time—from widespread, uncoordinated, spontaneous activity to highly organized, structured activity, and from broadly tuned to finely tuned response activity—is a key feature of complex adaptive systems (Miller & Page, 2007), and one that would help the inexperienced neonate to adapt to complex environments (M. H. Johnson, 2011b). Indeed, it has been identified in several developmental domains, including face perception (Pascalis et al., 2005), cognitive control (Crone, 2014), and emotional reactivity and regulation (Somerville & Casey, 2014). Earlier in this thesis I showed that the process of motor specialization leads to a better match between task-related demands and the activation of the limbs. While younger infants often activated multiple limbs when reaching for a small object, older infants were better at selectively activating only the limbs needed to interact efficiently with the environment. In other words, we saw increasing fit of the infant's limb activation to the environment emerging over development. Furthermore, the infants who showed more specialization for unimanual actions also exhibited better intermanual coordination. Thus, an increase in motor specialization is related to the ability to perform more complex adaptive actions.

5.1.1. Specialization as an active process

However, progressive specialization is not a passive process; it requires the infant to calibrate its internal operations to the external world by actively exploring (selecting, acting on) and sampling it (Buzsáki, 2006; Held & Hein, 1963; Piaget, 1954). If the infant lacks the cognitive tools to intelligently explore or sample the environment, or is exposed to an atypical or restricted environment that hampers exploration, then this will constrain the process of specialization and the infant is more likely to develop atypically (M. H. Johnson, Jones, & Gliga, 2015).

Infants' past experiences and current repertoire of abilities will constrain what aspects of the external environment, and what activities, the child will select and engage in (Kidd, Piantadosi, & Aslin, 2012; Rovee-Collier & Cuevas, 2009). In other words, individuals select their environments and generate their own experiences based on their histories and abilities; it is through this self-organizing process of development that specialization occurs. In the motor domain, extensive practice of emerging new skills has been described in ontogeny. For example, in *one* waking hour the average toddler takes 2,368 steps, which is the equivalent length of 7.7 American football fields (Adolph et al., 2012). However, it still takes several years before the movements they select in walking become adult-like (Adolph & Robinson, 2015). This highlights how extensive interaction with the environment is required before an adult-like state can emerge. In agreement with this position, I have also shown that locomotor experience is positively related to motor specialization (Study 1, Chapter 2 of this thesis).

According to M. H. Johnson and colleagues (2015), deficits in the ability to select and generate appropriate experience that best matches the capacity of the developing organism may impact the ability of the system to specialize. Furthermore, early atypical selection of experiences with the environment can push the organism into an atypically developing trajectory. Moreover, even if the sampling is appropriate (i.e., typical), abnormal processing of the gathered information can also impact the organism's developmental trajectory.

Because progressive specialization reflects changes in neural connectivity and the response properties of different neurons over developmental time (M. H. Johnson, 2011b), and because it is an experience-dependent process, the process of sampling the environment affects functional plasticity and the timing of developmental processes (Frankenhuis & Panchanathan, 2011a, 2011b). For example, an absence of visual input can prolong the critical period during which visual information may shape certain structures (e.g., ocular dominance columns) in primary visual cortex (Mower, Caplan, Christen, & Duffy, 1985). In human infants, interindividual variation in sampling can occur as a result of (1) variation in the external environment, and/or (2) differences between infants' 'internal' environments. I discuss these two constraints in detail below, using examples from the literature on bilingualism (variation in the external world) and neurodevelopmental disorders (internal differences).[2]

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[2] There is also likely to be an interaction between internal differences and the external world.

5.1.1.1. Differences in specialization due to the external environment

To illustrate how differences in the external environment affect specialization, take the example of language development in infants, a domain in which progressive specialization has been extensively studied. Language specialization emerges early in life. For example, human neonates are sensitive to a wide range of language contrasts, both native and non-native (e.g. Bertoncini, Bijeljac-Babic, Blumstein, & Mehler, 1987; Eimas, Siqueland, Jusczyk, & Vigorito, 1971; Streeter, 1976). However, between 6 and 12 months of age, their ability to discriminate between contrasts in their native language improves, while their sensitivity to non-native contrasts declines (Kuhl et al., 2006; Werker & Tees, 1984; Werker, Yeung, & Yoshida, 2012). In other words, the infant brain becomes progressively *selective* to its native language. This process of specialization, which involves neural commitment and thus co-occurs with a corresponding reduction in plasticity, increases the fit between infants and their specific language environment (Kuhl et al., 2008).

But what would happen if a child were exposed to a multilingual environment? It is likely that the child would be provided with fewer samples from each language than a child raised in a monolingual environment would receive from its one language (Byers-Heinlein & Fennell, 2014). Thus, it is likely to take longer for bilinguals to accumulate a sufficient amount of samples for them to specialize to their environment. Moreover, the challenge of acquiring sufficient sampling is exacerbated by bilingual exposure being particularly noisy, due to the presence of two languages, producing a less consistent environment. For many children exposed to bilingual environments, language input from two different languages may come from the same person, in the same environment, and even in the same sentence (Byers-Heinlein, 2013). Evidence that increased noise in the environment prolongs the process of specialization comes from animal studies. For example, rats exposed to white noise show protracted neural plasticity in primary auditory cortex (Chang & Merzenich, 2003). Taken together, less input from one language and extra noise may make the sampling of environment more challenging for bilingual infants than for monolinguals, which could prolong their specialization. Indeed, emerging evidence is consistent with this proposal (Pi Casaus, 2015; Sebastián-Gallés, Albareda-Castellot, Weikum, & Werker, 2012). However, neither bilinguals nor monolinguals are able to discriminate between unfamiliar languages in adulthood (Werker, 1986). This suggests that specialization in bilinguals may be initially protracted, but leads to a similar adult state. Yet even the adult state may be different in these two populations. Tremblay and Sabourin (2012) showed that although bi/multilinguals do not differ in their ability to discriminate nonnative contrasts from monolinguals in adulthood, bi/multilinguals show an enhanced ability to learn them. This suggests that developing in less predictable environments could lead to a protracted period of specialization and a more plastic brain that is more sensitive to environmental changes later on. Although this may be costly for the organism in terms of energy, it is an adaptive response to its environment.

Although there is currently a lack of studies in the motor domain focusing on the topic of motor specialization in human infants, I would expect similar mechanisms to those described above to operate here too. Cross-cultural differences in childrearing practices, such as constraining motor activity by swaddling infants in a 'gavora' cradle (a traditional rocking cradle used in Tajikistan), have been shown to delay the onset of certain motor skills (Karasik et al., 2015). I expect that these practices would also delay motor specialization, leading to a higher prevalence of extraneous movements later in development.

5.1.1.2. Differences in specialization due to the internal environment

As described above, the ability to discriminate contrasts in the native language improves over developmental time (Kuhl et al., 2006) while sensitivity to non-native contrasts declines (Werker & Tees, 1984; Werker et al., 2012). This specialization for native language increases the fit between infants and the environment. However, infants demonstrate considerable variability in their ability to adapt to the environment. Moreover, these early individual differences are associated with later developmental outcomes. Specifically, monolingual infants who show more specialization for their native language (e.g., better native, and/or worse non-native, phonetic perception skills) have on average better language outcomes as toddlers (Kuhl et al., 2008; Kuhl, Conboy, Padden, Nelson, & Pruitt, 2005; Tsao, Liu, & Kuhl, 2004). Similarly, I have also observed a relationship between motor specialization and functional behaviour in this thesis: the more motor specialization infants showed, the better they were in intermanual coordination (Study 3, Chapter 4).

If individual differences in sampling constrain development even in typically developing (TD) children, then might alterations in sampling in atypically developing populations affect developmental processes such as specialization to an even greater extent? In support of this possibility, there is some evidence that neural responses to speech input are initially diffuse in TD infants and only gradually become more focal (specialized) over developmental time (Brauer & Friederici, 2007; Minagawa-Kawai, Mori, Naoi, & Kojima, 2007). Furthermore, toddlers with autism spectrum disorder (ASD) show more diffuse patterns of activation than TD controls matched on chronological age (Coffey-Corina, Padden, & Kuhl, 2008). Moreover, low functioning toddlers with ASD show more diffuse patterns of activation than high functioning toddlers with ASD (Coffey-Corina et al., 2008). M. H. Johnson et al. (2015) propose that synaptic dysfunction in ASD (Bourgeron, 2009; Gilman et al., 2011; Zoghbi, 2003) results in poor sampling of the environment (reduced fidelity), which leads to prolonged specialization plus excessive plasticity and hence developmental delay. Indeed, poor evoked (neural) response reliability (i.e., less consistency across trials), yielding weaker signal-to-noise ratios in visual, auditory, and somatosensory systems, has been identified in adults with ASD relative to TD controls matched on chronological age and IQ (Dinstein et al., 2012). A similar theory of autism suggests that excessive neuronal information processing in local circuits (leading to hyper-perception, hyper-attention, hyper-memory, etc.) renders the world uncomfortably intense for individuals with the disorder, leading to social and environmental withdrawal (Markram, Rinaldi, & Markram, 2007; for similar theories, see also Rubenstein & Merzenich, 2003, and Simmons et al., 2009). This would also result in poor sampling of the environment.

ASD is not the only disorder for which synaptic dysfunction has been attributed however. In fact, a number of other neurodevelopmental disorders also show widespread abnormalities in synaptic function and plasticity (Blanpied & Ehlers, 2004; Zoghbi, 2003). For example, dendritic spine abnormalities (which result in synaptic dysfunction; Nimchinsky, Sabatini, & Svoboda, 2002) have been identified in Down, fragile X, Patau, Rett, and Williams syndromes (Chailangkarn et al., 2016; Irwin, Galvez, & Greenough, 2000; Kaufmann & Moser, 2000). At the same time, functional specialization in one or more domains may be atypical in these disorders. For example, whereas music (vs. noise or rest) elicits reliable, robust, and focal activations in superior and middle parts of the temporal lobe in typically developing adults, it elicits highly variable and diffuse activation in adults with Williams syndrome that involves regions in the amygdala, cerebellum, and brainstem (Levitin et al., 2003).

Although more evidence is needed to establish a link between synaptic abnormalities and protracted or atypical specialization, it is highly probable that synaptic disturbances affect development. Synapses enable brain cells to communicate with one another. They are not fixed; rather, they are modifiable, constantly being created, pruned, and altered throughout the lifespan. Although the development of neuronal circuitry is constrained by epigenetic activity, the size, shape, number, and pattern of synaptic connections are governed by experience (Fiala, Spacek, & Harris, 2002). Synaptic dysfunction could lead to sparser and less reliable sampling of environment, and hence a worse signal-to-noise ratio, which in turn may result in protracted plasticity and atypical specialization of function (Rubenstein & Merzenich, 2003). If individuals with neurodevelopmental disorders have difficulty sampling their environment efficiently, we should see prolonged or atypical specialization present in many of them—and this could be apparent relatively early in development.

5.2. Specificity of early predictors

Finding early markers of neurodevelopmental difficulties are especially important for neurodevelopmental disorders of unclear aetiology and which cannot be currently identified early in development (i.e., ADHD, ASD). Reliable early markers would enable earlier diagnosis or at least uncover potential atypically developing trajectories. This would allow for early intervention, which is likely to be critical for maximizing developmental outcomes (Shonkoff & Meisels, 2000; M. S. C. Thomas, Davis, Karmiloff-Smith, Knowland, & Charman, 2016; B. D. Ulrich, 2010).

Because the exact aetiology of some neurodevelopmental disorders remains unknown, diagnoses are often based on behavioural diagnostic criteria. However, many of these behaviours do not emerge clearly until later in development. This can be illustrated using one of the most common neurodevelopmental disorders: autism spectrum disorder (ASD). ASD affects around 1 in 100 children and adults in the UK (Baird et al., 2006; Elsabbagh et al., 2012). Currently, ASD is diagnosed by behavioural criteria including: (1) impairments in social interaction and communication, and (2) restricted or stereotype behaviours, interests, or activities (American Psychiatric Association [APA], 2013). In addition to these core features, individuals with ASD often present with sensory and motor difficulties, intellectual disability, and co-morbidities with other neurodevelopmental disorders (APA, 2013). Currently, the behaviours used to diagnose autism (see above) do not emerge clearly until two or three years of age. However, researchers are beginning to peer into infancy to attempt to identify early markers of ASD. They are doing this by carrying out prospective studies of younger siblings of children already diagnosed with autism (*sibs*, e.g., the British Autism Study of Infants Siblings [BASIS] in the UK). Studying sibs is an important strategy because they show a higher risk of developing ASD (around 19% of them will receive an ASD diagnosis; Ozonoff et al., 2011). The identification of early markers would not only contribute to our understanding of ASD, but they would also allow earlier intervention for individuals with ASD, which could significantly improve quality of life. Some promising early markers are already emerging. For example, infants' ability to selectively redirect attention was found to differentiate between sibs who were later diagnosed with ASD and TD controls (Elsabbagh et al., 2013). Using the Gap-Overlap task (similar to the task used in Study 1, Chapter 2), Elsabbagh et al. (2013) showed that sibs who were later diagnosed with ASD showed longer disengagement latencies when shifting their visual attention from a central stimulus towards a peripheral target.

However, it is important to discriminate between *syndrome-specific* and *syndrome-general* markers (D'Souza, 2014). Although the ability to selectively redirect attention is an early marker of ASD (Elsabbagh et al., 2013), other neurodevelopmental syndromes also show impairment in this domain (e.g., Down syndrome; D'Souza, 2014; Williams syndrome; Brown et al., 2003; D'Souza, 2014). Thus, disengagement difficulties might be an early manifestation of atypical development in general (i.e., a syndrome-general marker), rather than being a syndrome-specific marker for ASD. These attentional difficulties likely reduce the infant's ability to flexibly sample the environment, affecting the developmental process of specialization.

An overlap of early markers across disorders is to be expected since children with neurodevelopmental disorders cannot be described as static systems with 'impaired' and 'intact' modules, with some syndromes having an 'impaired' module for visual disengagement and others having an 'intact' module (Karmiloff-Smith, 1998; Karmiloff-Smith, Brown, Grice, & Paterson, 2003). Rather, neurodevelopmental difficulties are *emergent properties* of a developing organism. There is not a single domain that controls how the phenotype of a particular individual (with or without a neurodevelopmental disorder) is constructed. Development is an inherently probabilistic process (Gottlieb, 2007) during which many domains of the developing organism interact to give rise to a particular phenotype. The emerging properties of the system can be very difficult to predict. In order to truly understand how properties of an organism emerge, complex interactions between various domains need to be studied over developmental time.

Complex, dynamic systems tend to gravitate towards certain stable patterns of activity (*attractors*, Kitano, 2004). The most powerful attractor represents typical development. Thus, a typically developing individual is the outcome of a developmental trajectory that is relatively robust to perturbations over development. However, if the subsystems are compromised, new states (e.g., a neuro-developmental disorder) may emerge over time. A metaphor of this idea is provided in Waddington's (1957) *epigenetic landscape*. This landscape can be visualized as a series of ridges and valleys, which influence the journey each organism takes as it rolls down towards a relatively stable state. According to Waddington, the depth of each valley is shaped by the activity of genes; the deeper the valley is, the more robust to environmental factors the developing organism is. The epigenetic landscape as a metaphor of development emphasizes the importance of following individuals over time to understand how they are *channeled* into relatively stable states. Thus, it is possible that different developmental trajectories leading to various neurodevelopmental disorders start from a very similar place (e.g., with difficulties in sampling the environment) and gradually differentiate over time.

Thus, different neurodevelopmental disorders may share symptoms early in development, but tiny differences may cascade over developmental time leading to very distinct developmental profiles. Yet if symptoms overlap early in development, how can researchers find syndrome-specific markers? Although syndrome-specific markers may be rare, it is likely that markers will co-occur in a syndrome-specific fashion. By identifying the co-occurring markers of a disorder, researchers can construct unique developmental, *syndrome-specific* profiles. I believe that degree of motor specialization could be a particularly fruitful addition to the syndrome-specific profiles, as I explain in the section below.

5.3. Motor specialization as an early marker of neurodevelopmental difficulties

As shown above, prolonged or atypical specialization is likely to be a shared feature across many neurodevelopmental disorders. Therefore, it could serve as an important indicator of early developmental difficulties. I would like to propose that focusing on *motor* specialization could be particularly fruitful for several reasons. Firstly, M. H. Johnson et al. (2015) propose that delayed or atypical specialization resulting from difficulties with sampling experience will be specifically observed for domains when experiences are complex, dynamic, and less predictable. Motor development certainly qualifies to be such a domain. As Wolpert, Diedrichsen, and Flanagan (2011) put it: "*The exploits of Martina Navratilova and Roger Federer* *represent the pinnacle of motor learning. However, when considering the range and complexity that are involved in motor learning, even the mere mortals among us exhibit abilities that are impressive*" (p. 739). Although Wolpert et al. (2011) were referring to motor learning in adults, motor development in infants is also highly complex, as indicated by the amount of extensive practice a developing organism needs to generate over many years in order to reach an adult-like level of abilities (Adolph et al, 2012). When learning to act on the environment, an organism needs to extract and process sensory information relevant to the action, because visual, auditory, and tactile information influence our movements. Furthermore, the organism needs to control a large number of muscles and joints. Even when human adults are asked to repeatedly perform well-practiced action sequences, the stereotyped movement trajectories are not exactly the same (e.g., Schorer, Baker, Fath, & Jaitner, 2007; Sim & Kim, 2010).

Secondly, motor development is an interesting domain to focus on considering the timing of synaptic pruning (M. S. C. Thomas et al., 2015). The onset of pruning varies across different brain regions (Gogtay et al., 2004; Huttenlocher, 2002; Huttenlocher & Dabholkar, 1997). It occurs first in sensory and motor areas, followed by higher association areas and lastly in prefrontal cortex. Therefore, motor deficits may emerge before many other often co-occurring deficits. Indeed, problems in the motor domain are often observed before the emergence of cognitive and neurophysiological prodromal symptoms (e.g., ASD, Leonard et al., 2013; ADHD, Kroes et al., 2007). For example, a growing body of research on ASD shows differences in the motor domain that can discriminate a group of infants who go on to develop ASD from a group of infants who do not, in retrospective (in their first year of life) (Baranek, 1999; Esposito, Venuti, Maestro, & Muratori, 2009; Gernsbacher, Sauer, Geye, Schweigert, & Hill Goldsmith, 2008; Ozonoff, Heung, Byrd, Hansen, & Hertz-Picciotto, 2008; Teitelbaum, Teitelbaum, Nye, Fryman, & Maurer, 1998) and prospective studies (Flanagan, Landa, Bhat, & Bauman, 2012; Iverson & Wozniak, 2007; Leonard et al., 2014; Toth, Dawson, Meltzoff, Greenson, & Fein, 2007). However, most standardized tests of fine and gross motor development are not sufficiently sensitive to pick up on differences in the first year of life (Brian et al., 2008; Landa & Garrett-Mayer, 2006; Landa, Gross, Stuart, & Faherty, 2012; Ozonoff et al., 2010; Zwaigenbaum et al., 2005). This highlights the importance of using sensitive measures of motor development. The measures of extraneous movements developed in this thesis may be a particularly sensitive index of motor specialization. I have already shown this measure to be sensitive to individual differences in motor specialization in TD children: the extraneous movements were related to intermanual coordination skills in 12-month-olds while performance on a standardized developmental test (the Mullen Scales of Early Learning) was not (Study 3, Chapter 4 of this thesis).

Thirdly, motor development has cascading effects on many other areas of development. Take, for example, the association between motor and social development. At 3 months of age, training infants to manipulate and reach for objects affects their visual exploration of social agents (Libertus & Needham, 2010, 2011). Furthermore, the transition from crawling to walking changes interactions between infants and their caregivers, increasing opportunities for more advanced social interactions (Clearfield, Osborne, & Mullen, 2008; Karasik et al., 2011). Another domain that motor development seems to impact is perception. For example, crawling experience was found to increase sensitivity to optic flow information for balance (J. J. Campos et al., 2000) as well as mental rotation abilities (Schwarzer, Freitag, Buckel, & Lofruthe, 2013). Motor development was also found to be associated with language development. Walle and Campos (2014) found a positive relationship between walking and receptive and expressive language. If different domains (e.g., motor and language) are interconnected and interdependent, then a deficit in one domain (e.g., motor) may have cascading effects on other domain (e.g., language). Thus, identifying early atypicalities in the motor domain is important because of their potential cascading effects on other domains.

A final reason for focusing on motor specialization is the applicability of these measures in the clinical environment. For any early marker to be successfully implemented in clinical practice, it should be sufficiently easy and relatively inexpensive to obtain. Atypicalities in the motor domain are more easily observable than atypicalities in other domains, such as low-level perception. Also, costly equipment, such as magnetic resonance imaging (MRI) or electroencephalography (EEG), is not necessary for the detection and observation of differences in motor development. Taken together, for the reasons outlined above, the level of motor specialization as indicated by extraneous movements could be a promising and relatively easily obtainable early marker of neurodevelopmental difficulties.

5.3.1. Extraneous movements as an early marker of atypical development?

There is currently no literature exploring extraneous movements as a possible early marker of developmental difficulties in infancy or toddlerhood. This is striking since extraneous movements have been used as a neurological soft sign, or subtle sign[3], across many disorders later in development (Bombin, Arango, & Buchanan, 2005; Quitkin, Rifkin, & Klein, 1976; Shaffer et al., 1985; Tupper, 1987). Aggravated extraneous movements have been described in older children with various neurodevelopmental disorders including ADHD (e.g., Gilbert et al., 2011; MacNeil et al., 2011; Mostofsky et al., 2006, 2003), ASD (e.g., Jansiewicz et al., 2006), developmental coordination disorder (Miyahara & Möbs, 1995), and learning difficulties (J. A. C. Lazarus, 1994).

5.3.1.1. Autism spectrum disorder (ASD)

Jansiewicz et al. (2006) showed significant impairments on several measures of motor control in children with ASD compared to TD children, including an increased prevalence of extraneous movements. These results suggest that children with ASD show less motor specialization. This proposal is supported by neuroimaging evidence. The main brain structure linked to extraneous movements is the corpus callosum (Addamo et al., 2007). This structure was found to be reduced in adults with ASD (Casanova et al., 2009; Freitag et al., 2009). Importantly, J. J. Wolff et al. (2012) showed that the aberrant development of white matter pathways,

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[3] Neurological soft signs are described as neurological atypicalities which are neither part of a well-defined neurological syndrome nor mapped onto a specific brain region (Bombin et al., 2005).

including the corpus callosum, discriminates between infants who go on to develop ASD and those who do not, as early as 6 months of age. This suggests that aggravated extraneous movements may also be present in infants who will go on to developing ASD.

Apart from the atypical development of corpus callosum, a number of other neural differences have been described in ASD which are generally in line with reduced motor specialization as indicated by reduced or delayed network segregation (or differentiation) (Fishman, Keown, Lincoln, Pineda, & Müller, 2014; Rudie et al., 2013; Shih et al., 2011), perhaps, as Carper, Solders, Treiber, Fishman, and Müller (2015) suggested, due to impaired synaptic pruning (Tang et al., 2014). For example, overconnectivity of motor areas to brain areas outside of the motor network was found in children with ASD (Carper et al., 2015). Furthermore, brain activation in ASD was found to differ from TD individuals during a simple motor task (repetitive finger movement). Individuals with ASD showed greater variety in their functional maps in motor cortex and less distinct regional activation patterns than TD participants (Müller, Pierce, Ambrose, Allen, & Courchesne, 2001). Furthermore, an overlap in leg/trunk and upper limb/hand representations was found in 8- to 12-year-old children with ASD (Nebel et al., 2014). These results support the hypothesis that motor specialization is delayed or atypical in ASD.

The overlap between representations of limbs in ASD (Nebel et al., 2014) points to a possible explanation for the observation of extraneous movements in feet in typically developing infants (Study 1, Chapter 2). Perhaps representations of limbs are becoming more distinct over development, as a result of interactions with the environment. If children with neurodevelopmental disorders benefit less from interactions with the environment, or act less on the environment, this may result in abnormal or protracted specialization as indicated by less distinct representations of their limbs, possibly also underlying aggravated extraneous movements persisting over development. Overall, findings from individuals with ASD suggest that they show reduced specialization of the motor system.

5.3.1.2. Attention-deficit/hyperactivity disorder (ADHD)

Another neurodevelopmental disorder, which may also demonstrate a lack of specialization, is ADHD. Failure to adaptively implement strategies and modulate neural activity in response to varying task demands has been proposed to be a core problem in ADHD (Douglas, 1999; Durston, Mulder, Casey, Ziermans, & van Engeland, 2006; Fassbender et al., 2009). Indeed, ADHD medication seems to reduce superfluous neural activity in brain regions that are not necessary for success on a particularly challenging tasks, thus increasing signal-to-noise ratio and hence neural efficiency (e.g., Schulz, Newcorn, Fan, Tang, & Halperin, 2005; Schweitzer et al., 2004). In the motor domain, the difficulties with selecting appropriate responses to task characteristics would be identified as difficulties with accurate selection and control of motor responses.

One of the measures used to assess the ability of the brain to increase signal-to-noise ratio in the frontal cortex is a transcranial magnetic stimulation measure called *short-latency intracortical inhibition* (SICI; Rothwell, Day, Thompson, & Kujirai, 2009; Winterer & Weinberger, 2004). SICI was linked to extraneous movements in TD adults (Perez & Cohen, 2008). Gilbert et al. (2011) conducted a study investigating SICI in TD children and children with ADHD between 8 and 12 years of age. Within the ADHD group, less SICI was associated with more severe ADHD symptoms. SICI was significantly reduced in children with ADHD compared to TD children. Children with ADHD also obtained worse scores on a behavioural motor assessment, including increased extraneous movements. This suggests that children with ADHD have difficulties with selecting accurate movement, perhaps due to low signal-to-noise ratio in the frontal cortex. This may make it not only difficult to select accurate movement, but also affect the ability to sample from the environment and to specialize.

Difficulties with modulating signal-to-noise ratio (as indicated by reduced SICI) has been observed in many other disorders including ASD (Enticott et al., 2013), Tourette syndrome (Gilbert et al., 2004), dystonia (Avanzino et al., 2008), epilepsy (Di Lazzaro et al., 2004), and schizophrenia (Wobrock et al., 2008). These disorders also show increased extraneous movements (Caine et al., 1988; Hoy, Fitzgerald, Bradshaw, Farrow, et al., 2004; Sitburana & Jankovic, 2008). This is in line with my earlier proposal that extraneous movements could serve as an indicator of motor difficulties early in development. Yet, there is currently no study of extraneous movements in atypical populations in infancy and toddlerhood.

5.3.1.3. Developmental coordination disorder (DCD)

A lack of motor specialization has been also suggested for DCD. Individuals with DCD show motor difficulties that include a higher prevalence of extraneous movements (Licari, Larkin, & Miyahara, 2006). Hadders-Algra (2000) proposed that the motor difficulties observed in DCD are due to inappropriate specialization of neuronal groups, a process dependent on the interaction between the organism and the environment. This proposal is supported by findings from electrophysiological studies showing that children with DCD show increased coherence in cortical motor regions, which persist with age (de Castelnau, Albaret, Chaix, & Zanone, 2008). In TD children, increased coherence in cortical motor regions is associated with less skilled motor performance. As children develop their motor abilities, coherence decreases (Bell & Fox, 1996). This is in line with the finding that neural activity becomes more focal or less diffuse during typical development (Durston & Casey, 2006). Thus, increased coherence in children with DCD compared to TD children suggests protracted or atypical specialization.

5.4. Summary

The presence of aggravated extraneous movements across many conditions which has been documented in older children and adults suggest that extraneous movements could be a general marker of vulnerabilities early in development rather than a syndrome-specific marker of a particular neurodevelopmental disorder. Nonetheless, as I suggested above, it could be an important component for creating early profiles of various neurodevelopmental disorders. An advantage of using extraneous movements as part of the profile is that, compared to many other early markers which often require expensive technology (e.g., MRI, EEG), the identification of extraneous movements is low cost.

As mentioned above, there is currently no literature addressing whether the production of extraneous movements is increased in atypically developing children early in development. To shed some light on this issue, the following study (Chapter 6) focuses on examining extraneous movements in infants and toddlers with the most common neurodevelopment disorder of known genetic aetiology: *Down syndrome*. This neurodevelopmental disorder is usually identified very early in development (often prenatally), which allows us to examine young infants and toddlers with this neurodevelopmental syndrome. This is what differentiates Down syndrome from many others neurodevelopmental disorders. Behaviourally defined neurodevelopmental disorders such as ADHD, ASD, DCD, or cerebral palsy are usually identified later in childhood (e.g., most children are not diagnosed with ADHD until after 7 years of age; Centers for Disease Control and Prevention [CDC], 2016a). Also, many rare neurodevelopmental syndromes of known genetic origin are not usually tested for until later in development when developmental delay is noticed (e.g., in fragile X syndrome, the average age of diagnosis is around 3 years of age; CDC, 2016b).

Focusing on Down syndrome instead of other neurodevelopmental disorders therefore allows us to examine extraneous movements in atypically developing infants and toddlers. This is an important first step in understanding whether extraneous movements could be used as an early marker for neurodevelopmental disorders, since it is clear that the emerging phenotype of infants with Down syndrome will be atypical. If increased extraneous movements are found in infants and toddlers with Down syndrome, it would open a new line of enquiry; looking at early predictors in less clearly defined neurodevelopmental disorders.

CHAPTER 6

EXTRANEOUS MOVEMENTS AND INTERMANUAL COORDINATION IN INFANTS AND TODDLERS WITH DOWN SYNDROME (STUDY 4)

In Chapter 5 (Section 5.3.1), I suggested that motor specialization could serve as a particularly fruitful early marker of neurodevelopmental difficulties. Aggravated extraneous movements have been described in children with various neurodevelopmental disorders, including attention-deficit/hyperactivity disorder (ADHD; e.g., Gilbert et al., 2011; MacNeil et al., 2011; Mostofsky et al., 2006, 2003), autism spectrum disorder (ASD; e.g., Jansiewicz et al., 2006), developmental coordination disorder (DCD; Miyahara & Möbs, 1995), and learning difficulties (J. A. C. Lazarus, 1994). As discussed in the previous chapter, problems in the motor domain are often observed in these children before the emergence of cognitive and neurophysiological prodromal symptoms (e.g., ADHD; Kroes et al., 2007; ASD; Leonard et al., 2013). Thus, extraneous movements provide an excellent prospect for use as an early marker of developmental difficulties before the full profiles of these disorders emerge.

There is currently no literature addressing whether the production of extraneous movements is increased in atypically developing infants and toddlers. To help bridge this gap in our knowledge, the current study focuses on examining extraneous movements in infants and toddlers with a neurodevelopment disorder of clear genetic aetiology: *Down syndrome*. Studying a neurodevelopmental disorder that can be clearly identified based on its genetic profile is an important first step in understanding whether extraneous movements could be used as an early marker for neurodevelopmental disorders, since it is clear that the emerging phenotype of these individuals will be atypical. Focusing on Down syndrome is advantageous because it is usually diagnosed very early in development, often prenatally. This differentiates Down syndrome from disorders that are identified based on behaviour later in childhood (e.g., ADHD, ASD, cerebral palsy), as well as from disorders of known genetic origin that are not routinely tested for (e.g., fragile X syndrome, Williams syndrome). If increased extraneous movements are found in infants and toddlers with Down syndrome, it would open up a new line of enquiry investigating motor behaviours as early predictors of neurodevelopmental disorders that are not usually diagnosed until later on in childhood (e.g., ADHD, ASD).

Down syndrome (DS) is the most prevalent neurodevelopmental disorder of known genetic origin. It is caused by trisomy of human chromosome 21 (Has21; Lejeune, Gautier, & Turpin, 1959). DS occurs in one of every ~700 live births (Parker et al., 2010). It is the most common known genetic cause of intellectual disability, with an IQ that ranges from mild to severe disability (and an average IQ of around 50) (Chapman & Hesketh, 2000). Although many developmental domains are affected by DS (Newberger, 2000), the behavioural phenotype is characterized by a pattern of relative strengths and weaknesses. Domains of relative strengths are visual processing, receptive vocabulary, and social-emotional functioning, while relative weaknesses are spatial memory, verbal working memory, expressive language, attention, and motor ability (Fidler, 2005; Jarrold, Baddeley, & Hewes, 2000; Jarrold, Baddeley, & Phillips, 2002; Lanfranchi, Jerman, Dal Pont, Alberti, & Vianello, 2010; Laws & Gunn, 2004; G. E. Martin, Klusek, Estigarribia, & Roberts, 2009; Næss, Lyster, Hulme, & Melby-Lervåg, 2011; Opitz & Gilbert-Barness, 1990; Silverman, 2007; Tudella, Pereira, Basso, & Savelsbergh, 2011).

Based on the results of standardized tests, which often assess performance across different developmental domains (e.g., the Mullen Scales of Early Learning, the Bayley Scales of Infant and Toddler Development), motor development is a domain that infants with DS particularly struggle in. For example, in a longitudinal study, Carr (1970) tested children with DS and typically developing (TD) children on five separate occasions during the participants' first two years of life (6 weeks, 6 months, 10 months, 15 months, and 24 months), using the Bayley Infant Scales of Mental and Motor Development (now called the Bayley Scales of Infant and Toddler Development). A decline in both standardized cognitive and motor scores in DS, relative to TD children, was found and this decline was particularly steep from 10 to 15 months. In other words, as children with DS develop, they fall behind TD children. Moreover, from 6 months of age, mean standardized motor score was found to be lower than mean standardized mental score in DS. A deceleration of development with increasing chronological age in DS has also been found in other studies, as has the finding that motor standardized scores lags behind mental standardized scores (Harris, 1981; LaVeck & LaVeck, 1977). This suggests that the motor domain presents a particular challenge for the developing child with DS. From this it is reasonable to predict that behavioural atypicalities will be first observable in the motor domain (Section 5.3; M. S. C. Thomas et al., 2016).

Motor ability is an emergent property that arises from the interactions of multiple subsystems (Thelen & Smith, 1994). Many of these subsystems are atypical in infants with DS, which is likely to contribute to their motor difficulties. On the muscular and skeletal level, infants with DS experience hypotonia, joint laxity, and hypermobility (B. D. Ulrich & Ulrich, 1993). Most commonly mentioned is severe hypotonia (low muscle tone, Block, 1991; Cowie, 1970). Lower extremities are described as having lower muscle tone than upper limbs (Lauteslager, 2004). This may explain why motor abilities that require leg movements, such as walking, are more delayed. For example, while the average age of walking in TD children is 13 months and the age range is from 9- to 17-months, most children with DS learn to stand alone and walk between 1.5 and 3 years of age – with some DS children not able to walk even at 4 years of age (Palisano et al., 2001).

Brain abnormalities have also been described in DS (Dierssen, 2012), many of which are present prenatally or at birth (Haydar & Reeves, 2012; Imai et al., 2014). Since birth, the brain of individuals with DS shows a 20-50% reduction in the number of cortical neurons relative to TD controls (Schmidt-Sidor, Wisniewski, Shepard, & Sersen, 1990; Wisniewski, 1990; Wisniewski, Laure-Kamionowska, Connell, & Wen, 1986). Abnormal neuronal migration and synaptogenesis has already been identified at birth or soon after (Takashima, Becker, Armstrong, & Chan, 1981; Wisniewski et al., 1986), as was reduced dendritic arborization (Becker, Armstrong, & Chan, 1986; Benavides-Piccione et al., 2004; Purpura, 1975; Takashima, Ieshima, Nakamura, & Becker, 1989). Myelination is also delayed in individuals with DS (Wisniewski & Schmidt-Sidor, 1989).

In typical development, the number of neurons and synapses reaches its peak in early postnatal life. The synapses are initially weak but, as a result of experience, certain synaptic connections get strengthened (Hebb, 1949). Synapses that are unused become weaker and eventually eliminated (Colman, Nabekura, & Lichtman, 1997; Sengpiel & Kind, 2002). This process is essential for establishing optimally adaptive neural circuitry early in life, and hence specialization of the brain (M. H. Johnson, 2001a, 2011b). As described above, the brains of infants with DS have fewer neurons, altered synapses and dendrites, and delayed myelination. As described in the previous chapter, synapses enable neurons to communicate with each other. Also, the synapses are not fixed, they are constantly being created, pruned and altered by experience (Fiala et al., 2002). Synaptic dysfunction could lead to sparser and less reliable sampling of the environment, and hence a worse signal-to-noise ratio, which in turn may result in protracted plasticity and atypical specialization of function (Rubenstein & Merzenich, 2003). Therefore, it is likely that the DS brain does not specialize in the same way or to the same extent as the TD brain.

Although the literature exploring the process of specialization in DS is small, some evidence (albeit not in the motor domain) exists which support my proposal that specialization in this population is atypical. For example, fMRI (functional magnetic resonance imaging) activation patterns during passive story listening tasks were studied in young adults with DS and TD (Reynolds Losin, Rivera, O'Hare, Sowell, & Pinter, 2009). While TD participants showed different activation for language (forward speech) compared to non-language (backward speech), the DS group showed almost no difference in activation patterns between the two. This suggests that the DS brain had not specialized for hearing speech, at least not to the same extent as the TD brain.

Furthermore, Anderson et al. (2013) described decreased specialization of cortical networks in young adults with DS as they watched cartoon video clip, relative to TD young adults. These authors found that, compared to TD participants, adjacent brain regions in DS were more synchronized while the opposite was true for distant brain regions. More short-range connections with less long-range connectivity is a hallmark of the TD brain early in development. Over time, short-range connections decrease and long-range connectivity increases (Fair et al., 2007, 2009). This developmental process has, for example, been documented in animal research in a brain area directly relevant to motor development: motor cortex (Biane, Scanziani, Tuszynski, & Conner, 2015). Although there is currently no literature directly examining the link between decreased specialization of cortical networks and delayed motor specialization in Down syndrome, or in fact any other neurodevelopmental disorder, indirect support for this relationship is available in the ASD literature. As discussed in Section 5.3.1.1, less differentiation in motor cortex has been documented in ASD (Müller et al., 2001; Nebel et al., 2014), and ASD is a clinical population that also presents with aggravated extraneous movements (Jansiewicz et al., 2006). This suggests that aggravated extraneous movements could index delayed or atypical specialization. Therefore, based on the lack of functional specialization in the DS brain in other domains (described above), I predict that there will also be a lack of motor specialization, evident in a higher prevalence of extraneous movements in infants and toddlers with DS compared to TD controls.

Due to disrupted synaptogenesis in DS, the relatively fewer and weaker connections of neurons may be more vulnerable during the pruning process (Colman et al., 1997; Cowan, 1979) in individuals with DS. As mentioned in Section 5.3, the onset of synaptic pruning varies across different brain regions (Gogtay et al., 2004; Huttenlocher, 2002; Huttenlocher & Dabholkar, 1997). It occurs first in sensory and motor areas, followed by higher association areas and lastly prefrontal cortex. Therefore, the motor domain may be one of the first domains that show marked atypicalities in DS. Indeed, this is supported by the results from the standardized developmental scales: As mentioned above, whereas there were no differences between cognitive and motor scores in DS at 6 weeks of age, infants with DS were found to have consistently lower motor scores from 6 months of age onwards (Carr, 1970). This is in line with the proposal that neurodevelopmental difficulties will be observable in the motor domain before any other domain, due to the time course of the pruning process (M. S. C. Thomas et al., 2016). This highlights the importance of investigating specialization in the motor domain as a possible marker of early developmental difficulties.

Organisms contribute to their own specialization by generating activity. Typically developing organisms are likely to select aspects of the external environment or generate activity that best suits their own capacities (Kidd et al., 2012; Rovee-Collier & Cuevas, 2009). However, self-generated activity patterns in infants with DS differ from those in TD infants. Infants with DS produce fewer general movements (spontaneous motor activity in young infants) than TD infants (Mazzone, Mugno, & Mazzone, 2004). Infants with DS also produce more low-intensity and less high-intensity spontaneous leg motor activity than TD infants (Lloyd, Burghardt, Ulrich, & Angulo-Barroso, 2010; McKay & Angulo-Barroso, 2006). Moreover, infants with DS produce fewer complex leg movements (i.e., kicking patterns; B. D. Ulrich & Ulrich, 1995). The reduced early motor activity is likely to contribute to motor delay in DS. However, it is important to note that individual differences are also likely to play a role. For example, the intensity of leg kicks predicts onset of walking in DS; infants who showed more high-intensity leg motor activity at around 12 and 14 months of age started walking earlier than those who showed less of this activity (Lloyd et al., 2010). Furthermore, the effect of motor experience on the onset of walking was examined in a randomized controlled study. It was demonstrated that infants with DS who underwent a home-based stepping training intervention achieved independent walking by an average of 101 days earlier than infants with DS who were not part of this intervention (D. A. Ulrich, Ulrich, Angulo-Kinzler, & Yun, 2001). It is clear therefore that specific levels of motor difficulty in DS result from gene-environment interactions rather than purely neuromaturational factors.

Apart from engaging in less spontaneous motor activity, infants with DS also produce fewer object-oriented actions. For instance, infants with DS show lower levels of exploration through mouthing objects than TD infants (Frazier & Friedman, 1996; Mizuno & Ueda, 2001). Differences in self-generated activity have also been observed in the emergence of reaching. A. C. de Campos, da Costa, Savelsbergh, and Rocha (2013) followed DS and TD infants monthly, with a first assessment at the age of 4 months. As expected, the majority of TD infants were able to reach at the age of their first assessment (i.e., at 4 months; Spencer & Thelen, 2000). The TD infants subsequently showed a gradual increase in number of reaches. The age at which infants started reaching was a better predictor of later reaching behaviour than chronological age. This suggests that reaching behaviour is dependent on experience rather than on chronological age (Carvalho, Tudella, Caljouw, & Savelsbergh, 2008;

Eppler, 1995; Lobo & Galloway, 2013; Soska, Adolph, & Johnson, 2010). This conclusion is in line with the proposal that TD infants act and select aspects of their environment as a function of their current level of abilities (Kidd et al., 2012; Rovee-Collier & Cuevas, 2009). TD infants spontaneously repeat their actions and, in so doing, practice new emerging skills (Adolph et al., 2012). A. C. de Campos et al. (2013) observed the same trend in DS: that is, an increasing number of reaches after the onset of reaching. However, the average number of reaches that the infants with DS produced was significantly lower than the number produced by the TD infants. Thus, not only did the children with DS start reaching later, but they also practiced their actions less frequently than the TD infants.

Because the motor system undergoes specialization from broad to fine tuning (as Studies 1-3 of this thesis demonstrate), if time spent practicing skills is an important factor in the process of functional specialization, then we should expect infants with DS to have a less specialized motor system than TD infants as indicated by more extraneous movements. Furthermore, the basic building blocks of prehension skills such as reaching and exploratory behaviour are atypical in DS (Cadoret & Beuter, 1994; A. C. de Campos, Cerra, Silva, & Rocha, 2014). This is likely to affect the emergence of later, more complex, arm coordination skills. Therefore, I predict less well-developed intermanual coordination skills in DS. Furthermore, I propose a link between extraneous movements and intermanual coordination in DS (as observed in the TD sample in Study 3, Chapter 4).

No previous study has investigated the development of extraneous movements in infants and toddlers with DS (nor, in fact, in infants/toddlers with any other neurodevelopmental disorder). Thus, the current study is the first to examine early motor specialization in neurodevelopmental disorders by investigating extraneous movements in DS. The same reaching paradigm that was developed for Study 1 and Study 3 was used here. Furthermore, to explore the relationship between extraneous movements and intermanual coordination in DS, the current study also extends the paradigm that was used to investigate intermanual coordination in Study 3. Study 3 used a single task (a box with a hinged lid) to investigate intermanual coordination in 12-month-olds. However, the current study of extraneous movements and intermanual coordination in DS covers a broader age range. Thus, instead of relying on a single task, I developed a scale of intermanual tasks of varying difficulties in order to capture various levels of intermanual ability across development.

6.1. Methods

6.1.1. Participants

Thirteen infants and toddlers with DS were tested at Birkbeck, University of London as part of the London Down Syndrome (LonDownS) Consortium infant stream protocol. The participants had trisomy 21 and a clinical diagnosis of DS. Four additional children with DS were tested but excluded from analysis due to: (1) experimenter error (n = 1); (2) producing fewer than four unimanual reaches (n = 1); and (3) fussiness (n = 2). Because children with DS have a mental age (MA) of approximately half their chronological age (CA), they were matched to two groups of typically developing (TD) controls. Table 6.1 shows the characteristics of the groups included in the study. The first TD group (the *CA-matched group*) was matched on CA and did not significantly differ from the DS group on chronological age, $t(23) = 0.40$, $p = .696$. The second TD group (the *MA-matched group*) was matched on mental age. Mental age scores were obtained using the Mullen Scales of Early Learning (MSEL; Mullen, 1995; Section 6.1.2.1), and the MA-matched group did not significantly differ on mental age from the DS group, $t(29) = 0.34$, $p = .740$.

In order to carry out a cross-sectional developmental trajectory analysis (this analysis approach is explained below in Section 6.1.3.1 of this chapter), the DS group was also compared with a larger TD group (henceforth the *TD group*, Table 6.1). The age range of this TD group stretched from the youngest mental age in the DS group (11.75 months) to the oldest chronological age in the DS group (35.45 months), as recommended by M. S. C. Thomas et al. (2009). Four additional TD children were tested, but excluded from analysis because they produced fewer than four unimanual reaches. The TD participants were recruited via a database of parents who expressed an interest in participating in developmental studies. Ethical approval was gained from the Goldsmiths Research Ethics Committee. Prior to testing, informed consent was obtained from all parents. Testing only took place if the child was awake and alert. The participants were given a small gift (e.g., a T-shirt) in return for their participation.

Table 6.1

Participant characteristics in Study 4

Group	*n*	Sex	CA (months)	MA (months)
CA-matched	11	6f, 5m	27.42 (*SD* = 5.16)	28.61 (*SD* = 6.41)
MA-matched	17	9f, 8m	15.64 (*SD* = 4.02)	15.78 (*SD* = 3.85)
TD trajectory	24	13f, 11m	20.01 (*SD* = 7.88)	20.74 (*SD* = 8.70)
DS	14	8f, 6m	28.22 (*SD* = 4.94)	16.20 (*SD* = 2.88)

Note. CA = chronological age, MA = mental age, TD = typically developing, DS = Down syndrome.
Note. The DS group was compared with the CA- and MA-matched groups in one set of analyses, and with the TD trajectory group in a different set of analyses.

6.1.2. Procedure and materials

6.1.2.1. The Mullen Scales of Early Learning

This standardized developmental scale was also used in Study 3 (Chapter 4, Section 4.1.2.1). The Mullen Scales of Early Learning (MSEL; Mullen, 1995) comprises five subscales: (1) *Gross motor* (central motor control and mobility in supine, prone, sitting, and fully upright positions); (2) *Fine motor* (visually-directed motor planning, object manipulation, visual discrimination, and motor control); (3) *Visual reception* (visual perceptual ability, spatial awareness, and visual memory); (4) *Receptive language* (auditory comprehension, auditory memory, and the ability to process linguistic input); and (5) *Expressive language* (the ability to use sounds and language productively). These yield scores for each domain. Mental age was then computed as an average of Fine motor, Visual reception, Receptive language, and Expressive language scores (D'Souza et al., 2015; Mullen, 1995). This standardized test has high internal consistency and test-retest reliability (Mullen, 1995; see also Bishop et al., 2011, for estimates of convergent validity).

6.1.2.2. The reaching task

The reaching task used in Study 1 (Chapter 2, Section 2.1.2.1) was also used here. For each unimanual reach, the coder identified the timings of: (1) *the onset of the reach* (i.e., the moment when any part of the acting hand and/or arm from the fingertips to the shoulder started a continuous trajectory which ended in target contact), and (2) *contact* (i.e., the moment when the hand touched the target for the first time in the trial). Next, for each unimanual reach, the coder identified whether any extraneous movement occurred. If there was an extraneous movement during the reach, then the coder identified whether it was tightly linked to the onset of movement in the acting limb (starting +/- 100 ms around the onset of the reach of the acting hand).

As in Study 1 (Chapter 2, Section 2.1.2.1), the proportion of unimanual reaches accompanied by extraneous movement for each infant was calculated. The measure was computed separately for the non-acting hand/arm and the feet/legs. Furthermore, a proportion of reaches in which extraneous movement onset was tightly linked to the onset of movement in the acting limb (+/- 100 ms around the onset of the reach in the acting hand) was calculated. The proportion of unimanual reaches accompanied by these reach-onset-locked extraneous movements was computed separately for hand/arm and feet/legs. Because these data were proportional, they were arcsine transformed prior to carrying out inferential analyses. Raw data are presented in the figures. Outliers (+/- 2 *SD*) were excluded.

6.1.2.3. The intermanual coordination scale

In order to obtain a measure of intermanual coordination across the studied groups, an intermanual coordination scale was developed. The administration of the scale followed the reaching task. Infants were seated in an infant seat (Bébépod Flex, Prince Lionheart Inc., Santa Maria, CA, USA) and secured into place with adjustable straps around the waist so that movement of the trunk was restricted. This scale consists of seven intermanual tasks of varying difficulty. The tasks were presented to infants twice over two blocks, always preceded by the experimenter demonstrating the solution to the task. In each block, each task was presented once.

The order of tasks was randomized across infants within each block. Thus, each infant received in total 14 intermanual coordination trials. The intermanual coordination scale consisted of the following tasks: (1) *Cup*; (2) *Tube*; (3) *Two cups*; (4) *Doll*; (5) *Box*; (6) *Screw*; and (7) *Bottle*. The description of each task and retrieval strategy classification (adapted from Birtles et al., 2011; Fagard & Pezé, 1997; Ramsay & Weber, 1986) is provided in the following paragraphs.

Cup. For this task, a small red rubber object (4 cm in diameter) was inserted inside a semi-transparent plastic cup (9 x 4.5 cm, height x diameter). The task was to retrieve the rubber object from the cup. To succeed on this task the infant had to hold the cup with one hand and remove the rubber object with the other (intermanual coordination). Retrieval strategy was classified into four categories of intermanual coordination: (1) *Failure*: the infant engaged with the objects but did not retrieve the target object (score of 0); (2) *No differentiation*: The infant did not present any intermanual coordination. For example, the infant would use only one hand to retrieve the object from the cup (score of 1); (3) *Incomplete differentiation*: The differentiation between hands presented by the infant was incomplete. The infant grasped the cup with one hand, shifted it to the other and pulled the rubber object out with the first hand (score of 2); (4) *Complete differentiation*: One hand grasped the cup while the other pulled out the object (score of 3).

Tube. For this task (based on Fagard & Pezé, 1997), a small red plastic tube (7 x 1 cm, height x diameter) was inserted into a small plastic semi-transparent bottle (6.5 x 3 cm, height x diameter), with only the bright cap of the tube sticking out from the bottle. The purpose of the task was to extract the tube from the bottle. To succeed on this task, the infant had to hold the bottle with one hand, while removing the tube with the other. In other words, the task required intermanual coordination. The retrieval strategy the infant used was classified into four categories of intermanual coordination: (1) *Failure*: the infant engaged with the objects but did not retrieve the tube (score of 0); (2) *No differentiation*: The infant did not present any intermanual coordination. For example, the infant would use only one hand to retrieve the tube from the bottle (score of 1); (3) *Incomplete differentiation*: The differentiation between hands presented by the infant was incomplete. The infant grasped the bottle with one hand, shifted it to the other and pulled the tube out with the first hand (score of 2); (4) *Complete differentiation*: One hand grasped the bottle while the other pulled the tube out (score of 3).

Two cups. This task consisted of two plastic cups (9 x 6 cm, height x diameter). One of the cups was cut (2 cm from the top) so it could fit inside the other cup. A colourful rubber bracelet (6.5 cm diameter) was inserted in the hollow space created by joining the two cups. The task was to retrieve the bracelet. This required holding each of the cups with one hand and pulling the cups apart. The retrieval strategy the infant used was classified into three categories of intermanual coordination: (1) *Failure*: The infant engaged with the objects but did not retrieve the bracelet (score of 0); (2) *No differentiation*: The infant did not present any intermanual coordination. One hand disconnected the cups to retrieve the bracelet. The other hand was not used (score of 1); (3) *Complete differentiation*: Each hand held one of the cups. The infant then pulled apart the cups and retrieved the bracelet inside (score of 3).

Doll. For this task, a small plastic doll (6.5 cm height) was placed inside a rectangular cloth box (22.5 x 15.5 x 33 cm, width x height x depth) by lifting a flap (which was one of the two smaller sides of the box). To retrieve the doll, the infant had to lift the flap (the side of the box) with one hand while retrieving the object with the other hand. Retrieval with only one hand was almost, but not entirely, prevented by the fact that the flap had to be lifted up. In other words, if it were not held up, it would fall back down to its original closed position. The retrieval strategy the infant used was classified into four categories of intermanual coordination: (1) *Failure*: The infant engaged with the objects but did not retrieve the doll (score of 0); (2) *No differentiation*: The infant did not present any intermanual coordination. One hand raised up the side of the box and retrieved the doll. The other hand was not engaged in the task (score of 1); (3) *Incomplete differentiation*: The differentiation presented by the infant was incomplete. Two possible strategies belong to this category. One strategy involved the infant raising up the flap with the leading hand and then swapping the leading hand for the other hand in holding up the flap, while the leading hand then retrieved the doll. The second involved the infant raising up the flap with both hands, and then one of the hands kept the flap up while the other hand retrieved the doll (both strategies yield a score of 2); (4) *Complete differentiation*: One hand lifted up the flap, while the other reached inside for the doll (score of 3).

Box. This task was also used in Study 3 (Chapter 4, Section 4.1.2.3). A semi-transparent plastic box (16 x 7 x 8 cm, width x height x depth) was used. The lid of the box was hinged so the lid would fall back on the top of the box if not held (adapted from Birtles et al., 2011; Bruner, 1970; Fagard & Pezé, 1997; Ramsay & Weber, 1986). A small red and navy blue ball with a jingle bell inside (4 cm in diameter) was placed inside the box and produced a ringing bell sound as it moved around. To retrieve the ball, the infant had to raise the lid and hold it open with one hand while retrieving the toy with the other hand. Retrieval with only one hand was almost, but not entirely, prevented by the hinged lid (following Fagard & Pezé, 1997). The retrieval strategy the infant used was classified into four categories of intermanual coordination: (1) *Failure*: The infant engaged with the objects but the toy was not retrieved (score of 0); (2) *No differentiation*: The infant did not present any intermanual coordination. One hand raised the lid and retrieved the toy underneath. The other hand was not engaged in the task (score of 1); (3) *Incomplete differentiation*: The differentiation presented by the infant was incomplete. Two possible strategies belong to this category. In the first, the infant raised the lid with the leading hand and then swapped the leading hand for the other hand in holding the lid while the leading hand retrieved the ball. In the second, the infant raised the lid with both hands, then one of the hands held the lid while the other retrieved the ball (score of 2); (4) *Complete differentiation*: One hand raised the lid, the other reached for the object inside (score of 3).

Screw. This task consisted of a large plastic nut and bolt (6.5 x 5 cm, height x width; from the Mullen Scale of Early Learning testing kit; Mullen, 1995). The purpose of the task was to unscrew the nut from the bolt. The strategies that the infant used was classified into four categories of intermanual coordination: (1) *Failure*: The infant engaged with the object but did not unscrew the nut (score of 0); (2) *No differentiation*: The infant did not present any intermanual coordination. One hand unscrewed the nut by shaking or turning it, usually against the surface or the infant's own body. The other hand was not engaged in the task (score of 1); (3) *Incomplete differentiation*: The infant grasped the screw with one hand, shifted it to the other, and unscrewed the nut with the first hand (score of 2); (4) *Complete differentiation*: Each hand held one end of the screw, rotating the ends until the nut came off (score of 3).

Bottle. This task consisted of a semi-transparent plastic bottle (10 x 6 cm, height x diameter) with a screwable top. A colourful rubber bracelet (6.5 diameter) was inserted inside the bottle and the lid was screwed on. The task was to retrieve the rubber bracelet which required holding the bottle with one hand while unscrewing the lid with the other. The retrieval strategy that the infant used was classified into four categories of intermanual coordination: (1) *Failure*: The infant engaged with the object but did not retrieve the bracelet (score of 0); (2) *No differentiation*: The infant did not present any intermanual coordination. The infant managed to unscrew the lid using just one hand, usually by holding the bottle against his or her own body. The other hand was not used (score of 1); (3) *Incomplete differentiation*: The infant grasped the bottle with one hand, shifted it to the other, and then unscrewed the lid with the first hand to retrieve the bracelet (score of 2); (4) *Complete differentiation*: One hand held the bottle while the other twisted off the lid and retrieved the bracelet (score of 3).

For each child, an average score was computed for each task. If the infant did not engage with the task in a particular trial, the trial was not counted. The average scores per task were then summed up to create an intermanual coordination score.

6.1.3. Analysis

Since cognitive and motor profiles of neurodevelopmental disorders often show uneven distributions across subdomains, the first step in the analysis was to describe the profiles of each group based on their scores in a standardized test (the Mullen Scales of Early Learning). This was followed up with an exploratory correlational analysis between chronological age, mental age (as indicated by the Mullen Scales of Early Learning), and experimental measures. Then, differences in extraneous movements and intermanual coordination were examined separately between the DS and CA-matched groups and between the DS and MA-matched groups, as well as in a cross-sectional developmental trajectories analysis (see below Section 6.1.3.1 for details). Finally, the relationship between extraneous movements in the non-acting hand and intermanual coordination was explored across groups.

Since this is the first study to examine extraneous movements in atypically developing infants and toddlers, I included in the analysis all the variables that I had examined in my TD sample in Study 1 (overall extraneous movements in hand/arm, tightly linked extraneous movements in hand/arm, overall extraneous movements in feet/legs, tightly linked extraneous movements in feet/legs). I had no *a priori* predictions about which of these four variables would be the most relevant. I believe that this analysis is vital for the generation of more constrained hypotheses in future studies.

6.1.3.1. Building cross-sectional developmental trajectories

A cross-sectional developmental trajectory analysis was employed to compare whether cross-sectional developmental trajectories of extraneous movements and intermanual coordination differ between the DS and TD groups. Although this type of analysis is well established in the field of neurodevelopmental disorders (Annaz, Karmiloff-Smith, Johnson, & Thomas, 2009; Jarrold, Baddeley, & Phillips, 2007; Purser et al., 2015; M. S. C. Thomas, Purser, & van Herwegen, 2011), it is not as well known as other methods of analysis. This section will therefore describe this approach in more detail.

The cross-sectional developmental trajectories method was developed to compare typically developing trajectories with those of individuals with developmental disorders (M. S. C. Thomas et al., 2009). The method uses Analysis of Covariance (ANCOVA). However, whereas ANCOVA tests for differences between group means (while accounting for a covariate [continuous variable]), the cross-sectional developmental trajectories method uses a covariate and evaluates differences between regression lines which depict the developmental trajectory of each group. For group-based analyses, the average performance of each group is represented by a single number, while two numbers represent cross-sectional developmental trajectories – the *intercept* and *gradient*. The intercept represents the level at which performance starts. The gradient represents the rate at which performance changes (increases or decreases) with age. The use of intercepts and gradients allows researchers to look beyond differences between group means (which can only inform us whether groups differ or not) and provide insight into *how* groups differ.

In this chapter, following Jarrold et al. (2007) and M. S. C. Thomas et al. (2009), cross-sectional developmental trajectories were initially plotted separately for the DS and TD groups by conducting a series of regression analyses to examine how extraneous movements and intermanual coordination are related to chronological age and mental age in each group. Analysing the relationship with chronological and mental age in separate analyses rather than in one analysis is the recommended approach, because chronological and mental ages are usually closely related in TD individuals (M. S. C. Thomas et al., 2009). As a result, chronological age and mental age are unlikely to differ from each other in their association with extraneous movements and/or intermanual coordination. However, chronological and mental ages tend to be more dissociated among individuals with neurodevelopmental disorders. Any regression combining chronological and mental ages would therefore underestimate the differential effects of these two variables.

Once cross-sectional developmental trajectories were constructed separately for each group, the trajectories were directly compared. This made it possible to evaluate whether the DS developmental trajectory differed from the TD developmental trajectory in terms of its gradient and/or intercept. To compare the two trajectories, a modified version of ANCOVA was employed to test for a main effect of Age (chronological and mental age were examined in two separate analyses as explained above), Group (TD vs. DS), and the interaction between Age and Group. If the main effect of Group is significant, then the intercepts of the two groups are reliably different. We could then conclude that the disorder group exhibits *delayed onset* in development. If the interaction between Age and Group is significant, then we can conclude that the disorder group was developing more slowly on the experimental task, exhibiting a *slower rate* of development.

6.2. Results

6.2.1. Cognitive and motor profiles of the CA-matched, MA-matched, and DS groups

To describe cognitive and motor profiles within each group, scores on five Mullen Scales were compared separately in the CA-matched, MA-matched, and DS groups using three ANOVAs[4] (see Figure 6.1). Significant main effects were followed up by paired samples *t*-tests for which Bonferroni correction was applied ($\alpha = .005$ for ten t-tests). Although there was a trend for a main effect of Mullen Scale on scores in the CA-matched group ($F(1.9,17.1) = 3.49$, $p = .056$, $\eta^2 = .28$), no difference was found between individual scales when t-tests were used to tease apart the main effect, all *t*s < 3.30, all *p*s > .08. Mental age differed significantly across the five Mullen Scales in the MA-matched group, $F(2.53,40.48) = 5.91$, $p = .003$, $\eta^2 = .27$. Paired samples t-tests revealed that scores for Visual reception and Fine motor skills were significantly higher than Expressive language, $t(16) = 4.20$, $p = .007$, $d = 1.05$; $t(16) = 8.64$, $p < .001$, $d = 2.16$. For the DS group, scores differed significantly across the five Mullen Scales, $F(4,48) = 3.88$, $p = .008$, $\eta^2 = .24$. Paired samples *t*-tests revealed that the scores for Fine motor skills were significantly higher than both Receptive and Expressive language, $t(12) = 3.45$, $p = .048$, $d = 0.92$; $t(13) = 3.38$, $p = .049$, $d = 0.90$.

To test whether the MA-matched and DS groups were matched not only on overall mental age (see Section 6.1.1), but also on each scale in the MSEL, independent-samples t-tests were carried out. The t-tests revealed no significant differences on any of the subscales (all *t*s < 1.70, all *p*s > .100). This confirms that

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[4] A Greenhouse-Geisser correction was applied where appropriate.

the DS and MA-matched groups were well matched on each individual scale of the Mullen Scales of Early Learning.

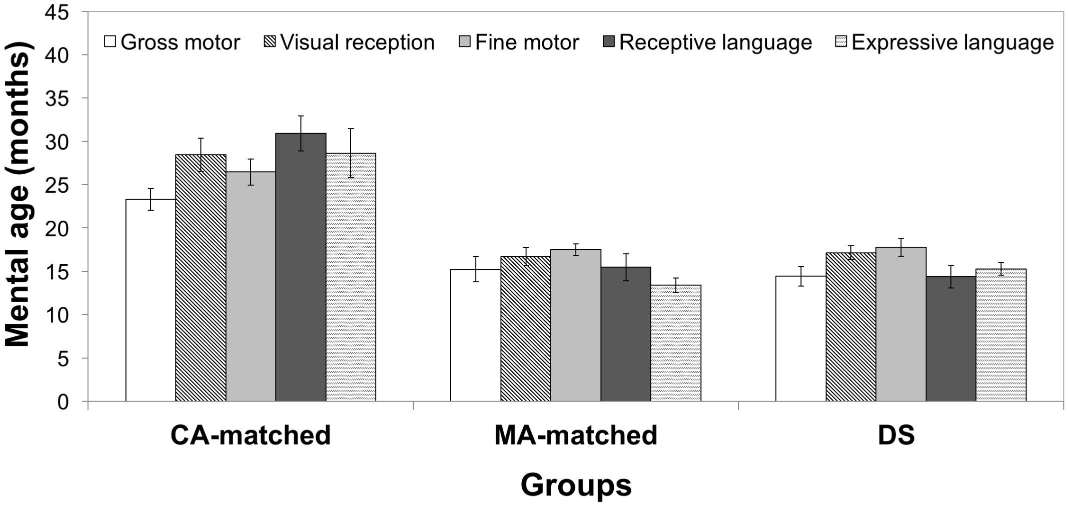


Figure 6.1. The five Mullen Scales in: (a) a typically developing group matched on chronological age to the Down syndrome group (CA-matched); (b) a typically developing group matched on mental age to the Down syndrome group (MA-matched); (c) the Down syndrome group (DS). No difference was found among the scales in the CA-matched group. In the MA-matched group, Visual reception and Fine motor were significantly higher than Expressive language. In the DS group, Fine motor was significantly higher than Receptive and Expressive language ability. There was no difference between the MA-matched and DS groups on any of the scales, showing that the groups were well matched on these measures. Error bars show +/- 1 *SE*.

6.2.2. Exploratory correlational analysis of measures in TD and DS groups

To explore whether chronological and mental age (including scores from individual Mullen scales) are related to the experimental measures, a correlation matrix was produced separately for the TD trajectory (see Table 6.2) and DS groups (see Table 6.3). A tight relationship between measures was present in the TD group. A very high correlation was observed between chronological and mental age in the TD group (.98). Furthermore, there were high correlations between all of the individual Mullen Scales in the TD group. This suggests that abilities tend to improve simultaneously across domains in TD children (e.g., when visual reception improves, so does language). Improvements across the Mullen Scales are tightly linked to chronological age (all correlations between chronological age and individual Mullen Scales are greater than .80). Furthermore, significant relationships

Table 6.2

Correlations in the TD group between chronological age (A), mental age (B), five Mullen Scales (C-G), and experimental measures (H-L)

	Age		**Mullen Scales**				
	A	B	C	D	E	F	G
Age							
A. Chronological	-						
B. Mental	.98*** (24)	-					
Mullen Scales							
C. Gross motor	.81*** (23)	.78*** (23)	-				
D. Visual reception	.95*** (24)	.97*** (24)	.73*** (23)	-			
E. Fine motor	.97*** (24)	.96*** (24)	.82*** (23)	.90*** (24)	-		
F. Receptive language	.95*** (24)	.98*** (24)	.78*** (23)	.96*** (24)	.90*** (24)	-	
G. Expressive language	.95*** (24)	.98*** (24)	.71*** (23)	.91*** (24)	.96*** (24)	.92*** (24)	-
Experimental measures							
H. Overall extraneous hand/arm movements	-.69*** (23)	-.74*** (23)	-.50* (22)	-.70*** (23)	-.69*** (23)	-.77*** (23)	-.70*** (23)
I. Tightly extraneous hand/arm movements	-.56** (23)	-.62** (23)	-.45* (22)	-.58** (23)	-.62** (23)	-.62** (23)	-.60** (23)
J. Overall extraneous feet/legs movements	-.64** (23)	-.62** (23)	-.63** (22)	-.62** (23)	-.58** (23)	-.70*** (23)	-.52* (23)
K. Tightly extraneous feet/legs movements	-.44* (23)	-.44* (23)	-.23 (22)	-.43* (23)	-.38 (23)	-.51* (23)	-.37 (23)
L. Intermanual coordination	.86*** (24)	.84*** (24)	.75*** (23)	.85*** (24)	.83*** (24)	.83*** (24)	.77*** (24)

Note. *p < .050, **p < .010, ***p < .001; N in brackets; correlations between experimental measures are affected by CA and MA and thus omitted.

Table 6.3

Correlations in the DS group between chronological age (A), mental age (B), five Mullen Scales (C-G), and experimental measures (H-L)

	Age		**Mullen Scales**				
	A	B	C	D	E	F	G
Age							
A. Chronological	-						
B. Mental	.56* (14)	-					
Mullen Scales							
C. Gross motor	.52 (14)	.52 (14)	-				
D. Visual reception	.43 (14)	.67** (14)	.41 (14)	-			
E. Fine motor	.62* (14)	.91*** (14)	.55* (14)	.56* (14)	-		
F. Receptive language	.35 (13)	.83*** (13)	.58* (13)	.28 (13)	.67* (13)	-	
G. Expressive language	.43 (14)	.81** (14)	.12 (14)	.44 (14)	.69** (14)	.57** (13)	-
Experimental measures							
H. Overall extraneous hand/arm movements	-.61* (13)	-.42 (13)	-.42 (13)	-.63* (13)	-.48 (13)	-.13 (12)	-.17 (13)
I. Tightly extraneous hand/arm movements	.24 (13)	.25 (13)	.24 (13)	-.23 (13)	.17 (13)	.45 (12)	.30 (13)
J. Overall extraneous feet/legs movements	-.24 (14)	-.02 (14)	-.46 (14)	-.11 (14)	-.19 (14)	.13 (13)	-.04 (14)
K. Tightly extraneous feet/legs movements	-.66* (13)	-.34 (13)	-.42 (13)	-.09 (13)	-.44 (13)	-.28 (12)	-.22 (13)
L. Intermanual coordination	.55* (14)	.40 (14)	.34 (14)	.46 (14)	.52 (14)	.19 (13)	.11 (14)

Note. *p < .050, **p < .010, ***p < .001; *N* in brackets; correlations between experimental measures are affected by CA and MA and thus omitted.

between age and experimental measures were consistently present in the TD group; the higher their chronological age and also the higher their motor and cognitive scores (as measured using the Mullen Scales of Early Learning), the better they were at producing more specialized movements (i.e., they produced fewer extraneous movements) and the better they were at intermanual coordination. The only experimental measure that did not consistently correlate the Mullen Scales of Early Learning and correlated most poorly with chronological and mental age in the TD group was a measure of tightly linked extraneous movements in feet/legs. I suspect that this was due to the floor effect. The TD children tested in this study did not produce many unimanual reaches with extraneous movements in their feet/legs at the onset of the reaches (*M* = 10%, *SD* = 10%).

In the DS group, correlations between the measures were not as high or consistent as the correlations in the TD group. The following comparisons come with the caveat that the DS sample size was relatively small and the range of ages was limited. While the correlation between chronological and mental age in the TD group was .98, it was only .56 in the DS group. This may be due to individual differences in the severity of difficulties associated with Down syndrome which may vary independently of chronological age. Furthermore, correlations between individual Mullen Scales were either non-existent or much weaker than in the TD group. This suggests that development in DS does not progress at the same rate across domains (e.g., improvements in visual reception are unrelated to development in the language domain). Furthermore, only Fine motor skills were linked to chronological age (.62). Relationships between age and experimental measures were also inconsistent in the DS group. Most correlations were between chronological age and experimental measures (overall extraneous movements in non-acting hand/arm: -.61; tightly linked extraneous movements in feet/legs: -.66; intermanual coordination: .55). Therefore, in line with what was observed in the TD group, the greater chronological age was in children with DS, the fewer extraneous movements they produced and the better they were at intermanual coordination. There was no consistent correlation between mental age and experimental measures or between the experimental measures and individual Mullen Scales. The only correlation found was between overall extraneous movements in the non-acting hand/arm and the Visual reception scale of the Mullen (-.63). To explore this relationship, I conducted a follow up correlation between Visual reception scale and overall extraneous movements in the non-acting hand/arm, partialling out chronological age. When chronological age was taken into account, the relationship between Visual reception abilities and overall extraneous movements in the non-acting hand/arm was no longer significant, $r(10) = -.419$, $p = .175$.

6.2.3. Extraneous movements

6.2.3.1. Overall extraneous movements in the non-acting hand/arm

Comparing the DS group with the CA- and MA-matched groups. Extraneous movements in the non-acting hand/arm were produced in 20% of unimanual reaches in the CA-matched group ($SD = 18\%$), 50% in the MA-matched group ($SD = 17\%$), and 80% in the DS group ($SD = 16\%$). The DS group produced significantly more extraneous movements than both the CA- and MA-matched groups, DS vs. CA: $t(22) = 6.53$, $p < .001$, $d = 2.67$; DS vs. MA: $t(26) = 4.35$, $p < .001$, $d = 1.65$.

DS and TD developmental profiles. Figure 6.2 shows developmental trajectories relating overall extraneous movements in the non-acting hand/arm to chronological and mental age in the TD group and in the DS group. Trajectories were initially explored separately according to group in order to assess the developmental profile of each group before comparing them against each other. The TD cross-sectional developmental trajectory revealed a significant relationship between chronological age (Figure 6.2a, Table 6.4a), as well as mental age (Figure 6.2b, Table 6.4b) and overall extraneous movements in the non-acting hand/arm, CA: $R^2 = .48$, $F(1,21) = 19.48$, $p < .001$; MA: $R^2 = .54$, $F(1,21) = 25.07$, $p < .001$. This is an important addition to Study 1, showing a further developmental decrease in extraneous movements beyond 12 months of age. Although chronological age predicted overall extraneous movements in the non-acting hand/arm in DS (Figure 6.2a, Table 6.4a), mental age did not (Figure 6.2b, Table 6.4b), CA: $R^2 = .38$, $F(1,11) = 6.59$, $p = .026$; MA: $R^2 = .17$, $F(1,11) = 2.32$, $p = .156$.

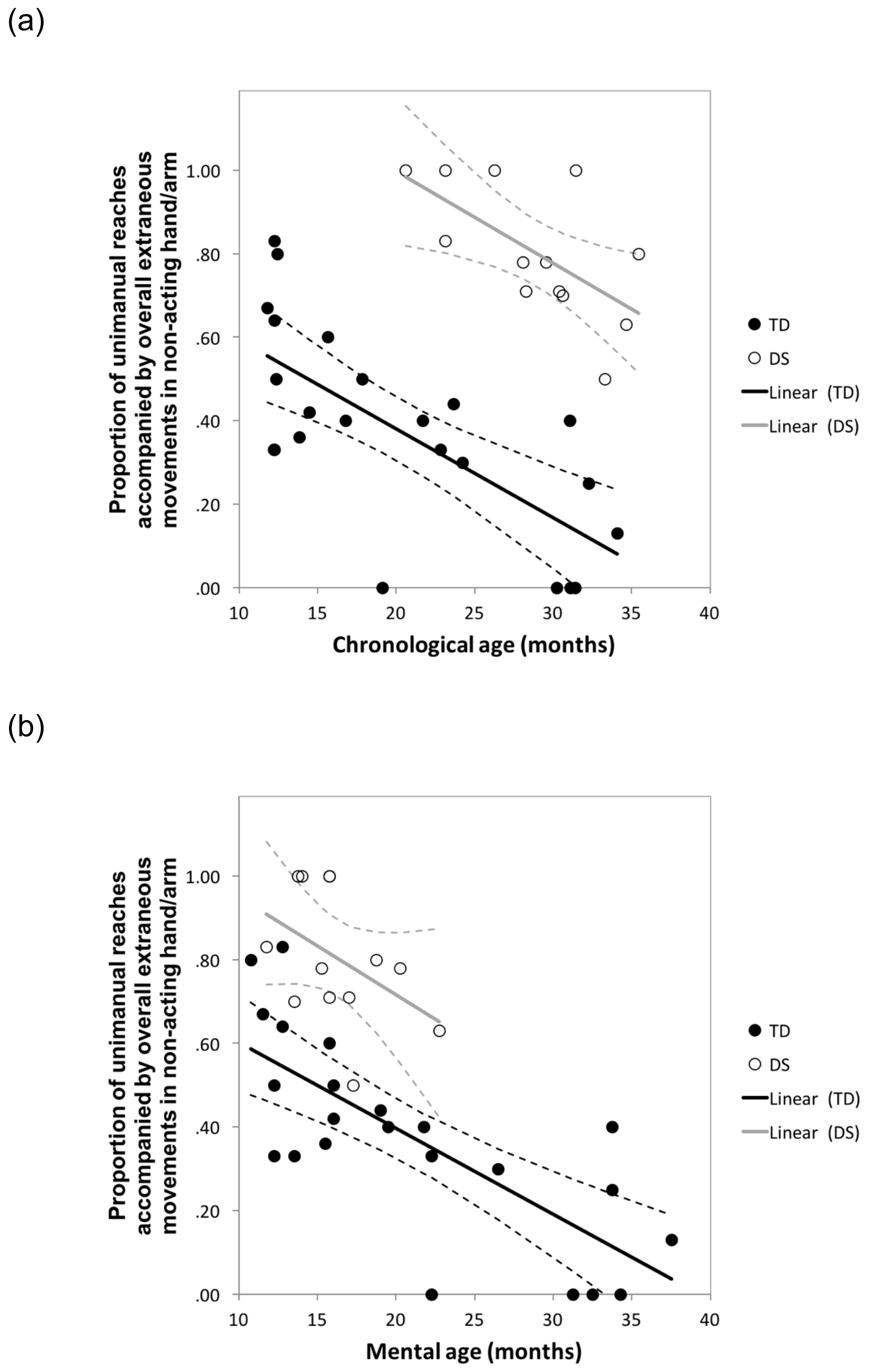


Figure 6.2. Proportion of unimanual reaches accompanied by overall extraneous movements in the non-acting hand/arm for typically developing children (TD) and children with Down syndrome (DS) plotted against: (a) chronological age; (b) mental age. Dashed lines represent 95% confidence intervals for the regression lines.

Table 6.4

Linear regression analysis predicting overall extraneous movements in the non-acting hand/arm from: (a) chronological age (CA); and (b) mental age (MA). Regressions were conducted separately for typically developing children (TD) and children with Down syndrome (DS).

(a)

	B	*SE B*	β
TD			
Constant	0.886	0.118	
CA	-0.024	0.005	-.694***
DS			
Constant	2.526	0.585	
CA	-0.051	0.020	-.612*

Note. TD: R^2 = .48 (p < .001); DS: R^2 = .38 (p = .026).
**p* < .050, ***p* < .010, ****p* < .001.

(b)

	B	*SE B*	β
TD			
Constant	0.886	0.105	
MA	-0.023	0.005	-.738***
DS			
Constant	1.917	0.583	
MA	-0.054	0.035	-.418

Note. TD: R^2 = .54 (p < .001); DS: R^2 = .17 (p = .156).
**p* < .050, ***p* < .010, ****p* < .001.

Comparing the DS and TD trajectories based on chronological age. The DS trajectory plotted against chronological age was compared with the TD trajectory plotted against chronological age using a general linear model predicting overall extraneous movements from chronological age with Group as a between-subject factor (Figure 6.2a). This model explained a significant proportion of variance, $F(3,32) = 26.35, p < .001, \eta_p^2 = .71$. As expected, there was a significant main effect of chronological age, $F(1,32) = 19.63, p < .001, \eta_p^2 = .38$, which indicates that across both groups, chronological age significantly predicts overall extraneous movements in the non-acting hand/arm. In other words, the greater the children's chronological age, the less overall extraneous movements in their non-acting hand/arm. Furthermore, in line with the group matched analysis above, there was a significant main effect of Group, $F(1,32) = 11.71$, $p = .002$, $\eta_p^2 = .27$. This indicates that the intercepts of the TD and DS groups were significantly different, with a higher intercept in the DS group. Thus, the DS group exhibits a delayed onset in development (M. S. C. Thomas et al., 2009). However, the gradient did not vary between groups because the interaction between Group and chronological age was not significant, $F(1,32) = 0.16$, $p = .116$, $\eta_p^2 = .08$. Thus, DS did not show a slower rate of development (M. S. C. Thomas et al., 2009).

Comparing the DS and TD trajectories based on mental age. The DS trajectory plotted against mental age was compared with the TD trajectory plotted against mental age using a general linear model predicting overall extraneous movements in the non-acting hand/arm from mental age with Group as a between-subject factor (Figure 6.2b). This model explains a significant proportion of the variance, $F(3,32) = 22.17$, $p < .001$, $\eta_p^2 = .68$. As expected, there was a significant main effect of mental age ($F(1,32) = 8.56$, $p = .006$, $\eta_p^2 = .21$) which indicates that, with both groups combined, mental age significantly predicts level of overall extraneous movements in the non-acting hand/arm. In other words, the greater the children's mental age, the less overall extraneous movements in their non-acting hand/arm. Furthermore, in line with the group matched analysis above, there was a significant main effect of Group, $F(1,32) = 5.35$, $p = .027$, $\eta_p^2 = .14$. This indicates that the intercepts of the two groups were significantly different in the DS group. The DS group therefore exhibits a delayed onset of development (M. S. C. Thomas et al., 2009). This suggests that even when mental age is taken into account, the DS group is still delayed in their developmental reduction of extraneous movements. However, as in the trajectory analysis built on chronological age, DS are not exhibiting a slower rate of development since there was no difference in gradient as indicated by a non-significant interaction between Group and mental age, $F(1,32) = 1.37$, $p = .251$, $\eta_p^2 = .041$.

6.2.3.2. Tightly linked extraneous movements in the non-acting hand/arm

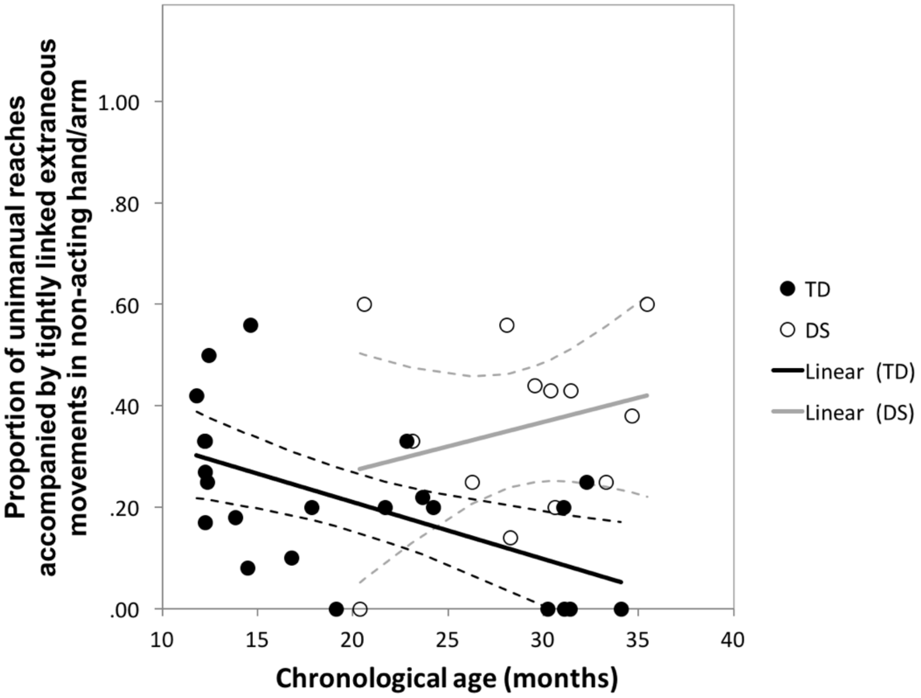
Comparing the DS group with the CA- and MA-matched groups. In order to investigate the presence of extraneous movements tightly linked to reach onsets, extraneous movements with an onset within a window of +/- 100 ms around reach onset (henceforth, ‘tightly linked extraneous movements’) were analysed. The CA-matched group produced tightly linked extraneous movements in the hand/arm in 13% of unimanual reaches (*SD* = 13%), the MA-matched group produced 28% (*SD* = 17%), and the DS group produced 35% (*SD* = 18%). DS showed significantly more tightly linked extraneous movements in the hand/arm than the CA- but not MA-matched group, $t(22) = 3.46$, $p = .002$, $d = 1.42$; $t(28) = 1.18$, $p = .247$, $d = 0.44$.

DS and TD developmental profiles. Figure 6.3 depicts developmental trajectories relating tightly linked extraneous movements in the hand/arm in the TD group and in the DS group according to chronological and mental age. Trajectories were initially explored separately by group to assess the developmental profile of each group before comparing them. In the TD group, there was a significant relationship between both chronological age (Figure 6.3a, Table 6.5a) as well as mental age (Figure 6.3b, Table 6.5b) and tightly linked extraneous movements in the hand/arm, CA: $R^2 = .32$, $F(1,21) = 9.76$, $p = .005$; MA: $R^2 = .39$, $F(1,21) = 13.21$, $p = .002$. Neither chronological (Figure 6.3a, Table 6.5a) nor mental age (Figure 6.3b, Table 6.5b) predicted tightly linked extraneous movements in DS, CA: $R^2 = .06$, $F(1,11) = 0.66$, $p = .433$; MA: $R^2 = .07$, $F(1,11) = 0.76$, $p = .402$.

Comparing DS and TD trajectories based on chronological age. The DS trajectory plotted against chronological age was compared with the TD trajectory plotted against chronological age using a general linear model predicting tightly linked extraneous movements from chronological age with Group as a between-subject factor (Figure 6.3a). This model explained a significant proportion of the variance, $F(3,32) = 5.27$, $p = .005$, $\eta_p^2 = .33$. There was no significant main effect. However, the interaction between chronological age and Group approached significance, $F(1,32) = 4.07$, $p = .052$, $\eta_p^2 = .11$. This hints that DS shows a slower rate of development than TD.

Comparing DS and TD trajectories based on mental age. The DS trajectory plotted against mental age was compared with the TD trajectory plotted against mental age using a general linear model predicting tightly linked extraneous movements from mental age with Group as a between-subject factor (Figure 6.3b). This model explains a significant proportion of variance, $F(3,32) = 6.17$, $p = .002$, $\eta_p^2 = .37$. There was no significant main effect. However, the interaction between mental age and Group approached significance, $F(1,32) = 3.24$, $p = .081$, $\eta_p^2 = .09$.

(a)



(b)

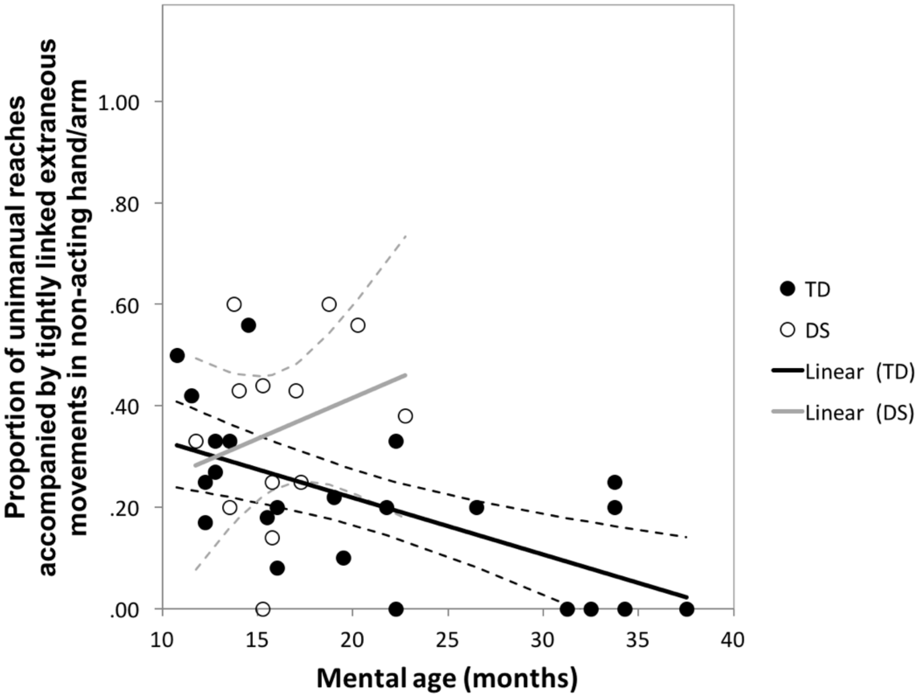


Figure 6.3. Proportion of unimanual reaches accompanied by tightly linked extraneous movements in non-acting hand/arm for typically developing children (TD) and children with Down syndrome (DS) plotted against: (a) chronological age; (b) mental age. Dashed lines represent 95% confidence intervals for the regression lines.

Table 6.5

Linear regression analysis predicting tightly linked extraneous movements in non-acting hand/arm from: (a) chronological age (CA); and (b) mental age (MA). Regressions were conducted separately for typically developing children (TD) and children with Down syndrome (DS).

(a)

	B	*SE B*	β
TD			
Constant	0.448	0.081	
CA	-0.012	0.004	-.563**
DS			
Constant	0.097	0.339	
CA	0.010	0.012	.238

Note. TD: $R^2 = .32$ ($p = .005$); DS: $R^2 = .06$ ($p = .433$).
**p* < .050, ***p* < .010, ****p* < .001.

(b)

	B	*SE B*	β
TD			
Constant	0.457	0.073	
MA	-0.012	0.003	-.621**
DS			
Constant	0.099	0.315	
MA	0.017	0.019	.254

Note. TD: $R^2 = .39$ ($p = .002$); DS: $R^2 = .07$ ($p = .402$).
**p* < .050, ***p* < .010, ****p* < .001.

This hints that DS still shows a slower rate of development than TD even when they are compared on mental age.

6.2.3.3. Overall extraneous movements in feet/legs

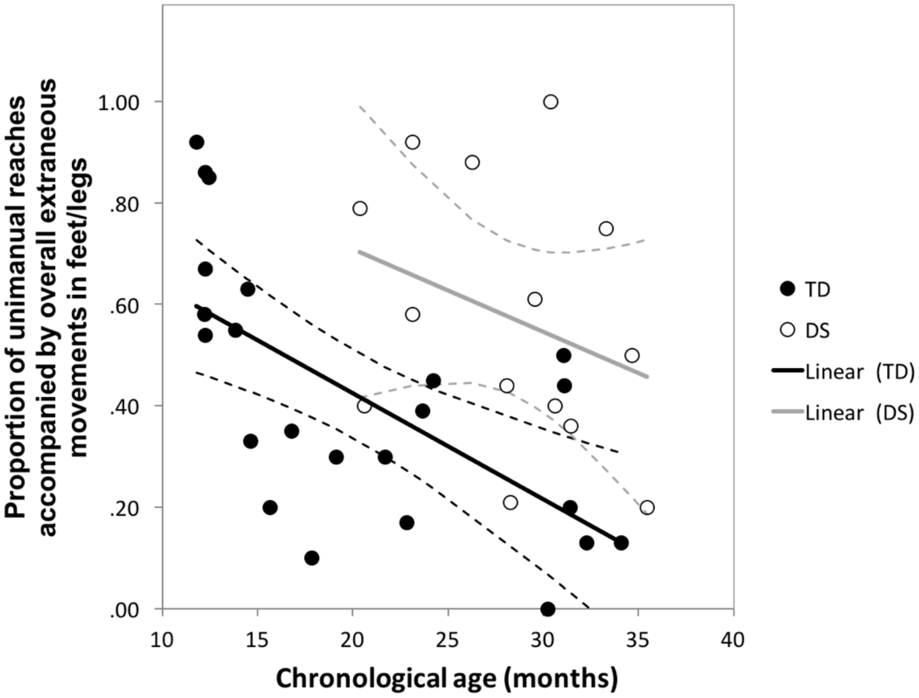
Comparing the DS group with the CA- and MA-matched groups. Overall extraneous movements in feet/legs were produced in 27% of unimanual reaches in the CA-matched group (*SD* = 16%), 51% in the MA-matched group (*SD* = 28%), and 57% in the DS group (*SD* = 26%). The DS group produced significantly more overall extraneous movements in feet/legs than the CA- but not MA-matched group, *t*(23) = 3.08, *p* = .005, *d* = 1.24; *t*(29) = 0.53, *p* = .597, *d* = 0.19.

DS and TD developmental profiles. Figure 6.4 depicts trajectories relating overall extraneous movements in feet/legs in the TD and DS groups to chronological age and mental age. Trajectories were initially analysed separately by group to assess the developmental profile of each group before comparing them. The TD cross-sectional developmental trajectory analysis revealed a significant relationship between overall extraneous movements in feet/legs and both chronological age (Figure 6.4a, Table 6.6a) as well as mental age (Figure 6.4b, Table 6.6b), CA: R^2 = .40, *F*(1,21) = 14.16, *p* = .001; MA: R^2 = .39, *F*(1,21) = 13.32, *p* = .001. This is an important addition to Study 1. The current finding goes beyond 12 months of age, showing a further developmental decrease of overall extraneous movements in feet/legs. Neither chronological age (Figure 6.4a, Table 6.6a) nor mental age (Figure 6.4b, Table 6.6b) predicted overall extraneous movements in the feet/legs in DS, CA: R^2 = .06, *F*(1,12) = 0.72, *p* = .412; MA: R^2 < .01, *F*(1,12) < 0.01, *p* = .946.

Comparing DS and TD trajectories based on chronological age. The DS trajectory plotted against chronological age was compared with the TD trajectory plotted against chronological age, using a general linear model predicting overall extraneous movements in feet/legs from chronological age, with Group as a between-subject factor (Figure 6.4a). This model explained a significant proportion of variance, *F*(3,33) = 4.82, *p* = .007, η_p^2 = .31. There was a significant main effect of chronological age (*F*(1,33) = 5.22, *p* = .029, η_p^2 = .14) which indicates that with the DS and TD groups combined, chronological age significantly predicts level of overall extraneous movements in feet/legs. In other words, the older the children become (in term of their chronological age), the fewer overall extraneous movements in their feet/legs. There was no other significant main effect or interaction.

Comparing DS and TD trajectories based on mental age. The DS trajectory plotted against mental age was compared with the TD trajectory plotted against mental age using a general linear model predicting overall extraneous movements in feet/legs from mental age with Group as a between-subject factor (Figure 6.4b). This model explains a significant proportion of variance, *F*(3,33) = 4.14, *p* = .014, η_p^2 = .27. However, no main effect or interaction was significant.

(a)



(b)

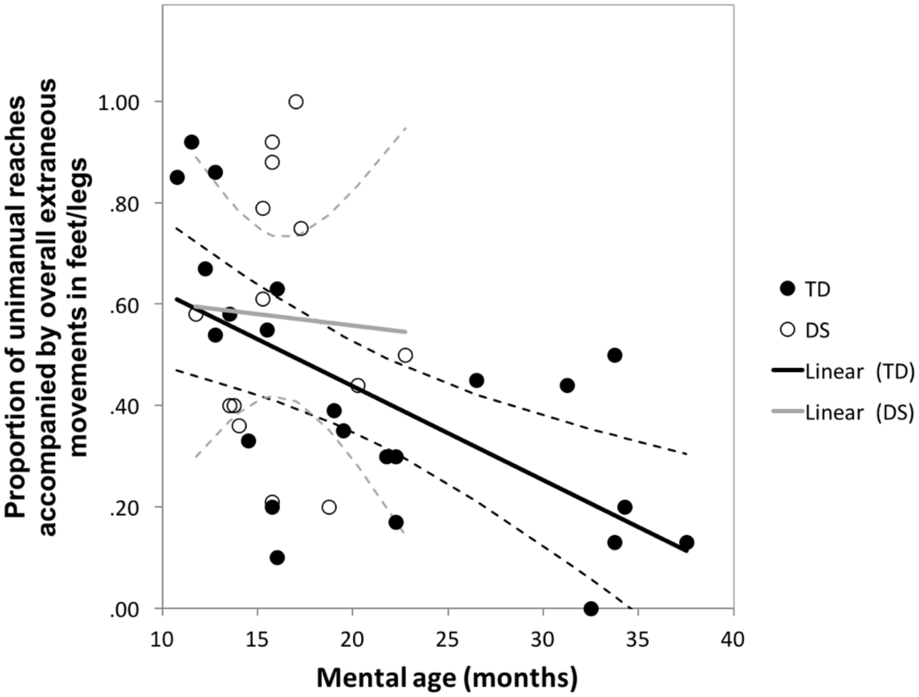


Figure 6.4. Proportion of unimanual reaches accompanied by overall extraneous movements in feet/legs for typically developing children (TD) and children with Down syndrome (DS) plotted against: (a) chronological age; (b) mental age. Dashed lines represent 95% confidence intervals for the regression lines.

Table 6.6

Linear regression analysis predicting overall extraneous movements in feet/legs from: (a) chronological age (CA); and (b) mental age (MA). Regressions were conducted separately for typically developing children (TD) and children with Down syndrome (DS).

(a)

	B	*SE B*	β
TD			
Constant	0.970	0.146	
CA	-0.025	0.007	-.635**
DS			
Constant	1.210	0.640	
CA	-0.019	0.022	-.239

Note. TD: $R^2 = .40$ ($p = .001$); DS: $R^2 = .06$ ($p = .412$).
*$p < .050$, **$p < .010$, ***$p < .001$.

(b)

	B	*SE B*	β
TD			
Constant	0.931	0.140	
MA	-0.023	0.006	-.623**
DS			
Constant	0.718	0.649	
MA	-0.003	0.039	-.020

Note. TD: $R^2 = .39$ ($p = .001$); DS: $R^2 < .01$ ($p = .946$).
*$p < .050$, **$p < .010$, ***$p < .001$.

6.2.3.4. Tightly linked extraneous movements in feet/legs

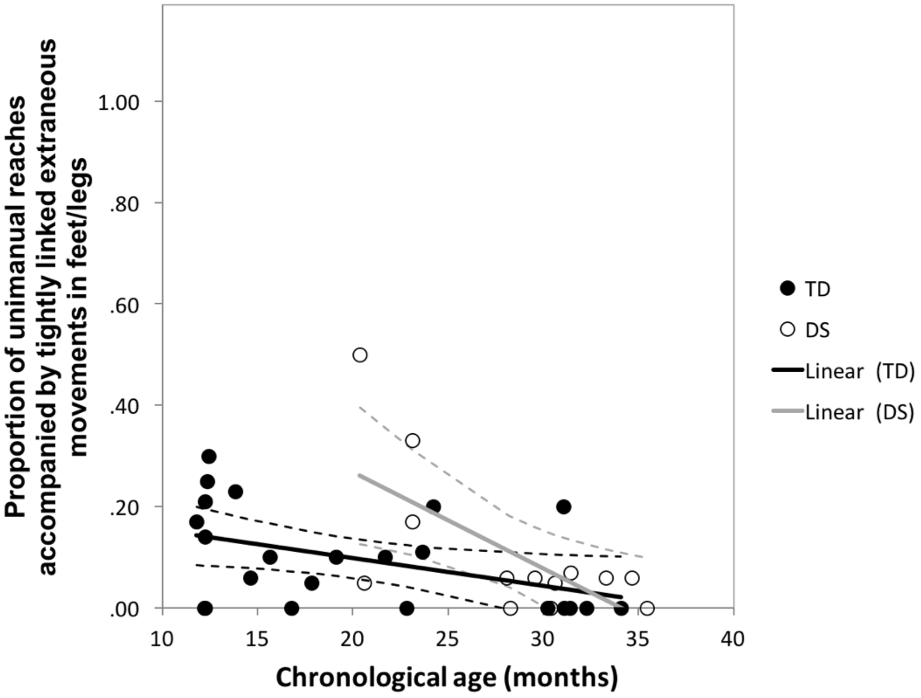
Comparing the DS group with the CA- and MA-matched groups. Tightly linked extraneous movements in the feet/legs were produced in 6% of unimanual reaches in the CA-matched group (*SD* = 8%), 11% in the MA-matched group (*SD* = 10%), and 11% in the DS group (*SD* = 15%). There was no significant difference between the DS and CA-matched groups or between the DS and MA-matched groups; DS vs. CA: $t(22) = 0.89$, $p = .386$, $d = 0.36$; DS vs. MA: $t(27) = -0.06$, $p = .950$, $d = 0.02$.

DS and TD developmental profiles. Figure 6.5 depicts developmental trajectories relating tightly linked extraneous movements in the feet/legs in the TD and DS groups according to chronological and mental age. Trajectories were initially analysed separately by group to assess the developmental profile of each group before comparing them. The TD cross-sectional developmental trajectory analysis revealed a significant relationship between tightly linked extraneous movements in feet/legs and both chronological (Figure 6.5a, Table 6.7a) as well as mental age (Figure 6.5b, Table 6.7b), CA: $R^2 = .19$, $F(1,21) = 4.94$, $p = .037$; MA: $R^2 = .19$, $F(1,21) = 4.99$, $p = .037$. This is an important addition to Study 1, which goes beyond 12 months of age, showing a further developmental decrease. In DS, chronological age (Figure 6.5a, Table 6.7a) predicted tightly linked extraneous movements in the feet/legs, but mental age (Figure 6.5b, Table 6.7b) did not, CA: $R^2 = .43$, $F(1,11) = 8.31$, $p = .015$; MA: $R^2 = .12$, $F(1,11) = 1.48$, $p = .250$.

Comparing DS and TD trajectories based on chronological age. The DS trajectory plotted against chronological age was compared with the TD trajectory plotted against chronological age using a general linear model predicting tightly linked extraneous movements in feet/legs from chronological age with Group as a between-subject factor (Figure 6.5a). This model explained a significant proportion of variance, $F(3,32) = 5.23$, $p = .005$, $\eta_p^2 = .33$. There was a significant main effect of chronological age ($F(1,32) = 15.43$, $p < .001$, $\eta_p^2 = .33$) which indicates that with the DS and TD groups combined, chronological age significantly predicts tightly linked extraneous movements in feet/legs. Furthermore, there was a significant main effect of Group, $F(1,32) = 6.88$, $p = .013$, $\eta_p^2 = .18$. This indicates that the intercepts of the TD and DS groups were significantly different, with a higher intercept in the DS group. Finally, the gradient between the groups was different, as indicated by a significant interaction between Group and chronological age, $F(1,32) = 4.99$, $p = .033$, $\eta_p^2 = .14$. However, using Cook's distances and depending on the exact procedure, up to three influential cases can be detected in the DS group. If these cases are removed, then the effects related to DS disappear.

Comparing DS and TD trajectories based on mental age. The DS trajectory plotted against mental age was compared with the TD trajectory plotted against mental age, using a general linear model predicting tightly linked extraneous movements in feet/legs from mental age, with Group as a between-subject factor

(a)



(b)

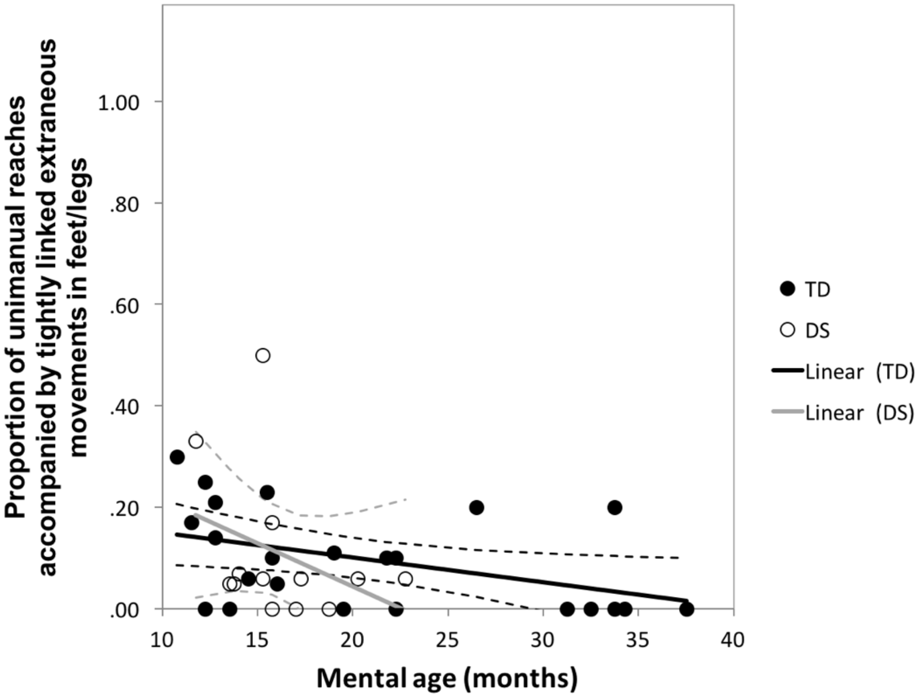


Figure 6.5. Proportion of unimanual reaches accompanied by tightly linked extraneous movements in feet/legs for typically developing children (TD) and Down syndrome (DS) plotted against: (a) chronological age; (b) mental age. Dotted lines represent 95% confidence intervals for the regression lines.

Table 6.7

Linear regression analysis predicting tightly linked extraneous movements in feet/legs from: (a) chronological age (CA); and (b) mental age (MA). Regressions were conducted separately for typically developing children (TD) and children with Down syndrome (DS).

(a)

	B	*SE B*	β
TD			
Constant	0.206	0.053	
CA	-0.005	0.002	-.436*
DS			
Constant	0.670	0.197	
CA	-0.020	0.007	-.656*

Note. TD: R^2 = .19 (p = .037); DS: R^2 = .43 (p = .015).
*p < .050, **p < .010, ***p < .001.

(b)

	B	*SE B*	β
TD			
Constant	0.199	0.050	
MA	-0.005	0.002	-.438*
DS			
Constant	0.397	0.239	
MA	-0.018	0.015	-.344

Note. TD: R^2 = .19 (p = .037); DS: R^2 = .12 (p = .250).
*p < .050, **p < .010, ***p < .001.

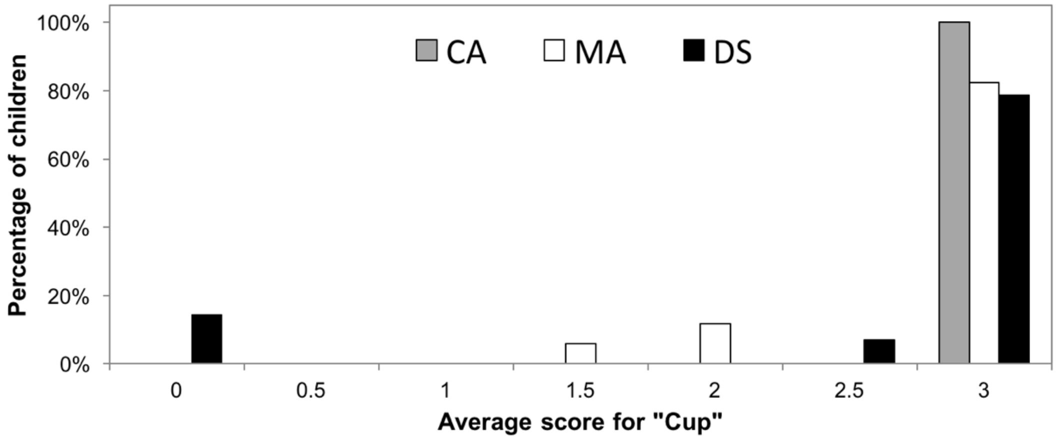
(Figure 6.5b). This model did not explain a significant proportion of variance, $F(3,32) = 1.92, p = .145, \eta_p^2 = .15$.

6.2.4. Intermanual coordination

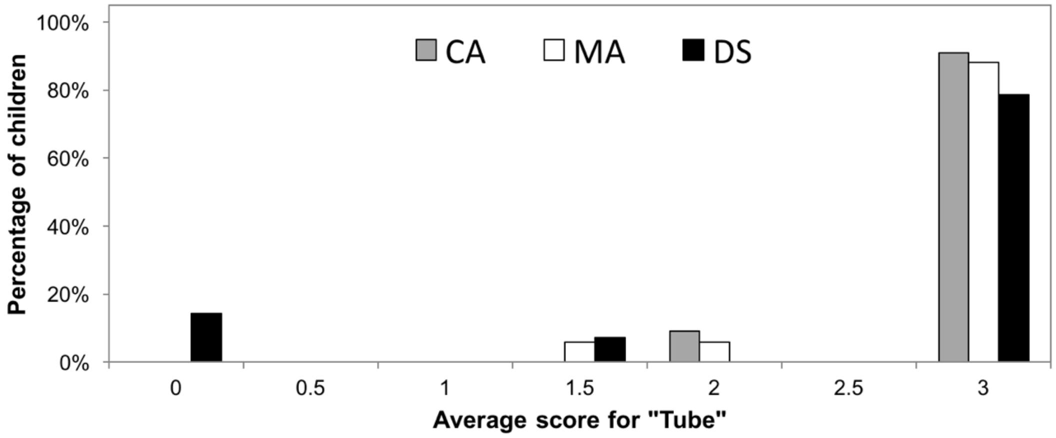
6.2.4.1. Individual items analysis

Figure 6.6 shows the distribution of average scores for each item in the intermanual coordination task. Since this is an ordinal variable, Fisher's exact tests were conducted for each of the items to analyse whether the distribution of average scores differed between the CA-matched and DS groups, and between the MA-

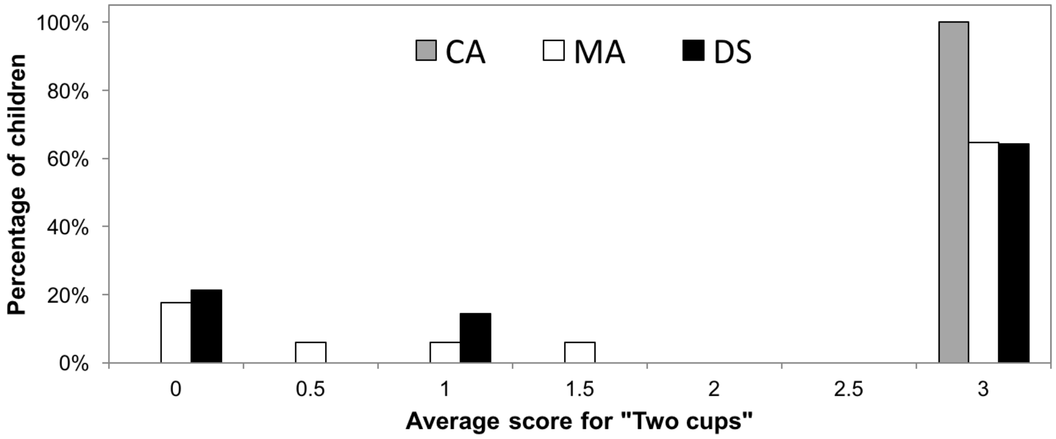
(a)


CA
MA
DS
Percentage of children
100%
80%
60%
40%
20%
0%
0
0.5
1
1.5
2
2.5
3
Average score for "Cup"

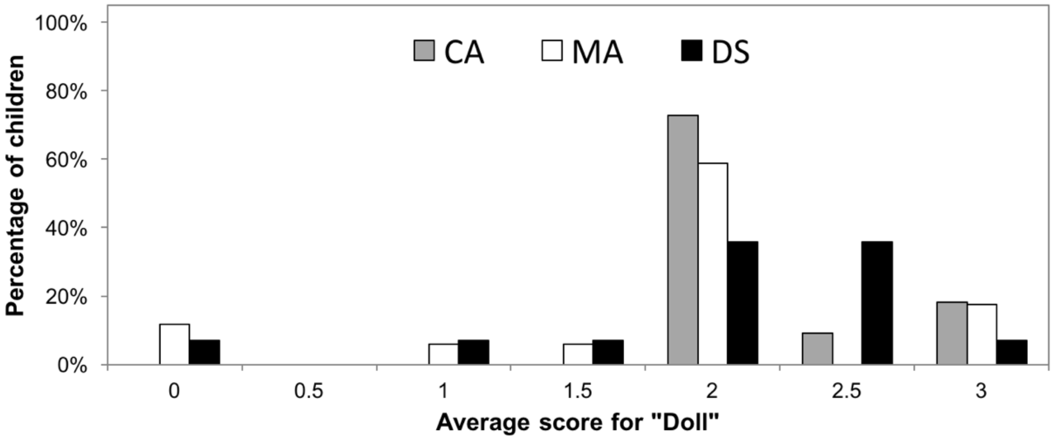
(b)


CA
MA
DS
Percentage of children
100%
80%
60%
40%
20%
0%
0
0.5
1
1.5
2
2.5
3
Average score for "Tube"

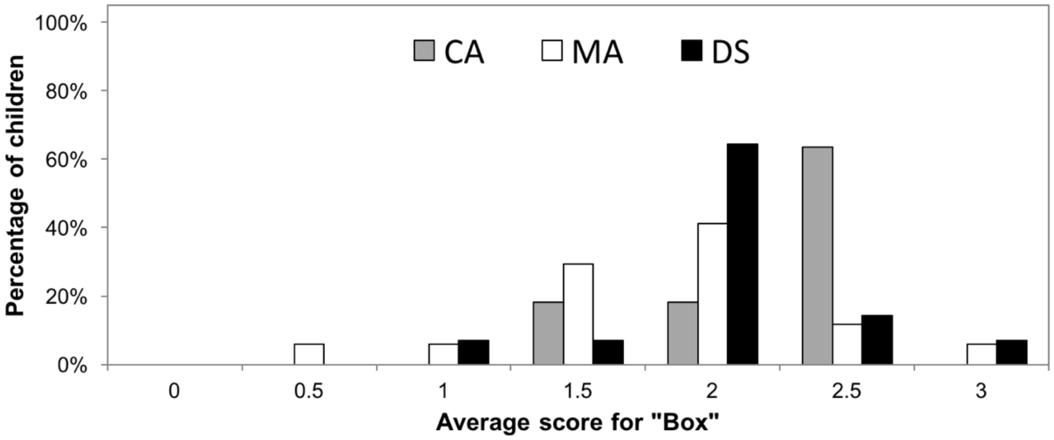
(c)


CA
MA
DS
Percentage of children
100%
80%
60%
40%
20%
0%
0
0.5
1
1.5
2
2.5
3
Average score for "Two cups"

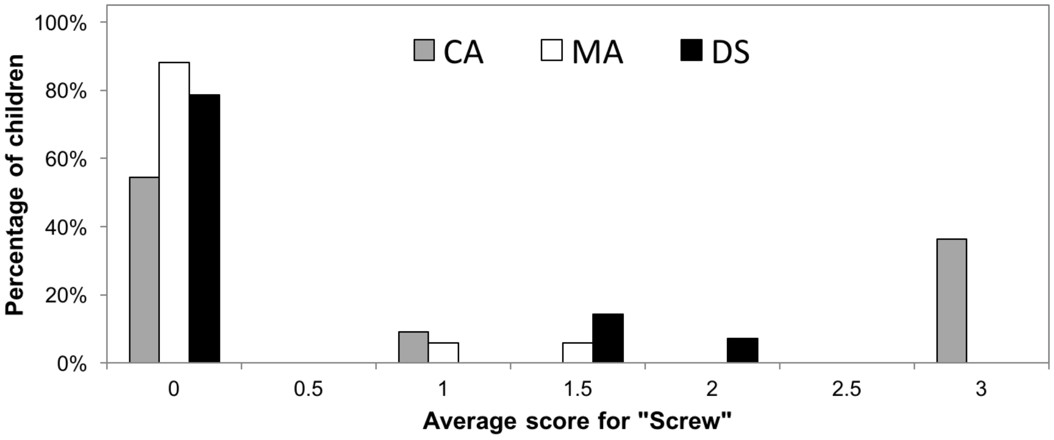
(d)


100%
80%
60%
40%
20%
0%
Percentage of children
CA
MA
DS
0
0.5
1
1.5
2
2.5
3
Average score for "Doll"

(e)


100%
80%
60%
40%
20%
0%
Percentage of children
CA
MA
DS
0
0.5
1
1.5
2
2.5
3
Average score for "Box"

(f)


100%
80%
60%
40%
20%
0%
Percentage of children
CA
MA
DS
0
0.5
1
1.5
2
2.5
3
Average score for "Screw"

(g)

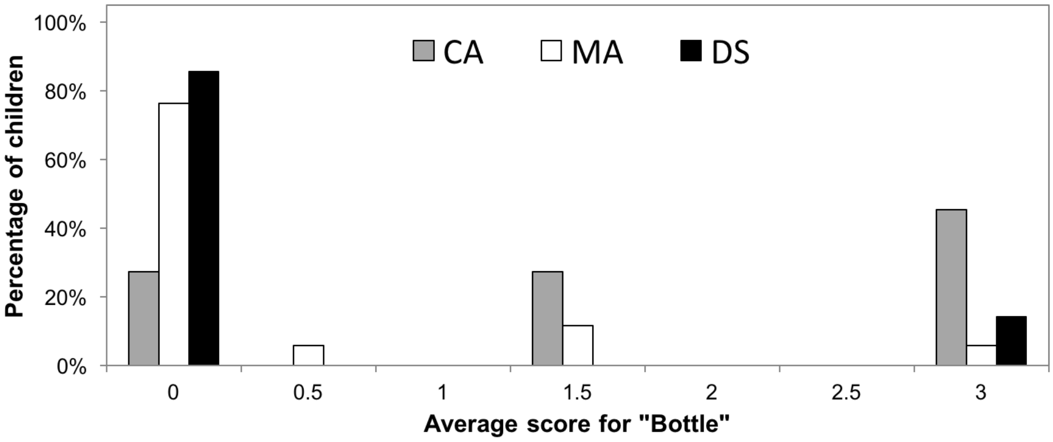


Figure 6.6. Distribution of average scores for each intermanual task in the chronological age matched group (CA), mental age matched group (MA), and Down syndrome group (DS). The intermanual tasks are: (a) Cup; (b) Tube; (c) Two cups; (d) Doll; (e) Box; (f) Screw; and (g) Bottle. The CA-matched group scored higher than the DS group in the last three items; i.e., (e) Box; (f) Screw; (g) Bottle. No differences were found between the MA and DS groups.

matched and DS groups. Fisher's exact test was used, because some of the cells contained fewer than five individuals. When the CA-matched group was compared to the DS group, there was no significant difference for the first four items (Cup: p = .487; Tube: p = .487; Two cups: p = .147; Doll: p = .199). However, significant differences were found on the last three items of the scale (Box: p = .023; Screw: p = .021; Bottle: p = .009). For the Box, based on residuals, more children from the DS group and fewer children from the CA-matched group reached a score of 2 than expected. Also, based on residuals, more children from the CA-matched group and fewer children from the DS group reached a score of 2.5 than expected. For the Screw, based on residuals, more children from the CA-matched group and fewer children from the DS group scored the maximum score (3) than expected. For the Bottle, based on residuals, more children from the DS group and fewer children from the CA-match group scored 0 than expected. Furthermore, again, based on residuals, more children from the CA-matched group and fewer children from the DS group scored 1.5 than expected. There was no significant difference in any of the items between the MA-matched and DS groups (Cup: p = .171; Tube: p = .435; Two cups: p = .958; Doll: p = .094; Box: p = .638; Screw: p = .555; Bottle: p = .607). Thus, for these intermanual tasks, the DS group performed at the level expected based on their mental age.

6.2.4.2. Overall intermanual coordination score

Comparing the DS group with the CA- and MA-matched groups.

Overall, the CA-matched group scored higher in the intermanual coordination (IMC) tasks ($M = 16.32$, $SD = 2.32$) than the DS group ($M = 11.89$, $SD = 3.53$), $t(23) = -3.59$, $p = .002$, $d = 1.44$. However, there was no difference in IMC scores between the DS and MA-matched groups ($M = 11.97$, $SD = 2.72$), $t(29) = -0.07$, $p = .945$, $d = 0.02$. These results are in line with the results of the individual item analysis presented above.

DS and TD developmental profiles. Figure 6.7 depicts developmental trajectories relating the IMC score in the TD group and in the DS group according to chronological and mental age. Trajectories were initially analysed separately by group to assess the developmental profile of each group before comparing them against each other. The TD cross-sectional developmental trajectory revealed a significant relationship between IMC score and chronological age (Figure 6.7a, Table 6.8a) as well as mental age (Figure 6.7b, Table 6.8b), CA: $R^2 = .73$, $F(1,22) = 59.93$, $p < .001$; MA: $R^2 = .70$, $F(1,22) = 52.44$, $p < .001$. Although chronological age predicted IMC score in DS (Figure 6.7a, Table 6.8a), mental age did not (Figure 6.7b, Table 6.8b), CA: $R^2 = .30$, $F(1,12) = 5.21$, $p = .041$; MA: $R^2 = .16$, $F(1,12) = 2.22$, $p = .162$.

Comparing DS and TD trajectories based on chronological age. The DS trajectory plotted against chronological age was compared with the TD trajectory plotted against chronological age, using a general linear model predicting IMC score from chronological age, with Group as a between-subject factor (Figure 6.7a). This model explains a significant proportion of variance, $F(3,34) = 16.89$, $p < .001$, $\eta^2 = .60$. As expected, there was a significant main effect of chronological age ($F(1,34) = 28.05$, $p < .001$, $\eta^2 = .45$) which indicates that with the DS and TD groups combined, chronological age significantly predicts IMC score. In other words, the older children become, the better their performance on the IMC task. There was no other main effect or interaction.

Comparing DS and TD trajectories based on mental age. The DS trajectory plotted against mental age was compared with the TD trajectory plotted against mental age, using a general linear model predicting IMC score from mental age, with Group as a between-subject factor (Figure 6.7b). This model explains a significant proportion of variance, $F(3,34) = 12.88$, $p < .001$, $\eta^2 = .53$. As expected,

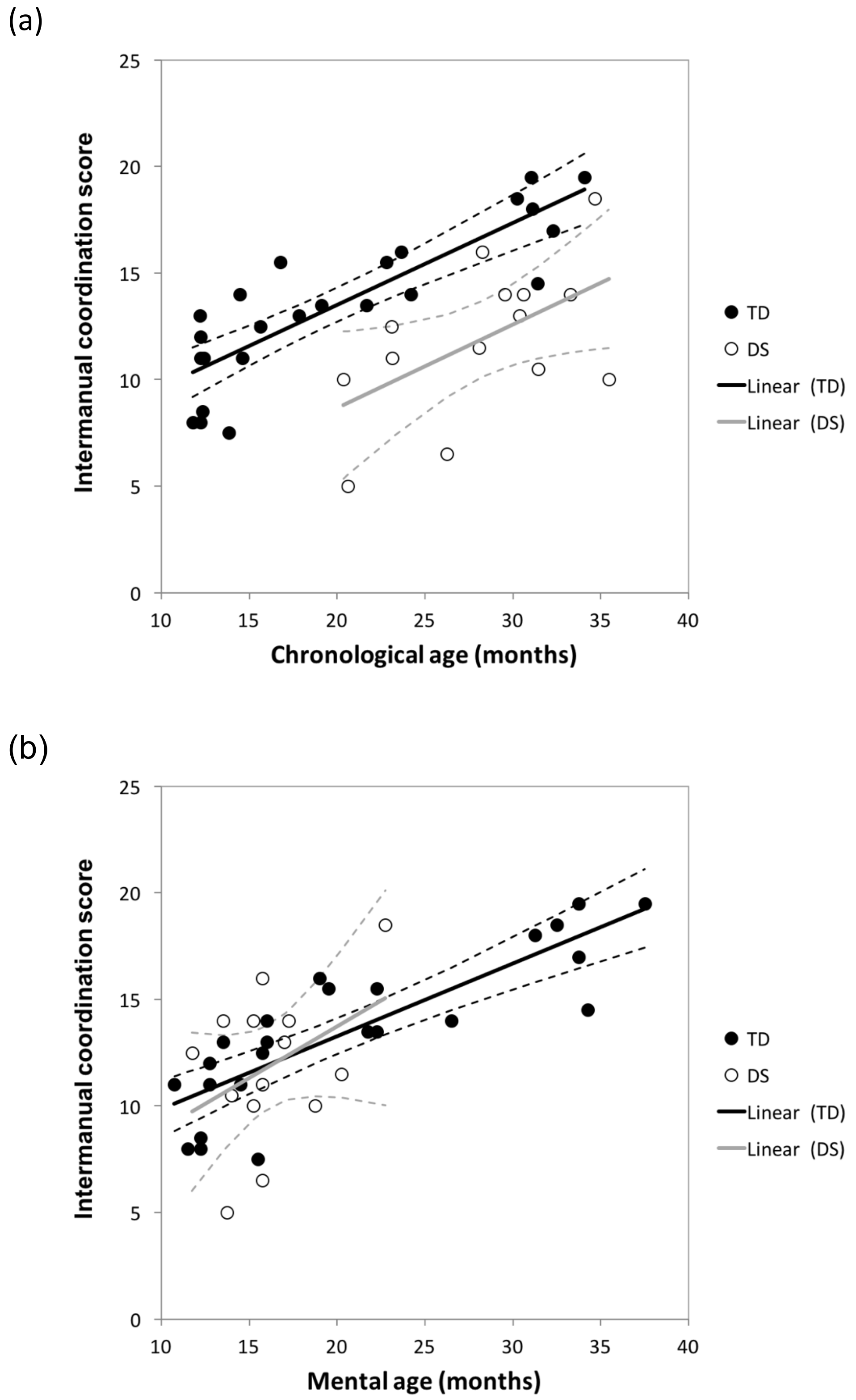


Figure 6.7. Intermanual coordination scores for typically developing children (TD) and children with Down syndrome (DS), plotted against: (a) chronological age; (b) mental age. Dashed lines represent 95% confidence intervals for the regression lines.

Table 6.8

Linear regression analysis predicting intermanual coordination from: (a) chronological age (CA); and (b) mental age (MA). Regressions were conducted separately for typically developing children (TD) and children with Down syndrome (DS).

(a)

	B	*SE B*	β
TD			
Constant	5.819	1.066	
CA	0.385	0.050	.855***
DS			
Constant	0.797	4.928	
CA	0.393	0.172	.550*

Note. TD: R^2 = .73 (p < .001); DS: R^2 = .30 (p = .041).
*p < .050, **p < .010, ***p < .001.

(b)

	B	*SE B*	β
TD			
Constant	6.423	1.060	
MA	0.342	0.047	.839***
DS			
Constant	4.043	5.340	
MA	0.485	0.325	.395

Note. TD: R^2 = .70 (p < .001); DS: R^2 = .16 (p = .162).
*p < .050, **p < .010, ***p < .001.

there was a significant main effect of mental age ($F(1,34) = 10.63$, $p = .003$, $\eta^2 = .24$) which indicates that with the DS and TD groups combined, mental age significantly predicts IMC score. In other words, the older children become in terms of their mental age, the better their intermanual coordination. There was no other significant main effect or interaction.

6.2.5. Extraneous movements and intermanual coordination

6.2.5.1. Overall extraneous movements in the non-acting hand/arm and age as predictors of intermanual coordination

Predicting intermanual coordination from overall extraneous movements in non-acting hand/arm and chronological age. Multiple regression analyses were conducted to evaluate which variables predict IMC score. In the initial set of regressions, I evaluated whether chronological age and overall extraneous movements in the non-acting hand/arm predicted IMC score in the TD and DS groups. The groups were initially analysed separately to assess the developmental profile of each group before comparing them. Using the Enter method, it was found that the linear combination of chronological age and overall extraneous movements in the non-acting hand/arm explained a significant amount of variance in the IMC score in both TD and DS groups, TD: $R^2 = .73$, $F(2, 20) = 27.19$, $p < .001$; DS: $R^2 = .62$, $F(2, 10) = 8.22$, $p = .008$. In TD, chronological age made a significant contribution to the prediction equation, while overall extraneous movements in the non-acting hand/arm did not (see Table 6.9). The opposite pattern emerged in the DS group. In DS, overall extraneous movements in the non-acting hand/arm made a significant contribution to the prediction equation, whereas chronological age did not (see Table 6.9). Thus, the fewer overall extraneous movements participants with DS produced, the better they were in intermanual coordination.

To assess whether the models predicting IMC in the TD and DS groups significantly differed, a general linear model was used to predict IMC score from chronological age, overall extraneous movements in the non-acting hand/arm, and Group. This model explains a significant proportion of variance, $F(5,30) = 14.20$, $p < .001$, $\eta^2 = .70$. There was a significant main effect of chronological age ($F(1,30) = 13.11$, $p = .001$, $\eta^2 = .30$), which indicates that with the DS and TD groups combined, CA significantly predicts IMC score. In other words, the older children become (the greater their chronological age), the better they are at intermanual coordination. There was no other significant main effect. The three-way interaction between Group, chronological age, and overall extraneous movements in the non-acting hand/arm was significant, $F(2,30) = 3.36$, $p = .048$, $\eta^2 = .18$. This confirms that the relationships between extraneous movements, chronological age, and IMC scores described in Table 6.9 were significantly different across groups. Whereas chronological age predicted IMC in the TD group, overall extraneous movements in the non-acting hand/arm were the significant predictor in the DS group.

Table 6.9

Multiple regression analysis (Enter method) predicting intermanual coordination from chronological age (CA) and overall extraneous movements in the non-acting hand/arm (Overall extra mov hand). Regressions were conducted separately for typically developing children (TD) and children with Down syndrome (DS).

	B	*SE B*	β
TD			
Constant	4.722	2.175	
CA	0.414	0.072	.921***
Overall extra mov hand	1.301	2.097	.100
DS			
Constant	16.694	7.393	
CA	0.084	0.195	.106
Overall extra mov hand	-6.789	2.322	-.719*

Note. TD: R^2 = .73 (p < .001); DS: R^2 = .62 (p = .008).
*p < .050, **p < .010, ***p < .001.

Predicting intermanual coordination from overall extraneous movements in the non-acting hand/arm and mental age. A series of multiple regression analyses was conducted to evaluate which variables predict IMC score. In the initial set of regressions, I evaluated whether mental age and overall extraneous movements in the non-acting hand/arm predicted IMC score in the TD and DS groups. The groups were initially analysed separately to assess the developmental profile of each group before comparing them. Using the Enter method, it was found that the linear combination of mental age and overall extraneous movements in the non-acting hand/arm explained a significant amount of variance in IMC in both TD and DS, TD: $R^2 = .71$, $F(2, 20) = 24.62$, $p < .001$; DS: $R^2 = .62$, $F(2, 10) = 8.12$, $p = .008$. As Table 6.10 shows, in TD, mental age made a significant contribution to the prediction equation, while overall extraneous movements in the non-acting hand/arm did not. The opposite pattern emerged in the DS group. In DS, overall extraneous movements in the non-acting hand/arm made a significant contribution to the prediction equation whereas mental age did not. Thus, the fewer overall extraneous movements participants with DS produced, the better they were in intermanual coordination.

To assess whether the models predicting IMC in the TD and DS groups significantly differed, a general linear model was used to predict IMC score from mental age, overall extraneous movements in the non-acting hand/arm, and Group. This model explains a significant proportion of variance, $F(5,30) = 14.35, p < .001, \eta^2 = .71$. There was a significant main effect of mental age ($F(1,30) = 15.01, p = .001, \eta^2 = .33$) which indicates that with the DS and TD groups combined, mental age significantly predicts IMC score. In other words, the older children get in terms of their mental age, the better they are at intermanual coordination. There was a significant main effect of Group ($F(1,30) = 12.77, p = .001, \eta^2 = .30$), indicating that IMC score differs across groups. The three-way interaction between Group, mental age, and overall extraneous movements in the non-acting hand/arm was significant, $F(2,30) = 5.41, p = .010, \eta^2 = .27$. This confirms that the relationships between extraneous movements, mental age, and IMC scores described in Table 6.10 were significantly different across groups. Whereas mental age predicted IMC in the TD group, overall extraneous movements in the non-acting hand/arm was the significant predictor in the DS group.

Table 6.10

Multiple regression analysis (Enter method) predicting intermanual coordination from mental age (MA) and overall extraneous movements in the non-acting hand/arm (Overall extra mov hand). Regressions were conducted separately for typically developing children (TD) and children with Down syndrome (DS).

	B	*SE B*	β
TD			
Constant	4.519	2.337	
MA	0.392	0.073	.960***
Overall extra mov hand	2.202	2.319	.169
DS			
Constant	18.017	5.523	
MA	0.088	0.261	.072
Overall extra mov hand	-7.114	2.028	-.754**

Note. TD: $R^2 = .71$ ($p < .001$); DS: $R^2 = .62$ ($p = .008$).
*$p < .050$, **$p < .010$, ***$p < .001$.

6.2.5.2. Tightly linked extraneous movements in the non-acting hand/arm and age as predictors of intermanual coordination

Predicting intermanual coordination from tightly linked extraneous movements in the non-acting hand/arm and chronological age. Multiple regression analyses were conducted to evaluate which variables predict IMC score. In the initial set of regressions, it was evaluated whether chronological age and tightly linked extraneous movements in the non-acting hand/arm predicted IMC score in the TD and DS groups. The groups were initially analysed separately to assess the developmental profile of each group before comparing them. Using the Enter method, it was found that the linear combination of chronological age and tightly linked extraneous movements in the non-acting hand/arm explained a significant amount of variance in IMC in both TD and DS groups, TD: $R^2 = .73$, $F(2, 20) = 27.41$, $p < .001$; DS: $R^2 = .49$, $F(2, 10) = 4.83$, $p = .034$. As Table 6.11 shows, in both groups, chronological age made a significant contribution to the prediction equation, while tightly linked extraneous movements in the non-acting hand/arm did not (Table 6.11).

Table 6.11

Multiple regression analysis (Enter method) predicting intermanual coordination from chronological age (CA) and tightly linked extraneous movements in the non-acting hand/arm (Tightly extra mov hand). Regressions were conducted separately for typically developing children (TD) and children with Down syndrome (DS).

	B	*SE B*	β
TD			
Constant	6.040	1.781	
CA	0.379	0.063	.839***
Tightly extra mov hand	-0.654	3.065	-.030
DS			
Constant	0.905	4.899	
CA	0.493	0.173	.660*
Tightly extra mov hand	-8.229	4.341	-.440

Note. TD: $R^2 = .73$ ($p < .001$); DS: $R^2 = .49$ ($p = .034$).
*$p < .050$, **$p < .010$, ***$p < .001$.

To assess whether the models predicting IMC in the TD and DS groups significantly differed, a general linear model was used to predict IMC score from chronological age, overall extraneous movements in the non-acting hand/arm, and Group. This model explains a significant proportion of variance, $F(5,30) = 11.17$, $p < .001$, $\eta^2 = .65$. There was a significant main effect of chronological age ($F(1,30) = 15.61$, $p < .001$, $\eta^2 = .34$), which indicates that with the DS and TD groups combined, chronological age significantly predicts IMC score. In other words, the older children get (the greater their chronological age), the better they are at intermanual coordination. No other main effect was significant. Nor was there a three-way interaction between Group, chronological age, and tightly linked extraneous movements in the non-acting hand/arm.

Predicting intermanual coordination from tightly linked extraneous movements in the non-acting hand/arm and mental age. Multiple regression analyses were conducted to evaluate which variables predict IMC score. In the initial set of regressions, I evaluated whether mental age and tightly linked extraneous movements in the non-acting hand/arm predicted IMC score in the TD and DS groups. The groups were initially analysed separately to assess the developmental profile of each group before comparing them. Using the Enter method, it was found that the linear combination of mental age and tightly linked extraneous movements in the non-acting hand/arm explained a significant amount of the variance of IMC in the TD group, but not in the DS group, TD: $R^2 = .71$, $F(2, 20) = 23.98$, $p < .001$; DS: $R^2 = .31$, $F(2, 10) = 2.27$, $p = .154$. As Table 6.12 shows, in the TD group, mental age made a significant contribution to the prediction equation, while tightly linked extraneous movements in the non-acting hand/arm did not (Table 6.12).

To assess whether the models predicting IMC in the TD and DS groups significantly differed, a general linear model was used to predict IMC score from mental age, overall extraneous movements in the non-acting hand/arm, and Group. This model explains a significant proportion of variance, $F(5,30) = 7.85$, $p < .001$, $\eta^2 = .57$. There was a significant main effect of mental age ($F(1,30) = 8.78$, $p = .006$, $\eta^2 = .23$), which indicates that with the DS and TD groups combined, mental age significantly predicts IMC score. No other main effect was significant. Nor was the three-way interaction between Group, mental age, and tightly linked extraneous movements in the non-acting hand/arm.

Table 6.12

Multiple regression analysis (Enter method) predicting intermanual coordination from mental age (MA) and tightly linked extraneous movements in the non-acting hand/arm (Tightly extra mov hand). Regressions were conducted separately for typically developing children (TD) and children with Down syndrome (DS).

	B	*SE B*	β
TD			
Constant	6.032	1.917	
MA	0.352	0.063	.859***
Tightly extra mov hand	0.694	3.392	.032
DS			
Constant	4.899	5.315	
MA	0.609	0.332	.498
Tightly extra mov hand	-7.654	5.069	-.410

Note. TD: $R^2 = .71$ ($p < .001$); DS: $R^2 = .31$ ($p = .154$).
*$p < .050$, **$p < .010$, ***$p < .001$.

6.3. Discussion

This study contributes to our knowledge in four ways. Firstly, it extends the findings from Study 1 of this thesis (Chapter 2), demonstrating that extraneous movements during unimanual reaching continue to decrease over development between 1 and 3 years of age. Secondly, it contributes to the literature on the atypical development of extraneous movement, showing increased extraneous movements in infants and toddlers with DS compared to TD children. This is in line with my hypothesis that infants and toddlers with DS show delay in motor specialization. The DS group showed aggravated extraneous movements, not only in comparison with TD children of the same chronological age, but also with TD children of the same mental age. In other words, children with DS show more extraneous movements than expected for their developmental level. Thirdly, as expected, this study showed that children with DS are delayed in intermanual coordination (IMC). Finally, extraneous movements in the non-acting hand/arm predicted IMC, but only in the DS group. I will now discuss these contributions in more detail.

The analysis of cross-sectional developmental trajectories went beyond group statistics and revealed new insights. For typically developing children, decrease of extraneous movements was associated with age (both chronological and mental).

This relationship was strong across all types of extraneous movements. This is an important finding which further extends Study 1 of this thesis (Chapter 2) which showed that extraneous movements decrease between 9 and 12 months of age. Using an identical reaching task, the current study shows that extraneous movements continue to decrease after 12 months of age with children around 3 years of age producing unimanual reaches often without the activation of non-acting limbs. This finding also provides an important bridge between Study 1, which investigated 9- and 12-month-olds, and studies investigating extraneous movements in older children and adults (Addamo et al., 2007; Gasser, Rousson, Caflisch, & Jenni, 2010; Largo et al., 2001; P. H. Wolff, Gunnoe, & Cohen, 1983). How does the high degree of motor specialization in older TD toddlers in the current study fit with findings in the literature that report extraneous movements in older children? To explain this discrepancy, it is important to consider the activities children are engaged in when exhibiting extraneous movements, and how these activities vary across studies. In this thesis, the movements young children were required to perform were unimanual reaches. Infants start reaching very early in development (at around 4 months of age; Spencer & Thelen, 2000). It is an action that children practice extensively from the time of its emergence (A. C. de Campos et al., 2013). This is arguably because reaching is crucial for efficient interaction with the environment. Therefore, a high degree of specialization by toddlerhood for unimanual reaching is to be expected. In contrast, studies with older children and adolescents often induce extraneous movements by using actions that are challenging to perform (Connolly & Stratton, 1968; Gasser et al., 2010; P. H. Wolff et al., 1983). For example, Largo et al. (2001) conducted a large scale cross-sectional study of around 660 children from 5 to 18 years of age. The children were asked to perform actions of various complexity including repetitive, alternating, or sequential movements. The developmental changes in extraneous movements were described as a function of the complexity of the motor task. The extraneous movements decreased earlier for repetitive actions, which are relatively easy to perform, and later for more challenging actions including alternating and sequential movements. Therefore, when charting developmental trajectories of extraneous movements, it is important to consider what actions participants were asked to perform. The timing of specialization for different actions may differ depending on their complexity. This also highlights the importance of always including an appropriate control group when drawing conclusions about an atypically developing group.

The cross-sectional developmental trajectories analysis revealed differential relationships between chronological and mental age and the experimental measures in the typically developing and Down syndrome groups. In the typically developing group, extraneous movements in the hand/arm and feet/legs were negatively linked to both chronological and mental age. This is to be expected since chronological and mental age are strongly correlated with each other in TD participants. However, in the DS group, only a relationship with chronological (but not mental) age was observed. Although this result needs to be replicated with a larger sample and broader age range, one could take this as evidence of maturational processes underlying the decrease in extraneous movements in DS. However, a purely maturational account of the development of motor specialization in DS would seem to fly in the face of multiple demonstrations of the importance of experiential factors in motor development in typically developing children (Study 1 of this thesis; Adolph et al., 2009, 1998, 2003; D. Corbetta & Bojczyk, 2002; Fogel, 1992; Fogel et al., 1992; Libertus & Needham, 2010; Lobo & Galloway, 2008). An alternative explanation is that the negative correlation between extraneous movements and chronological age may, at least partially, reflect the *amount* of motor experience participants have had. In previous studies, infants with DS were found to generate less spontaneous (Lloyd et al., 2010; Mazzone et al., 2004; McKay & Angulo-Barroso, 2006; B. D. Ulrich & Ulrich, 1995) and object oriented (A. C. de Campos et al., 2013; Frazier & Friedman, 1996; Mizuno & Ueda, 2001) activity, which is likely to protract or alter the specialization of their motor system. It is likely that the older infants with DS were able to accumulate more experience with their environment (even though it may not have been as much or as relevant as the motor experience accumulated by the typically developing children, hence the delay) than the younger infants with DS in this study—just because they have had more opportunity. This may be why chronological age was associated with a decrease in extraneous movements. This hypothesis can be tested in the future by examining the relationship between experience with various motor skills and extraneous movements in infants and toddlers with Down syndrome. I attempted to gather this information for the current study. However, in contrast with Study 1 (Chapter 2) where the motor milestones I asked about were relatively recent achievements considering the fact that the participants were no older than 12 months of age, the parents in the current study struggled to pinpoint retrospectively when in development various milestones appeared (the oldest child in this study was around 3 years of age). Thus, the parents were unable to recall the onset of various motor milestones with confidence. In order to reliably capture when various milestones emerge, children should be tracked longitudinally in a future study. Future studies could also assess whether providing children with Down syndrome with early intervention promoting reaching (Libertus, Joh, & Needham, 2015; Libertus & Needham, 2010; Williams et al., 2015) leads to a decrease of extraneous movements. Finally, intervention studies promoting crawling and walking could also provide insight into motor specialization for unimanual reaching in infants and toddlers with Down syndrome, since Study 1 of this thesis (Chapter 2) found that locomotion experience is linked to a decrease in extraneous movements in feet/legs during unimanual reaching in 9- and 12-month-olds.

How does the development of extraneous movements differ between typically developing and Down syndrome groups? The cross-sectional developmental trajectory analysis provides insight into whether the developmental trajectories are delayed or atypical. Differences between the developmental trajectories of the two types of extraneous movements in the non-acting hand/arm (overall vs. tightly linked) are of interest. For overall extraneous movements in the non-acting hand/arm, the developmental trajectory in the Down syndrome group was found to be delayed but similar to the typically developing trajectory in its rate of change. However, for extraneous movements in the non-acting hand/arm that are tightly linked to the onset of the reach, the rate of development was slowed. In this case, no developmental change was detected in the production of tightly linked extraneous movements in Down syndrome in this study. Although this result needs to be replicated with a larger sample and broader age range, it suggests that extraneous movements accompanying the initiation of a movement are more pervasive over development. Why would this be the case? As was pointed out above, previous studies have shown that children with Down syndrome interact less with the environment than typically developing children (A. C. de Campos et al., 2013; Frazier & Friedman, 1996; Mizuno & Ueda, 2001). Less interaction with the environment was suggested to protract and alter specialization (M. H. Johnson et al., 2015). This is indeed in line with findings from the current study that infants and toddlers with Down syndrome show aggravated overall extraneous movements in the non-acting hand/arm, not only compared to typically developing children of the same chronological age, but also typicaly developing children on the same developmental level.

One possible explanation for the developmental delay in overall extraneous movements in the non-acting hand/arm and pervasiveness of tightly linked extraneous movements in non-acting hand/arm is that children with DS may be generating a lot of activity that, in fact, fosters the coupling of limbs. For example, some children with DS use a ‘symmetrical’ strategy (i.e., they move their limbs symmetrically along the body midline) to lift themselves up from a prone position into a sitting position which involves doing the splits (Lydic & Steele, 1979). This was proposed to be a compensatory movement strategy arising from a lack of trunk rotation due to hypotonia and hypermobility of joints (Åkerström & Sanner, 1993; Kugel, 1970) or reduced posture reactions (balance and self-righting; Haley, 1986). Infants and toddlers with Down syndrome have also been reported to use a symmetrical strategy when rising up from the floor into a standing position; they tend to simultaneously use both hands and both feet to provide maximum support (Lauteslager, 1995). Furthermore, from my personal observations, young children with DS often use alternative locomotion strategies to crawl before they learn to walk. I have frequently noticed children with Down syndrome ‘bum-shuffle’, i.e., sitting and pushing themselves around by their lower or upper and lower limbs. This, again, presents a symmetrical locomotor strategy (limbs moving symmetrically along the body midline), in contrast to crawling, which is a reciprocal locomotion strategy (limbs producing alternating movements along the body midline).

If infants with DS employ symmetrical strategies across a variety contexts, this may lead to a reduced sensorimotor experience of differentiated hands. In other words, I would like to propose that the symmetrical strategies that children with Down syndrome use to compensate for problems with balance and low muscle tone may potentially impact manual strategies even when these children are reaching in a stable sitting posture. This proposal is commensurate with the *transfer of learning* account (D. Corbetta & Bojczyk, 2002; D. Corbetta et al., 2014), according to which limb use during one activity can transfer to other limbs in a different context. The most extensively studied example of this is the increase of two-handed reaching which, in typically developing children, occurs toward the end of the first year of life when infants are learning to walk (Babik et al., 2014; Berger, Friedman, & Polis, 2011; D. Corbetta & Bojczyk, 2002). Novice walkers hold their arms high to control their balance when stepping (D. Corbetta & Bojczyk, 2002; Kubo & Ulrich, 2006). Studies have shown that the coupling of arms during early walking impacts reaching, leading to increases in bimanual reaching (D. Corbetta & Bojczyk, 2002). How would early walking impact reaching? When infants attain a new skill, they show extensive practice of it (Adolph et al., 2012). Thus, when infants start walking, they practice walking a lot and, as mentioned above, early walkers hold their arms in high guard. Therefore, these early walkers spend a lot of time with their upper limbs coupled, which is reflected in organizational changes at the level of the brain, leading to more coupling at homologous prefrontal/central scalp locations in early walkers compared to pre-walkers and experienced walkers (D. Corbetta et al., 2014). If infants with Down syndrome use a number of symmetrical strategies across various contexts, it is possible that they subsequently have difficulties decoupling their limbs when the context requires them to do so – i.e., due to experience-driven neural reorganization or lack thereof. This may constrain motor specialization, potentially affecting the development of other skills. This may explain why increased extraneous movements in the non-acting hand/arm were identified in the children with Down syndrome in this study.

The transfer of symmetrical strategies across contexts could also explain why infants with DS perform poorly on intermanual coordination tasks relative to controls matched on chronological age. However, in contrast with the results of the extraneous movements analysis, the scores on the intermanual coordination scale used in this study did not differ between the mental age matched group and the Down syndrome group. This suggests that the Down syndrome group show intermanual coordination skills at the level expected for children of their mental age. Yet, some caution needs to be taken before we can reach that conclusion. Future studies should investigate the exact extent to which each limb is engaged in intermanual coordination and the precise timings of actual movements (as in Britles et al., 2011). Many of the strategies that children with DS use are revealed to be atypical when put under detailed scrutiny (e.g., as discussed above, although children with Down syndrome can sit up, many of them do it in an atypical way [‘doing the splits’]).

It is important to note that although the symmetrical motor strategies used by individuals with Down syndrome may negatively impact their motor specialization, it is possible that they are an adaptive solution for the atypically developing system. Many processes across various levels of description are altered in Down syndrome. For example, abnormalities in the cerebellum and brain stem are related to hypotonus in DS (Åkerström & Sanner, 1993; Dierssen, 2012; Kugel, 1970). Furthermore, infants with Down syndrome have been reported to have overall fewer neurons than typically developing children, as well as altered synapses (Schmidt-Sidor et al., 1990; Takashima et al., 1981; Wisniewski, 1990; Wisniewski et al., 1986; Wisniewski & Schmidt-Sidor, 1989). This may constrain the ability of young children with Down syndrome to generate appropriate activity and benefit from experience. Symmetrical movement strategies may emerge as an adaptive solution of the atypically developing system to help it to achieve major motor milestones (e.g., it is more advantageous to sit up by 'doing the splits' than not to sit up at all; it is more advantageous to 'bum shuffle' around than not locomote at all). These considerations are important when one wants to understand how the system develops and plan appropriate and timely interventions.

The current study has shed some light on the relationship between extraneous movements and intermanual coordination. In the typically developing group, extraneous movements, chronological age, and mental age were all strongly correlated. Therefore, without conducting an intervention study, it is difficult to disentangle the possible mechanisms underlying the development of intermanual coordination. Yet a different pattern emerged in the Down syndrome group. Here, extraneous movements in the non-acting hand/arm predicted intermanual coordination. This suggests, that there might be a direct link between the ability to control limbs separately and the ability to coordinate the limbs in intermanual coordination tasks. This relationship was also reported with typically developing 12-month-olds in Study 3 of this thesis (Chapter 4). Thus, bringing together the results from the typically and atypically developing populations, specialization for using a single limb during a unimanual task seems to be related to the ability to engage in more complex movements.

One neural structure that may be linked to both extraneous movements and intermanual coordination is the corpus callosum. Global anomalies of callosal geometry have been reported in individuals with Down syndrome; the corpus callosum was found to be thinner and more circular in individuals with Down syndrome than in chronologically matched controls and also individuals with

Williams syndrome (a rare neurodevelopmental disorder of known genetic origin) (P. P. Wang, Doherty, Hesselink, & Bellugi, 1992). This is consistent with behavioural findings in school-aged children and adults with Down syndrome showing that, although all areas of motor development are impaired, intermanual coordination is particularly challenging for this population (Ringenbach, Chua, Maraj, Kao, & Weeks, 2002; Spanò et al., 1999). Intermanual coordination has repeatedly been found to be delayed in various other neurodevelopmental disorders (e.g., ADHD; Klimkeit, Sheppard, Lee, & Bradshaw, 2004; ASD; Isenhower et al., 2012; developmental coordination disorder; Albaret, Zanone, & De Castelnau, 2000; Volman & Geuze, 2000; see also Swinnen & Carson, 2002). This is in line with the idea that motor specialization could potentially be used as a syndrome-general marker.

A further topic that remains to be investigated in future studies is the development of extraneous movements in feet/legs in infants and toddlers with Down syndrome. While overall extraneous movements in feet/legs were found to be higher in the Down syndrome group than in the chronological age matched group in the group analysis, no clear developmental pattern emerged from the trajectory analysis. This is likely to be because extraneous movements in feet/legs mostly did not correlate with either chronological or mental age in the Down syndrome group. If this finding is confirmed with a larger sample and a broader age range, then future studies could explore what other variables may explain individual variability in extraneous movements in feet/legs in individuals with Down syndrome. It may be that hypotonia plays an important role. Severity of hypotonia in individuals with Down syndrome may be independent of chronological and mental age. However, severity of hyptonia may influence the onset and proficiency of various locomotor skills, which in turn would influence motor specialization in the feet/legs as indicated by findings reported in Study 1 with TD children (Chapter 2). Because hypotonia has been reported as affecting lower limbs more than upper limbs in DS (Lauteslager, 2004), it may also explain the differential relationship between chronological age and extraneous movements in the upper limbs compared to lower limbs in the Down syndrome group. Hypotonia may play a more important role in the development of extraneous movements in the lower than upper limbs, while age may be more predictive for the development of extraneous movements in the upper limbs which are not as severely impacted by hypotonia.

The current study found that the number of extraneous movements produced by children with Down syndrome was above what would be expected for typically developing children of the same mental age. Together with findings from other studies (Carr, 1970; Harris, 1981; LaVeck & LaVeck, 1977), this supports the hypothesis that motor development is an area of particular difficulty for individuals with Down syndrome. Furthermore, this is consistent with the general proposal that neurodevelopmental difficulties can be detected in the motor domain before they can be detected in other domains (M. S. C. Thomas et al., 2016). This proposal is based on the developmental timing of neural pruning, which happens early in motor areas (Gogtay et al., 2004; Huttenlocher, 2002; Huttenlocher & Dabholkar, 1997). Due to synaptic abnormalities in many neurodevelopmental disorders, including Down syndrome, the relatively few and immature connections of neurons may be more vulnerable during the pruning process (Colman et al., 1997; Cowan, 1979). This may be why the motor domain presents early difficulties not only for Down syndrome but also for other neurodevelopmental disorders, including autism spectrum disorder (Flanagan et al., 2012; Iverson & Wozniak, 2007; Landa & Garrett-Mayer, 2006; Leonard et al., 2014; Toth et al., 2007).

Importantly, the current study contributes to the ongoing discussion on the extent to which standardized tests are sensitive enough to detect early markers of neurodevelopmental disorders. While extraneous movements were more frequent than that expected of their given mental age, no systematic disparities were observed between motor and cognitive scores in infants and toddlers with Down syndrome; although a common finding in previous studies with standardized assessment is that motor scores are lower compared to cognitive scores (Carr, 1970; Harris, 1981; LaVeck & LaVeck, 1977). In fact, fine motor scores were significantly higher than language scores in the current study. These differences between current findings and previous studies may be attributed to the use of different developmental scales (other studies often used the Bayley Scales, the current study used the Mullen Scales). Fine motor scores were found to be higher than language scores not only in the Down syndrome group but also in the mental age matched group (but not in the chronologically age matched group). One of the possible reasons why we see disparity between fine motor scores and language in participants with a lower mental age is that the scale was standardized on an American sample while the current study was conducted in the UK. Perhaps cultural differences in rearing practices between countries may differentially impact various domains. These differences may start disappearing as a result of formal education which children start receiving when they are older.

Furthermore, it is possible that the results of standardized tests, such as the Mullen Scales, show a lack of sensitivity to early developmental difficulties. For example, while many experimental measures show a difference in early motor development between typically developing children and children who later receive a diagnosis of autism spectrum disorder, standardized measures of motor development often fail to detect a difference in the first year of life (Brian et al., 2008; Landa & Garrett-Mayer, 2006; Landa et al., 2012; Ozonoff et al., 2010; Zwaigenbaum et al., 2005). The proposed lack of sensitivity of standardized measures is supported by the weak correlation between the Gross and Fine motor scales of the Mullen Scales of Early Learning and extraneous movements or intermanual coordination in the Down syndrome group in this chapter and also in typically developing children in Study 3 (Chapter 4). The issue of sensitivity of standardized measures is especially important to consider if they are to be used as early markers of neurodevelopmental difficulties.

The finding in the current study of increased extraneous movements in infants and toddlers with Down syndrome, a neurodevelopmental disorder of clear genetic origin, provides an important first step in support of extraneous movements being used as an early marker of neurodevelopmental disorders. Future research could examine infants and toddlers with other genetic disorders, such as Williams syndrome, to show whether increased extraneous movements is a syndrome-general or syndrome-specific characteristic. Based on studies showing increased extraneous movements across various neurodevelopmental disorders in older children, I would predict that aggravated extraneous movements in infancy are a syndrome-general feature of a vulnerable organism. However, the processes underlying aggravated extraneous movements might differ between disorders. Furthermore, extraneous movements could be a promising early marker of neurodevelopmental disorders of unclear aetiology which are not possible to be currently diagnosed early in development (e.g., ASD, ADHD). Thus, extraneous movements could be investigated as one of the measures in prospective studies in children who are at risk of developing a particular disorder. Although it is unlikely that aggravated extraneous movements would be a syndrome specific marker, they could be an important, easily identifiable feature of the early profile of various neuro-developmental disorders.

CHAPTER 7

DISCUSSION

7.1. Key findings

In this thesis I have documented for the first time a substantial decrease in extraneous movements in the non-acting hand/arm and feet/legs accompanying unimanual object-directed reaching between 9- and 12-months of age (Study 1). This developmental trend is reflected in a simultaneous decrease in the spatiotemporal congruency of movements between arms during unimanual shaking (Study 2). Fewer extraneous movements in the infants' non-acting hands/arms during unimanual object-directed reaching were related to better intermanual coordination (Study 3). Moreover, I showed that the developmental trajectory of extraneous movements in infants and toddlers with Down syndrome is delayed compared to the typically developing trajectory even when mental age is taken into account (Study 4). Finally, the fewer extraneous movements children with Down syndrome produced, the better was their intermanual coordination (Study 4).

7.2. Extraneous movements

7.2.1. Decrease in extraneous movements over development

This thesis extends previous work with 4.5- to 7.5-month-olds that demonstrated that infants' actions with one hand are often accompanied by goal-irrelevant movements in other limbs, such as clenching, splaying, or wiggling of the fingers and toes (Soska et al., 2012). Although Soska et al. (2012) did not find any developmental change across the studied ages, the extraneous movements they documented in the first year of life contrast with the skilled purposeful movements of adults and even young children (Addamo et al., 2007). The current thesis provides a bridge between infancy and young childhood by identifying a decrease in extraneous movements from 9 to 12 months of age during unimanual reaching (Study 1), which continues until at least 3 years of age (Study 4). An important contribution of this thesis is the converging evidence and replication it provides across multiple studies. Study 1 (Chapter 2) showed that extraneous movements decrease between 9 and 12 months of age during unimanual reaches. Study 2 (Chapter 3) validated and extended these findings in infants of the same age by showing a decrease in the spatiotemporal congruency of arm movements during a different unimanual activity (shaking). In Study 3, I identified a link between the extraneous movements and intermanual coordination in 12-month-olds. Not only does this study provide support for the hypothesis that the presence of extraneous movements is linked to functional motor behaviour (intermanual coordination in this case), but also it replicated findings from Study 1. More specifically, the prevalence of extraneous movements in the non-acting hand/arm was tested using an identical reaching paradigm in the same age group (12-month-olds) twice in this thesis (Studies 1 and 3) and the prevalence of extraneous movements was similar across both studies. This suggests that the paradigm and the coding scheme I developed for assessing the presence of extraneous movements is reliable.

Studies 1 and 4 of this thesis reported a developmental decrease in extraneous movements in infancy and toddlerhood. However, there seems to be a discrepancy between the high degree of motor specialization reported in toddlers in Study 4 and studies showing the presence of extraneous movements in older children (Addamo et al., 2007; Gasser et al., 2010; Largo et al., 2001; P. H. Wolff et al., 1983). Here I argue that to reconcile these findings it is important to consider the activities that the children were engaged in when the researchers measured their extraneous movements. In this thesis, I investigated extraneous movements during unimanual reaching. This is a motor action that infants start performing very early in development (at around 4 months of age; Spencer, Vereijken, Diedrich, & Thelen, 2000) and practice extensively from the onset of its acquisition (Carvalho et al., 2008; Eppler, 1995; Lobo & Galloway, 2013; Soska et al., 2010). This makes reaching an activity that can easily be used for assessing extraneous movements across many age groups starting from non-verbal infants making their first successful reaches.

The early onset and extensive practice of reaching suggest that it is a core motor skill that is crucial for efficient interaction with the environment. Thus, a high degree of specialization by toddlerhood (Study 4) is to be expected for reaching. In contrast, studies with older children report a high prevalence of extraneous movements during actions that are far from being a core motor skill (Connolly & Stratton, 1968; Gasser et al., 2010; P. H. Wolff et al., 1983). For example, Largo et al. (2001) asked children to perform actions of varying complexity including repetitive, alternating, or sequential movements which were not purposeful in that particular context. The authors observed that extraneous movements decreased earlier in development for repetitive actions, which are relatively easy to perform, and later for alternating and sequential actions, which are more challenging. Thus, the difficulty of action performed is an important factor that modulates the prevalence of extraneous movements. This aspect was also reported in the current thesis in Study 2: increasing action demands (i.e., speed) led to an increase in extraneous movements. The current thesis focused specifically on movements in reaching, shaking, and intermanual coordination. Future research could explore the emergence of specialization in different motor sub-domains which may differ in difficulty of acquisition and thus show different developmental timings for changes in extraneous movements.

7.2.2. Alternative explanations of extraneous movements

In this thesis, I have argued that developmental changes in extraneous movements can provide a window into motor specialization. But are there any alternative explanations of what might underlie the observed developmental changes in these movements? One possibility is that the extraneous movements are merely the result of a highly aroused motor system (e.g., Thelen, 1981), and correspondingly that a greater prevalence of extraneous movements in younger infants represents greater arousal of the motor system. When in an aroused state, infants move their limbs in a variety of different ways. For example, they often wave and shake their arms, kick their legs, and rub their feet together (Thelen, 1979). However, it is unlikely that the developmental changes in movements described in this thesis can be explained purely by changes in arousal for the following reasons. Firstly, both Soska et al. (2012) and this thesis (Studies 1, 3, and 4) found infants to be calm rather than aroused when performing the observed motor tasks. This is with the possible exception of Study 2 of this thesis, when some of the shaking sequences were vigorous. However, the analysis employed in Study 2 was very specific and robust: using motion capture, I measured in fine detail the spatiotemporal coupling between movements in acting and non-acting hands/arms during the action of shaking a rattle with a single hand, focusing on the analysis of spatiotemporal coupling between arms rather than the amount of movement in the non-acting arm. An account based on arousal does not explain the precise spatiotemporal coupling between arms. Similarly (and secondly), as Soska et al. (2012) pointed out, and this was also observed in the reaching paradigms in Studies 1, 3, and 4 of this thesis, a large proportion of extraneous movements were tightly linked to the onset of the action. If movements of the non-acting hand simply reflected motor arousal, then it seems likely that the movements would be randomly distributed across the reach rather than tightly linked to its onset.

Another alternative account of these findings is that extraneous movements are postural compensations for maintaining balance, and a developmental reduction would represent increasing efficiency of postural control. Again, Soska et al. (2012) present several arguments against this interpretation that are consistent with the observations in this thesis. Firstly, in Soska et al. (2012) parents physically supported their children, lessening postural demands. Similarly, in this thesis, postural demands were reduced by placing infants in an infant seat. I also further limited potential postural disruptions by presenting the target object at the infant's arm distance, ensuring that infants did not have to lean forward to reach for it (Rochat & Goubet, 1995). Secondly, like Soska et al. (2012), I observed that extraneous movements usually took the form of finger or toe wriggles and wrist or ankle twists. It is unlikely that these small movements would be able to provide compensation for postural disruption. Thirdly, as observed by both Soska et al. (2012) and me (Studies 1, 3, and 4 in this thesis), extraneous movements are often produced when the non-acting hand/arm is in a resting position (lying on a chair or the body of the infant). These extraneous movements cannot be postural compensations. Finally, the youngest infants tested in this study were 9-month-olds. By this age, infants have already accumulated a large amount of experience with reaching while sitting (Rochat, 1992), so it seems unlikely that they would produce extraneous movements for the purpose of maintaining balance. An important finding that supports this line of reasoning comes from Study 1: there was no relationship between experience with sitting and the prevalence of extraneous movements. Similarly, Soska et al. (2012) also did not find a relationship between sitting experience and extraneous movements.

Future studies could directly address the question of whether extraneous movements are postural compensations by manipulating the level of support provided to the infant. I would, however, question whether such a design would provide a clear and definitive answer to this concern. Providing infants with less support could make reaching more difficult, which may increase the prevalence of extraneous movements they produce. This would not necessarily be because the infants need to compensate for postural perturbations, but could be because the infants are unable to sustain the same level of differentiation of movement when the demands of the task are increased by the additional demands of keeping the torso upright (e.g., Rochat & Goubet, 1995). As mentioned above, increasing task demands results in an increasing number of extraneous movements in older children and adults (Addamo et al., 2007). Commensurate with this concern, increasing task demands were related to changes in extraneous movements in the infants in Study 2 of this thesis. In that study I observed higher spatiotemporal congruency between arms when the speed of shaking was higher. Similarly, Soska et al. (2012) also found a higher prevalence of extraneous movements with increasing task demands in infants; infants produced more extraneous movements when manipulating objects in a supine position than they did in a sitting position. Soska et al. (2012) argued that this was because, during exploration in the supine position, the infants needed to constantly hold the toy aloft against additional gravitational constraints. Thus, even if future studies were to show more extraneous movements in infants receiving less postural support, it may mean that the global task demands were more difficult for the infants, resulting in a higher prevalence of extraneous movements, rather than the extraneous movements indexing merely postural compensations. Employing electromyography (EMG) to capture the fine temporal aspect of motor activity would help us to study differences between postural compensations and extraneous movements.

7.2.3. Extraneous movements as an indicator of motor specialization

In this thesis, I have argued that the substantial decrease in extraneous movements accompanying unimanual actions, described in the various studies I have reported, reflect a wider developmental process of gradual motor specialization over the first year of life. I would like to suggest that extraneous movements may be a property of the endogenous organization of certain functionally related muscle groups (*synergies*, Bernstein, 1967). Such movement synergies are typically characterised as building blocks for generating coordinated movements, such as bilateral hand movements (Kelso, Southard, & Goodman, 1979a, 1979b). Building on the proposal that the infant brain is broadly tuned to environment stimuli (e.g., M. H. Johnson, 2011), I propose that, early in development, synergies are very simple and broad in the sense of involving co-activation of multiple limbs and muscle groups across various contexts. Indeed, recent evidence supports this view (Kato et al., 2014). Kato et al. (2014) demonstrated that spontaneous movements at 3-4 months of age can be decomposed into five simple synergies: four corresponding to single-limb movement and the fifth being the synchronous movement of all limbs. Over development, new synergies emerge. For example, while stepping in neonates can be explained by only two basic synergies, two additional synergies are required to explain stepping in toddlers (Dominici et al., 2011). Thus, motor development could be viewed as an increase in the number of synergies through developmental differentiation. This allows infants' motor responses to action goals to become increasingly specialized to their purpose, resembling the developmental processes of specialization seen in other domains, including language and face processing (Gervain & Mehler, 2010; Lewkowicz & Ghazanfar, 2009; Maurer & Werker, 2014; Pascalis et al., 2005; Scott & Monesson, 2010; Werker & Tees, 1984).

Future studies are needed to examine the extent to which specialization in the motor domain emerges independently from specialization in other domains (if at all). Some degree of independence may be assumed considering that the timing of pruning varies across different brain regions (Gogtay et al., 2004; Huttenlocher, 2002; Huttenlocher & Dabholkar, 1997). Pruning generally occurs first in sensory and motor areas, followed by higher association areas and lastly prefrontal cortex. This suggests that the process of specialization may be at least partly independent across domains with pruning in motor areas occurring earlier than in other domains.

7.2.4. Extraneous movements as an indicator of neurodevelopmental difficulties

Considering that motor areas are among the first to undergo synaptic pruning, motor deficits may be one of the first markers of neurodevelopmental difficulties (M. S. C. Thomas et al., 2016). Indeed, problems in the motor domain are often observed before the emergence of cognitive and neurophysiological prodromal symptoms (e.g., in autism spectrum disorder [ASD], Leonard et al., 2013; attention-deficit/hyperactivity disorder [ADHD], Kroes et al., 2007). Thus, extraneous movements could serve as an easily obtainable marker of early neurodevelopment difficulties. Support for this proposal comes from Study 4 of this thesis, where extraneous movements were shown to be aggravated in children with Down syndrome (DS).

To investigate extraneous movements in infants and children with DS (Study 4), I utilised a cross-sectional developmental trajectories analysis (following M. S. C.

Thomas et al., 2009). In this analysis, I linked chronological and mental age to extraneous movements, and this allowed me to go beyond group statistics and revealed new insights. Importantly, this analysis showed that although the rate of developmental decrease of extraneous movements in infants and toddlers with Down syndrome is often similar to the rate in typically developing (TD) individuals, overall they show a higher prevalence of extraneous movements; even beyond what would be expected based on their mental age. This highlights motor development as a domain of difficulty in infants and toddlers with Down syndrome. Indeed, other studies using standardized tests identify motor difficulties in DS beyond what would be expected for TD children of the same mental age (Carr, 1970; Harris, 1981; LaVeck & LaVeck, 1977). It also dovetails with M. S. C. Thomas et al.'s (2016) proposal that motor difficulties will be one of the first areas in which neurodevelopmental difficulties will be observed.

In a search of the literature, I could not identify any other study that had investigated extraneous movements in neurodevelopmental disorders early in development. I believe that this thesis is the first step in a potentially very important line of enquiry into extraneous movements as an early predictor of neuro-developmental disorders of unclear genetic origin such as ASD and ADHD. Although previous studies have already pointed to motor development as a domain of early difficulties in ASD (Flanagan et al., 2012; Iverson & Wozniak, 2007; Landa & Garrett-Mayer, 2006; Leonard et al., 2014; Toth et al., 2007), more sensitive measures which would reliably capture these early motor difficulties remain to be identified (many standardized measures of motor development often fail to detect any difference in the first year of life; Brian et al., 2008; Landa & Garrett-Mayer, 2006; Landa et al., 2012; Ozonoff et al., 2010; Zwaigenbaum et al., 2005). The extraneous movements investigated in this thesis may be such a measure.

Even though, as argued above, I would expect that specialization across domains happens with a certain degree of independence, I assume that various domains are interdependent and thus linked over developmental time. This has been documented in studies that have demonstrated cascading effects of the motor domain on other domains. For example, training of object manipulation and reaching at 3 months of age changes patterns of attention to others (Libertus & Needham, 2010, 2011). Furthermore, a positive relationship between walking and receptive and expressive language has been described (Walle & Campos, 2014). These findings suggest that motor specialization has the potential to influence other domains, perhaps by changing the ways in which infants interact with their environment (Clearfield et al., 2008; Karasik et al., 2011). Therefore, if motor specialization is atypical in many neurodevelopmental disorders, it could impact many other domains over development, contributing to atypical emerging phenotypes.

7.2.5. The adaptive purpose of extraneous movements

Although extraneous movements may seem like unnecessary by-products of a developing system unable to perform well differentiated motor actions, it is likely that they serve an adaptive purpose in early life. It may be that such movements are a vestige of our evolutionary past. Movements in the feet/legs during reaching and manipulation (Soska et al., 2012) could be driven by a phylogenetically older, quadrupedal system of movement (Dietz, 2002). It is possible that the dramatic decline in such extraneous feet/legs movements observed in this thesis may signify the progression to a more recently evolved mode in which the manual system operates independently of quadrupedal movement (Dietz, 2002).

Similarly, but without the proposal of an independent manual system, it may be that infants become gradually more competent at controlling redundant degrees of freedom and developing efficient movement synergies (Bernstein, 1967; Sporns & Edelman, 1993). Irrespective of this question, however, it is likely that extraneous movements play an adaptive role in ontogenetic development. It may be that the broad motor tuning reflected by extraneous movements facilitates specialization by enabling the selection of the most efficient movements for a given action as sensorimotor experience progresses. A further possibility is that extraneous movements provide motor activity and reafferent sensory feedback which is crucial to activity dependent processes of development in the nervous system (see Blumberg, 2015).

7.3. Neural correlates of extraneous movements

The high prevalence of extraneous movements (Study 1, 3, 4) and spatiotemporal coupling between arms (Study 2) in younger infants are in line with proposals that control over limbs is symmetrical early in development (Dennis, 1976; Diamond, 1991; Duque et al., 2007; Goldfield & Michel, 1986a; Meyer et al., 1995; Swinnen, 2002). According to this proposal, young infants have difficulty controlling their arms independently (e.g., Diamond, 1991; Fagard & Jacquet, 1989; Fagard & Lockman, 2005; Fagard & Marks, 2000; Ramsay & Weber, 1986). Indeed, initial reaching attempts in infancy are often described as bimanual or symmetrical (e.g., D. Corbetta & Thelen, 1996; Fagard, 2000; Flament, 1974, 1975). For example, Flament (1974, 1975) reported that during early reaches infants often extend both hands/arms toward an object, even if only one of them grasps the object. This default symmetry of the motor system is also supported by findings in this thesis; because a large proportion of the extraneous movements in the hand were produced at the same time as the onset of the reach in the acting hand (i.e., *motor overflow*), it can be assumed that they originated from the same motor command.

In order to better understand the process of motor specialization, it is important to understand what happens in the brain. Various neural structures have been proposed to be associated with changes in the default symmetry of the motor system. In the following section, I will discuss some of them. The most commonly studied in terms of explaining the presence of extraneous movements is the *corpus callosum*. Some authors have also focused on the *corticospinal system*, but this structure has been studied to a much lesser extent than the corpus callosum in relationship to extraneous movements (Addamo et al., 2007). The same applies for another brain structure, whose developmental changes are likely to contribute to changes in extraneous movements – *motor cortex*. However, it is very likely that other neural structures contribute to the developmental decrease in extraneous movements (e.g., the basal ganglia, which I will briefly discuss in the section on attention).

7.3.1. Corpus callosum

If the motor system is initially symmetrical, as has been proposed in the section above, then the initial symmetry of the motor system needs to be modified over development in order to control the body efficiently in a unilateral manner and also to intermanually coordinate two different sides of the body. The main brain structure which is proposed to break the initial symmetry is the *corpus callosum* (CC; Koerte et al., 2009; J. A. Lazarus & Todor, 1987; Mayston, 1997; Mayston et al., 1999; Qiu et al., 2011). CC develops across early life reaching its adult size and myelination in later adolescence when extraneous movements typically decline to an adult level (Addamo et al., 2007; Fling, Peltier, Bo, Welsh, & Seidler, 2011; Giedd et al., 1999). However, there is evidence that brain activation remains to some extent symmetrical, even in older children when the overt action is unimanual (Huo et al., 2011).

One of the parts of the CC, the splenium, has been identified as a rapidly developing part of the CC in the first year of life (Provenzale, Isaacson, & Chen, 2012). The ratio of the thickness of the splenium to the rest of the CC, has been positively correlated with motor function in children with diplegia, the paralysis of corresponding limbs on both sides of the body (Iai, Tanabe, Goto, Sugita, & Niimi, 1994). The larger the splenium relative to the CC, the better the motor performance. Furthermore, P. Mathew et al. (2013) found a positive relationship between diffusion tensor imaging (DTI) measures of CC and motor function in preterm infants. More specifically, better motor scores were associated with more advanced callosal organization, callosal myelination, and the microstructure integrity of a part of the CC that connects the premotor and primary motor cortices (mid-body). More advanced callosal organization is likely to provide more efficient transmission of interhemispheric neural signals. This would allow for more optimal processing and integration of information between the hemispheres. Taken together, perhaps rapid developmental changes in CC can be associated with the rapid changes in the extraneous movements in the infants and toddlers I observed in the current thesis. However, this link has yet to be established empirically in these age groups.

Although there is a lack of research on the relationship between CC and extraneous movements early in development, a number of studies have investigated this association in older children and adults (e.g., Abercrombie et al., 2008; Baliz et al., 2005; Bodwell et al., 2003; Cohen et al., 1967; Lazarus & Todor, 1987; Mayston et al., 1999; Shinohara et al., 2003). These studies have mostly focused on *motor overflow*—extraneous movements that begin with the onset of goal-directed movement (e.g., if fingers on the left hand start moving at the moment when the right hand starts reaching for an object). Overflow movements that are symmetrical to the movements of the acting limb along the body midline are called *mirror movements* (Addamo et al., 2007). Because of their tight temporal synchrony to the onset of the movement of the acting limb, it has been suggested that motor overflow and mirror movements reflect motor commands that leak from one body part to others (Addamo et al., 2007). In adults, when a unilateral motor command is generated in one hemisphere, the interhemispheric connections of the CC usually inhibit the corresponding area in the other hemisphere (Grefkes et al., 2008). However, this inhibition can be reduced by specific tasks such as finger tapping, squeezing, or applying force, which leads to motor overflow and mirror movements (e.g., Addamo et al., 2007; Armatas et al., 1996; Hoy et al., 2004; Perez & Cohen, 2008). The increase in spatiotemporal congruency with speed observed in Study 2 points to a role for inhibition in the modulation of extraneous movements in infancy. I further showed that the ability to modulate extraneous movements improves with development. While infants at 9 months of age showed inter-limb congruency even at a slow speed of shaking, it was present only for fast shaking in 12-month-olds.

Apart from its proposed contribution to the production of unimanual actions, CC has also been implicated in the development of a range of other motor behaviours such as laterality (Sacco et al., 2006). Moreover, the development of the CC and developmental decreases in extraneous movements might both be related to the development of intermanual coordination abilities (Diamond, 1991; Muetzel et al., 2008). The relationship between intermanual coordination and unimanual movements was described in Study 3 of this thesis. Twelve-month-olds who were better at activating only one hand/arm for unimanual reaching were also better at coordinating their upper limbs when performing a complex intermanual action. This relationship was also found in the atypically developing individuals, i.e., the infants and toddlers with Down syndrome, tested in Study 4. It is possible that CC contributes to the ability to decouple the limbs, which would be associated with both the ability to selectively activate only the limbs needed for the action and also to coordinate the hands efficiently.

7.3.2. The corticospinal system

Another brain structure that may contribute to changes in extraneous movements is the *corticospinal system* (Addamo et al., 2007). The corticospinal system is essential for adaptive and skillful motor functions (Porter & Lemon, 1995). In adults, most corticospinal terminations are contralateral to their origin in the cortex; however, a large number of ipsilateral corticospinal projections exist in infants (Eyre, Taylor, Villagra, Smith, & Miller, 2001; J. H. Martin, 2005). This may explain why passive sensory motor stimulation on the left and right hand in preterm and term neonates showed significant bilateral activation of cortex and thalamus using fMRI (Erberich et al., 2006). Furthermore, when TMS is applied over one hemisphere, bilateral arm motor effects were found in both preterm and term infants (Eyre et al., 2001). The amplitude of the ipsilateral effect decreases over the first year of life and, at the same time, the amplitude of contralateral effects increases. These findings suggest that corticospinal projections undergo heavy pruning, especially in the first year of life, though pruning in this structure may continue until early adolescence (Carson, 2005). This again coincides with developmental changes in the production of extraneous movements. Nevertheless, a direct link between the corticospinal system and extraneous movements across development remains to be empirically investigated.

7.3.3. Motor cortex

Apart from the development of corpus callosum and the corticospinal system, there may be many other brain changes that relate to the production of extraneous movements. For example, extensive developmental changes have been described in cortex. At birth, the synaptic circuitry of the cortex is diffuse, nonspecific, and overlapping (Goldman-Rakic, 1987; Innocenti & Price, 2005; Katz & Callaway, 1992). Over development, brain regions become more segmented due to a developmental decrease in short-range connections (i.e., pruning). Simultaneously, there is an increase in long-range connectivity, a process which increases interconnectedness of more distant brain regions (Fair et al., 2007, 2009; Supekar et al., 2009).

Recent studies in the animal literature have documented a decrease in short-range connectivity and an increase in long-range connectivity in the motor cortex of rats (Biane et al., 2015). Early in development, motor cortex shows high short-range connectivity which gradually decreases as the system develops. Due to this early synaptic arrangement, corticospinal neurons which control separate muscle pools are coupled. Therefore, it is likely that early in development any activation would spread easily across motor cortex, leading to the co-activation of muscles. This may contribute to the presence of extraneous movements. With the experience-dependent reduction of short-range connectivity, the ability to perform more differentiated movements is likely to emerge. Furthermore, increases in inter-regional long-range connectivity (such as the one between hemispheres) may be important for the emergence of complex coordinated actions (such as the intermanual coordination examined in Study 3 and 4) and multi-joint synergies.

The organization of motor cortex in animals is often mapped by directly stimulating different parts of motor cortex and observing what movement is induced. Chakrabarty and Martin (2000) used this approach to map the motor cortex of kittens of different ages. In line with findings from Biane et al. (2015) described in the previous paragraph, Chakrabarty and Martin (2000) showed how motor cortex maps become progressively more elaborated over development with the emergence of multi-joint sites. These may be important for enabling the system to perform more differentiated movements. These multijoint sites were shown to result from experience: whereas training the animals on a prehension task increased the number of multijoint sites, disuse reduced them (J. H. Martin, Engber, & Meng, 2005).

The findings from the animal literature can also explain some of the findings with infants in the current thesis. Increased local connectivity in motor cortex could lead to the simultaneous activation of multiple limbs. Over development, the neuronal map in motor cortex is becoming more refined. This would allow for more differentiated movements and also for movements with higher complexity. This experience-dependent refinement of neuronal maps in motor cortex could explain why the infants with greater gross motor experience produced fewer extraneous movements in the feet (Study 1). Their synergies involving hand and leg movements may be more differentiated because they have greater experience with controlling their upper and lower limbs separately but in a coordinated manner (more experience in crawling, walking with assistance etc.). Subsequently, perhaps when a hand needs to be activated to unimanually reach for an object, infants with a more specialized brain do not activate the leg as much as infants with a less specialized brain since their synergies have been differentiated.

Currently, very few studies focus on specialization of motor cortex in humans, even though the few studies that exist provide intriguing results. Nebel et al. (2014) investigated the parcellation of resting-state functional connectivity of primary motor cortex in typically developing (TD) children and children with autism spectrum disorder (ASD). Parcellation analysis applied to MRI data is based on identifying patterns of connectivity between individual primary motor cortex voxels and all voxels outside of primary motor cortex. The authors found that the motor cortex of the children with ASD lacked differentiation between lower limb/trunk regions and upper limb/hand regions compared to the motor cortex of the TD children. This may have been due to a delay in functional specialization within the motor cortex. This may explain why extraneous movements in feet/legs are produced during reaching more in young infants than in older infants (Study 1). Future studies could investigate whether infants who show higher parcellation of motor cortex also show fewer extraneous movements.

Furthermore, cross-syndrome studies may reveal whether reduced parcellation of motor cortex is specific to children with ASD (i.e., it is a syndrome-specific marker) or whether it is present among a wider range of neurodevelopmental disorders (i.e., whether it is a syndrome-general marker). I would expect the latter, based on findings that motor difficulties including aggravated extraneous movements are common to several neurodevelopmental disorders including ADHD (e.g., Gilbert et al., 2011; MacNeil et al., 2011; Mostofsky et al., 2006, 2003) and Down syndrome (Study 4 of this thesis).

7.4. Factors influencing motor specialization

7.4.1. The role of experience

It is likely to be the case that the undifferentiated activity of the early motor system is fine-tuned over developmental time through interactions with the environment (Gibson & Pick, 2000; Sporns & Edelman, 1993). For example, in Experiment 1, 9-month-olds activated multiple limbs even though they only needed to activate one hand to retrieve the object. Limb-specific feedback over many repetitions of successful attempts to retrieve an object may, over developmental time, result in the ability to retrieve an object without movement of redundant limbs. This may be reflected in the observed decrease in extraneous movements by 12 months of age (Studies 1 and 4).

The link (observed in Study 1) between greater motor experience and fewer extraneous movements in feet/legs (but not in the non-acting arm) suggests that motor specialization is an experience-dependent process. When reaching for an object, infants with greater locomotor experience made fewer extraneous movements in their feet/legs than infants with less locomotor experience. Because infants must learn to move their feet/legs independently in order to acquire certain locomotor skills, coupling between motor skills and extraneous movements of the feet/legs supports the proposal that motor learning is specific to the mode of action (Adolph, 2000). Further research is needed to ascertain how motor experience interacts with neural mechanisms over developmental time to increase motor specialization.

As outlined in Chapter 5, it is important to emphasize that the organism is not passively receiving environmental stimuli. Rather individuals actively select their environments and generate their own experiences based on their history and abilities. It is through this self-organizing process of development that specialization occurs. The developing organism has the drive to practise the skills necessary for it to adapt to its environment. For example, in *one* waking hour the average toddler takes 2,368 steps, which is the equivalent length of 7.7 American football fields (Adolph et al., 2012). Yet it still takes several years before walking becomes adult-like (Adolph & Robinson, 2015). Therefore, extensive interaction with the environment is necessary for an adult-like state to emerge.

As M. H. Johnson et al. (2015) suggest, factors intrinsic to the child itself may alter the child's ability to perceive, select, process, and adaptively respond to environmental stimuli, and thus disturb or delay the process of specialization. I propose here that the delayed motor specialization I observed in infants and toddlers with Down syndrome (Study 4) may be a result (at least partially) of how these children interact with their environment. Studies suggest that children with Down syndrome have less rich interactions with their environments than typically developing children (e.g., they are reaching less often, their exploration is limited; A. C. de Campos et al., 2013; Frazier & Friedman, 1996; Mizuno & Ueda, 2001). This could protract and alter the developmental process of functional specialization (M. H. Johnson et al., 2015), and lead to a delay in the decrease in extraneous movements that I observed in Study 4.

Apart from less richly exploring and interacting with their external environment, children with DS may produce activity that actually reinforces (rather than breaks) the coupling of their limbs. This could potentially explain why I observed pervasive extraneous movements in this atypically developing group. For example, some children with DS have been described as using a symmetrical strategy when transitioning from a prone to sitting position (Lydic & Steele, 1979). A symmetrical strategy has also been reported in children with DS when rising up from the floor into a standing position (Lauteslager, 1995). Additionally, I have personally observed children with DS use various symmetrical locomotion strategies (e.g., 'bum-shuffling') prior to learning to walk. These symmetrical motor strategies employed across various contexts may be adaptive compensatory movement strategies for children with Down syndrome which arise as a solution for a lack of trunk rotation due to hypotonia and hypermobility of joints (Åkerström & Sanner, 1993; Kugel, 1970) or reduced postural reactions (balance and self-righting; Haley, 1986).

Perhaps the use of symmetrical strategies actually constrains opportunities that require differentiation of the limbs, leading to pervasive extraneous movements and difficulties with intermanual coordination. I am basing this proposition on the *transfer of learning* account (D. Corbetta, 2009; D. Corbetta & Bojczyk, 2002; D. Corbetta & Thelen, 2002; D. Corbetta, Williams, & Snapp-Childs, 2006). According to this account, limb use in one context can affect limb use in different contexts. The most commonly studied example of this is the increase of bimanual versus unimanual reaching when infants are learning to walk (Babik et al., 2014; Berger, Friedman, & Polis, 2011; D. Corbetta & Bojczyk, 2002, see Chapter 6 for more details). This was shown to be the result of early walkers spending a lot of time with their hands held in a high guard position to balance when practising walking (D. Corbetta & Bojczyk, 2002; Kubo & Ulrich, 2006; Ledebt, 2000). This leads to organizational changes at the level of the brain, leading to more coupling at homologous prefrontal/central scalp locations in early walkers than in pre-walkers and experienced walkers (D. Corbetta et al., 2014). I propose that the same mechanism may be behind the high prevalence of extraneous movements in infants and toddlers with Down syndrome as well as their difficulties with intermanual coordination. If children with Down syndrome use various symmetrical strategies to compensate for their motor difficulties, it may be possible that this leads to more coupling (or lack of decoupling) on a neural level, leading to behaviour consistent with a lack of motor specialization (a lack of experience which would lead to differentiation of synergies). Future studies should investigate this proposal by combining training facilitating decoupling of the system and neuroimaging. This would be an important step not only for understanding motor specialization in developing organisms but also for developing potential new remediation techniques or recommending interventions.

7.4.2. The role of attention

In adults, the brain areas involved in movement preparation overlap substantially with those implicated in selective attention (Allport, 1989; Astafiev et al., 2003; M. Corbetta et al., 1998; Perry & Zeki, 2000; Rizzolatti & Camarda, 1987). Attention has been implicated in the modulation of extraneous movements in school-aged children (e.g., Waber et al., 1985) and adults (e.g., Addamo et al., 2007; Baliz et al., 2005; Bodwell et al., 2003). However, there is very limited evidence of any link between attention and extraneous movement in infancy. Soska et al. (2012) found that infants produce fewer extraneous movements when they are looking at an object they are manipulating than when they are looking away. But the current thesis is the first to show that extraneous movements in infancy are associated with attentional performance, more specifically with the ability to disengage attention.

In Study 1, I found that infants who are better at disengaging/shifting visual attention are better at producing movements that are more tailored to their goal (i.e., fewer extraneous movements), indicating an overlap in early development between selective attention and limb activation (Bacher & Robertson, 2001; Robertson & Johnson, 2009). The ability to shift attention between sensory stimuli, which emerges during the first few months of life (Colombo, 2001; Richards & Casey, 1992), is likely to provide the basis for the selective processes that are required for the development of sophisticated motor skills which are not perfected until well beyond infancy (Addamo et al., 2007; Koerte et al., 2010).

Even though only a limited number of studies have explored the link between attention and extraneous movements in infancy, the tight coupling between attention and motor development more generally has been shown to be especially strong in infancy (e.g., Bacher & Robertson, 2001; Robertson & Johnson, 2009). At around 3 months of age, attention undergoes a major transformation when it is described as ‘obligatory’ or ‘sticky’ because the infants have difficulty disengaging from a fixated stimulus (Atkinson et al., 1992; Rothbart et al., 1994). At the same time, the motor system undergoes a transition from one that spontaneously produces general movements to one that produces more controlled actions (Einspieler et al., 2005; Prechtl, 1997; Prechtl & Hopkins, 1986). These changes may be underpinned by development of the corticobasal ganglia network (Atkinson et al., 1992; Dalton & Bergenn, 2007; Hood & Atkinson, 1993; M. H. Johnson, 2011a; Rothbart et al., 1994). The basal ganglia have been suggested to broadly inhibit all movements while the frontal lobe selectively disinhibits the desired movements (Alexander & Crutcher, 1990; Kostović & Jovanov-Milošević, 2006; Mink, 1996, 2003; Watanabe et al., 2011). In relation to Study 1 of this thesis, it is possible that infants whose frontal lobe was better at selectively disinhibiting desired movements demonstrated better (i.e., more specific) movements as well as attentional abilities (better disengagement). This could also explain findings that attention-related disorders are associated with an increased production of extraneous movements (Licari & Larkin, 2008; Licari et al., 2006). If attention and movement production are coupled early in infancy, then difficulties in one will likely be accompanied by problems in the other, as has been reported, for instance, in attention-deficit/hyperactivity disorder (ADHD; Bush, Valera, & Seidman, 2005; Castellanos et al., 2002; Teicher et al., 2000). Importantly, the interaction between motor activity and attention at the age of 3 months, but not motor activity or attention per se, is predictive of a number of attentional problems eight years later (Friedman, Watamura, & Robertson, 2005). Thus, examining the relationship between attention and the motor domain could have highly significant clinical implications (Addamo et al., 2007) and potentially open new avenues for early diagnosis and intervention.

7.5. Limitations and future directions

7.5.1. Cross-sectional versus longitudinal designs

Although this thesis has significantly contributed to our understanding of the development of extraneous movements, many aspects of this research domain require further investigation. Firstly, the designs used in this thesis were cross-sectional rather than longitudinal. Cross-sectional studies cannot provide answers related to research questions about motor learning and the process of developmental change, however they are useful for establishing normative patterns of development (Thelen & Corbetta, 2002). Since this thesis is focused on the latter, the choice of a cross-sectional design was an appropriate one. The decision was also motivated by practical concerns, particularly time constraints. This was especially a consideration for Study 4 when the ages of interest spanned from 1 to 3 years of age. Another reason for choosing a cross-sectional design for Study 4 is the difficulty with recruiting atypically developing children within the tight age range. Finally, longitudinal designs are associated with high dropout rates. If a participant misses one time point, the sample size is reduced. In order to learn more about trajectories using cross-sectional designs, I employed a cross-sectional developmental trajectories analysis (M. S. C. Thomas et al., 2009) in Study 4. This analysis gave some insight into how the development of extraneous movements unfolds over time in typically and atypically developing children. However, the results of this trajectory analysis need to be verified using a longitudinal design, because while trajectories constructed cross-sectionally may represent well the general trajectory of the group under scrutiny, they may not represent well each individual within that group, and this is a concern especially in atypically developing populations (M. S. C. Thomas et al., 2009).

What would future longitudinal studies add? Firstly, they could help to trace the development of infant motor skills (e.g., reaching, crawling, walking) as they emerge and examine their relationship with extraneous movements. This would allow us to get around one limitation of the current thesis: parents find it very challenging to recall the onset of various motor milestones. Tracing the onset of milestones as they emerge would ensure that the infant's experience with various motor milestones is measured reliably.

However, perhaps the greatest prospect from future longitudinal studies would be the implementation of active training in order to identify the direction (if any) of the relationship between extraneous movements and motor experience, as well as of the relationship between extraneous movements and attention. I proposed that improvements in motor skills are associated with a reduction in extraneous movements. Indeed, I found a negative correlation between experience with motor skills and extraneous movements (Study 1). However, future training studies could help to elucidate the direction of this relationship. This also applies to the relationship between attention and extraneous movements. Would training in the attentional domain improve specificity of movement? Would motor training improve attention? Answers to these questions may not only help us to understand how various domains cascade on to each other but would also be of importance for designing interventions.

7.5.2. Neural correlates of motor specialization

In the current thesis, I made a number of proposals about the neural correlates of extraneous movements. Some of them motivated the design of particular studies in this thesis (e.g., the role of the corpus callosum in breaking the initial symmetry of the motor system between the hands). Future studies need to measure these neural correlates to further understand the mechanisms behind extraneous movements. However, measuring the neural correlates of motor activity in infants would be challenging. This is because the most useable technique for measuring brain activity in infants (electroencephalography [EEG]) is highly sensitive to motor artefacts. It is possible to reduce or eliminate motor artefacts in adults by providing them with instructions to stay still before reaching for an object, establishing a clear onset of motion (e.g., Urbano, Babiloni, Onorati, & Babiloni, 1997). However, this poses a problem in infant research, as infants lack the ability (or perhaps the motivation) to follow instructions.

Furthermore, the spatial resolution of EEG is limited. This is a constraint because, in order to understand the neural correlates of progressive motor specialization across development, it is necessary to examine which brain areas are activated when the infants perform the motor task. As an alternative to EEG, functional near-infrared spectroscopy (fNIRS) provides reasonable spatial resolution, allowing researchers to locate haemodynamic activity in the brain (a proxy for neural activity). FNIRS is also more robust to certain movement artefacts than EEG, making it more suitable for studying movement in awake infants. Therefore, fNIRS may be the method of choice in order to provide insight into both typical and atypical motor development of extraneous movements as well as any brain changes associated with intervention in young age groups.

Another neuroimaging approach which could bring insight into motor specialization is analysis of resting state data collected using magnetic resonance imaging (MRI). An advantage of this approach over the fNIRS approach proposed in the paragraph above is that there are already a lot of existing resting state datasets across various age groups (including very young age groups, such as preterm infants, Smyser et al., 2010), which could be used for analysis. Parcellation of resting-state functional connectivity using spectral clustering approaches has been shown to provide information about functional organization within the brain (A. L. Cohen et al., 2008; Kelly et al., 2010; Kim et al., 2010; van den Heuvel, Mandl, & Pol, 2008). Recently, Nebel et al. (2014) applied this approach to motor cortex in children, showing that motor cortex shows less parcellation in children with autism spectrum disorder than in typically developing children. Extending this to infants and toddlers and also different neurodevelopmetnal disorders could provide a deeper understanding of the neural correlates of extraneous movements.

7.5.3. Cross-syndrome comparisons of motor specialization

This thesis has shown that infants and toddlers with Down syndrome show aggravated extraneous movements compared to typically developing infants and toddlers, even when mental age is taken into account. Based on this finding, I argue that extraneous movements have the potential to serve as an early marker of neurodevelopmental difficulties. Future studies could examine extraneous movements in other disorders of known genetic origin, such as fragile X or Williams syndrome, to show whether aggravated extraneous movements are syndrome-specific or syndrome-general. This would provide a basis for investigation of extraneous movements as an early marker of neurodevelopmental disorders of unclear aetiology which are not possible to be currently diagnosed early in development (e.g., ASD, ADHD). Although it is unlikely that aggravated extraneous movements would be a syndrome specific marker, they could be an important, easily identifiable feature of the early profile of various disorders.

7.6. Conclusion

This thesis provides new insights into the processes by which infants learn to select appropriate limb movements for purposeful action. In early development, the infant motor system is ‘broadly tuned’, with the activation of redundant limbs. But over the first year of life, motor responses become progressively more specialized. In my view, broad motor tuning in early infancy likely fulfils an adaptive function by providing young infants with a wide repertoire of responses to their environment from which they can select the most effective. The process of motor specialization documented here has wide-reaching implications for the development of a range of motor abilities such as object exploration, locomotion, intermanual coordination, the emergence of lateralised action, and tool use.

Furthermore, this thesis provides insight into motor specialization in neurodevelopmental disorders by showing aggravated extraneous movements in infants and toddlers with Down syndrome. Combined with other evidence of increased extraneous movements in children with attention-deficit/hyperactivity disorder and autism spectrum disorder, I suggest that extraneous movements may serve as an early marker of neurodevelopmental difficulties.

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