FROM THE DEPARTMENT OF WOMAN AND CHILD HEALTH,
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ON THE DEVELOPMENT OF POSTURAL ADJUSTMENTS IN SITTING AND STANDING

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To my family

ABSTRACT

Postural control constitutes an inseparable part of any posture or movement and is organized to ensure the maintenance of equilibrium (Massion 1994). Within the first two years of life the infant masters to control equilibrium well enough to be able to sit, stand and walk independently. We studied postural adjustments, i.e., muscle activity elicited by external perturbations in typically developing infants during the periods in life when independent sitting and standing emerge. We also studied two types of motor control (voluntary and automatic) in children with cerebral palsy (CP), and in a group of age-matched, typically developing children.

Already at the age of one month, the infants were able to produce direction specific postural muscle activity, during unsupported **sitting**. Translations in the *bw* direction, evoked direction specific postural adjustments in 85% of the trials, and translations in the *fw* direction, in 72% of the trials. The postural adjustments were noted in all recorded muscles and particularly, direction specific postural adjustments were found in the neck muscles. The ‘complete’ pattern, i.e., when all direction specific muscles were activated during the same trial, became more frequent with age. However, the development of postural adjustments was not linear. We found that at 3 months the infants, used the ‘complete’ pattern less often that at 1 and 2 months, during both *fw* and *bw* translations. From 3 and 4 months onwards the activation rate gradually rose.

Infants aged 8 and 10 months, who are not yet able to stand independently exhibited direction specific postural adjustments during **standing** both *with* and *without support*. Therefore, we argue that direction specificity might constitute a prerequisite for the development of independent standing. We also found that the development of postural control in standing resembles that of sitting, i.e., great variation in the postural adjustments at early age, and fine-tuning to the situation with increasing age and experience. This strengthens the proposal that postural control develops through a selection process of the most suitable postural adjustments for the situation from a repertoire of direction specific postural adjustments (Forssberg 1999, Hadders-Algra 2000). Additionally, differences in response rates were noted between the two standing positions, indicating that already before independent standing is established, sophisticated sensorimotor integration enables task specific postural adjustments.

We also examined two types of motor control, i.e., **voluntary ankle dorsiflexion** and **automatic postural adjustments** (during external perturbations in standing *without* support) in nine children aged 9-15 years with hemiplegic CP. The ability to dorsiflex the ankle was investigated using the Selective Motor Control scale and by recording muscle activity during dorsiflexion. During both voluntary dorsiflexion and automatic control of the leg muscles the children with CP activated more muscles than the typically developing children, both synergistic and antagonistic muscles. In the group of CP, there was a significant correlation ($rho=-0.71$, $p<0.05$) between the number of muscles activated during dorsiflexion (1-7 muscles) and the SMC scores (1-4). A trend for positive correlation between the numbers of muscles activated during the two tasks was noted.

SAMMANFATTNING

Att kunna hålla balansen är en förutsättning för grovmotorisk utveckling, t ex för att kunna sitta eller stå självständigt. Vilka mekanismer som styr denna tidiga utveckling av balanskontroll är till stor del okända och det förekommer argument både för att utvecklingen styrs genetiskt, och att den styrs av miljöfaktorer och erfarenhet. Vi har undersökt balansreaktioner genom att låta barn sitta eller stå på en plattform som plötsligt förskjutits framåt eller bakåt. Den grundläggande principen för detta är att om underlaget förskjuts framåt, svajar kroppen bakåt och det är då adekvat att aktivera muskler på kroppens framsida för att återupprätta jämvikten, detta är s.k. riktningsspecifik muskelaktivitet.

Redan vid en månads ålder, när barnen testades i **sittande** utan stöd, aktiverade barnen riktningsspecifika muskler. Förskjutning av underlaget bakåt, vilket fick barnet att svaja framåt, utlöste riktningsspecifika posturala reaktioner i 85% av försöken, förskjutningar av underlaget framåt gav riktningspecifika svar i 72% av försöken. Postural aktivitet noterades i alla testade riktningsspecifika muskler och särskilt ofta aktiverades nackmuskulaturen. Det 'kompletta' mönstret, dvs då alla riktningsspecifika muskler aktiverades vid samma försök, blev allt vanligare ju äldre barnen blev. Balanssvaren utvecklades däremot inte linjärt. Vid tre månaders ålder aktiverade barnen det 'kompletta' mönstret mer sällan än vid både en och två månaders ålder. Från tre till fyra månaders ålder ökade sedan svarsfrekvensen för det kompletta mönstret.

Barn i åldrarna 8 och 10 månader, som ännu inte kunde stå självständigt, uppvisade riktningsspecifika balanssvar både då de testades **stående** *med* stöd och *utan* stöd. Utvecklingen av balansreaktionerna i stående bar likheter med utvecklingen av balanssvaren i sittande; vi fann stor variation och muskelaktiviteten anpassades alltmer till situationen med ökad ålder och erfarenhet. Detta styrker idén om att postural kontroll utvecklas genom en urvalsprocess i vilken de bäst lämpade muskelsvaren för en viss situation stärks. Vi fann skillnader i muskelaktiveringsmönster mellan de två positionerna (stående *med* och *utan* stöd). Detta tolkade vi som en indikation på att muskelaktivitet kan anpassas efter olika förhållanden redan innan förmågan att stå självständigt är fullt utvecklad.

Vi undersökte även **viljemässig** och **automatisk** motorisk kontroll hos barn med CP. Uppgiften för viljemässig kontroll var att aktivt dorsalflektera i fotleden. Automatisk motorisk kontroll (balanskontroll) undersöktes som ovan, i stående utan stöd. Nio barn i ålder 9-15 år med CP hemiplegi ingick i undersökningsgruppen. Förmågan att aktivt dorsalflektera fotleden undersöktes med bedömningsinstrumentet Selective Motor Control, som mäter förmåga till aktiv dorsalflexion, samt genom att muskelaktiviteten registrerades med EMG. Både vid viljemässig och automatisk kontroll av fotleden aktiverade barnen med CP fler muskler än barnen i kontrollgruppen. Antalet muskler som aktiverades vid dorsalflexion (1-7 st) korrelerade ($rho=-0.71$, $p<0.05$) till bedömningen på SMC skalan (1-4). Vi fann en trend till positiv korrelation mellan antal aktiverade muskler vid viljemässig och automatisk motorisk kontroll hos barnen med CP.

LIST OF PUBLICATIONS

The thesis is based upon original articles listed below. They will be referred to in the text by their Roman numerals.

I. **Hedberg Å**, Forssberg H, Hadders-Algra M
Postural adjustments due to external pertubations in sitting in one-month-old infants. Evidence for the innate origin of direction specificity
Experimental Brain Research 2004;157(1):10-17

II. **Hedberg Å,** Brogren Carlberg E, Forssberg H, Hadders-Algra M
Development of postural adjustments in sitting position during the first half year of life
Developmental Medicine and Child Neurology 2005; 47:312-320

III. **Hedberg Å**, Schmitz C, Forssberg H, Hadders-Algra M
Early development of postural adjustments in standing, with and without support
Experimental Brain Research, in press

IV. **Hedberg Å,** Oscarsson J, Forssberg H
Voluntary and automatic motor control in children with cerebral palsy
Manuscript

CONTENTS

LIST OF ABBREVIATIONS

AIMS	Alberta Infant Motor Scale
bw	Backward
COM	Centre of Mass
CP	Cerebral Palsy
CPG	Central Pattern Generator
EMG	Electromyography
fw	Forward
GM	General Movements
GMFCS	Gross Motor Function Classification System
MR	Magnet Resonance
NGST	Neuronal Group Selection Theory
SIAS	Spinae Iliaca Anterior Superior
SMC	Selective Motor Control

1 INTRODUCTION

Postural control constitutes an inseparable part of any posture or movement. We constantly and unconsciously position our body segments in relation to each other in a purposeful way which allows us to pursue the motor tasks we are engaged in, without loosing our balance. Postural control is thus organized to ensure the maintenance of equilibrium (Massion 1994). This means that the projection of the centre of mass (COM) must be kept within the stability limits of the body during quiet positions as well as when the body is in motion.

The organization of postural control involves complex sensorimotor integration (Massion 1994). The position of the head and, the movement of the head in space, for example, are identified by visual and vestibular systems (Gehz 1991). These systems are closely linked to the motor system, especially those of the eyes and the neck. Maintaining equilibrium is more than just keeping the head in a stable position, the rest of the body also needs to be aligned. This brings almost every other muscle of the body into the picture; the muscles of the trunk and spine, the muscles of the legs and, if you increase the postural difficulty, the arms will also become involved. Proprioceptive sensors supply the nervous system with information on the position of limbs and segments as well as forces acting on the body (Massion 1994). While maintaining equilibrium in any position, small adjustments may be required to reassure or to regain the well balanced position. These adjustments can be self induced, in combination with self produced movements or induced by external stimuli, i.e., compensatory postural adjustments (Cordo and Nashner 1982; Massion 1994). Compensatory postural adjustments are the main focus of this thesis.

1.1 Postural sensorimotor integration

1.1.1 The moving surface of support paradigm

Compensatory postural adjustments, i.e., rapid muscle activity elicited for the protection of equilibrium have been studied by exposing subjects to unexpected, external perturbations (e.g. Elner et al. 1972; Nashner 1976, 1977; Cordo and Nashner 1982; Forssberg and Nashner 1982; Horak and Nashner 1986; Woollacott et al. 1987; Forssberg and Hirschfeld 1994; Hirschfeld and Forssberg 1994; Hadders-Algra et al. 1996a,b; Sundermier et al. 1998; Roncesvalles et al. 2004; Woollacott et al. 2005). By translating or rotating the surface of support of the subjects COM is moved in relation to the support surface and projects towards the stability limits and equilibrium is perturbed. By the translation of surface of support forward, COM will be projected backwards towards the stability limits behind the subject. If no action is taken in compensation, the person will fall backward. A translation of the surface of support backwards will move COM forward in relation to the support surface and as a consequence the person risks falling forward. To compensate for such threats to equilibrium muscle activity to counteract the movement of COM will be elicited. Direction specific muscle activity to compensate for movements of COM forward is that of dorsal muscles and, direction specific muscle activity to counteract movements of COM backward is that of ventral muscles. This is the basic rationale for the term direction specificity. The term direction specificity refers to adequate postural sensorimotor integration, i.e., that the nervous system integrates sensory information to trigger direction specific postural adjustments.

1.1.2 Neural organization of postural adjustments

Nashner who did pioneering work using the moving surface of support paradigm, proposed that postural muscle activity is not the consequence of segmental stretch reflex activity but reflects a more complex machinery (1976, 1977). He introduced the concept of 'fixed patterns of activation' which means that the nervous system will elicit a pre-programmed response to perturbations, which is conceptually different to reflex activity. He showed that these fixed patterns can be modified with experience and that the same stretch to the muscle in two different postural situations would eventually elicit two different postural responses.

The complexity of the task is induced by the redundancy in degrees of freedom resulting from the many muscles and joints involved in postural activity (Massion 1994). It is now widely accepted that the nervous system solves the problem imposed by the large number of motor possibilities by a functional organisation of basic synergies (Horak and Nashner 1986; Keshner et al. 1988; Forssberg and Hirschfeld 1994; Dietz 1992). Forssberg and Hirschfeld proposed in 1994, that postural adjustments are governed by central pattern generators (CPGs), on brainstem or spinal level. Neural networks, like the CPGs for locomotion or breathing, provide the specification for the postural muscle activity. The CPGs receive sensory information on forces acting on the body and trigger a motor response. The proposed CPG-model has a functional organisation in two levels (Figure 1, Forssberg and Hirschfeld 1994; Hadders-Algra et al. 1996a). The *first level* is involved in the generation of the basic direction specific response pattern. Direction specificity means that perturbations inducing a forward sway of the body primarily elicit activity in the muscles on the dorsal side of the body, while perturbations inducing a backward body-sway primarily evoke activity in the ventral muscles. The *second* level of control is involved in the fine-tuning of the basic response patterns. Modulation can be achieved by changing the order in which the agonist muscles are recruited, by modifying the size of muscle contraction or by altering the degree of antagonistic activity.

The CPG model

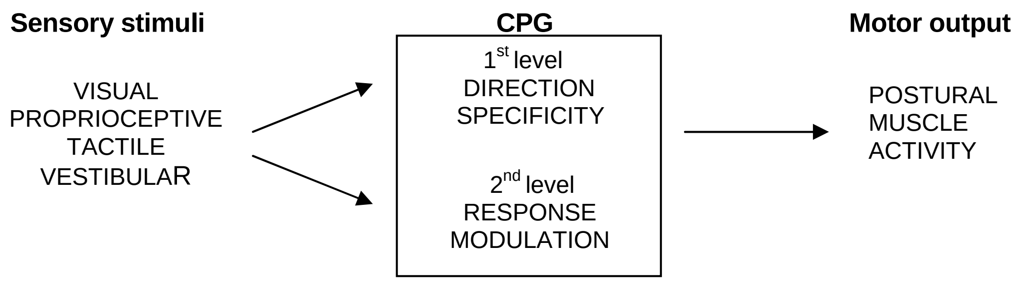

Figure 1. Sensory stimuli are processed at two levels within the CPG model. The first level generates direction specificity the second level the finetuning of the response.

Several sensory systems are contributing with information (Gehz 1991). Receptors within the joints and muscles give proprioceptive information on the position of the joints and the length or tension in muscles (Forssberg and Hirschfeld 1994; Hirschfeld and Forssberg 1994; Bloem et al. 2000; Dietz 1998). From the skin, mechanoreceptors provide important information on changes in pressure to and stretching of the skin. The tactile system is highly sensitive and gives fast and precise information on for example the direction a stimulus, which is important for the muscle recruitment of the postural adjustment (Johansson and Westling 1984, 1987; Edin 2001; Olaussen 2000). Even, specific graviceptors, specialized in detecting gravitational forces acting on the body have been proposed to exist (Mittelstaedt 1998). And as mentioned previously, visual and vestibular systems pass on information to the CPG networks. Finally, input from supraspinal regions are thought to influence the postural networks and thereby also the postural muscle activity triggered by them (Nashner 1977). This multitude of information is processed within the CPG networks and muscle responses are triggered accordingly.

1.2 Development of compensatory postural adjustments

1.2.1 Compensatory postural adjustments in infants

Assessments of postural adjustments in sitting infants, using the movable surface of support paradigm, have been conducted in as young as 3½ months old infants (Woollacott et al. 1987). The infants tested were sitting in an infant seat attached to the platform. Although direction specific postural adjustments were not consistently reported, direction specific postural adjustments were present already at this young age. Still, the authors concluded that at this age postural adjustments are not correctly organized due to inconsistency in direction specific responses. At four months of age, appropriate and consistent neck muscle activity were found, but only when the infants were deprived of visual stimuli (Woollacott et al. 1987). Harbourne and co-workers (1993) also found, direction specific responses in infants aged four months, but not in infants aged 2-3 months. The infants in their study were exposed to 'natural' perturbations in sitting, i.e., the support given by the experimenter was withdrawn and the infants consequently lost equilibrium. It is plausible that neither of these situations, i.e., the natural perturbation and the perturbation while sitting in an infant seat, is stressing the system as much as unsupported sitting during external perturbations. From the age of five months infants, exposed to external perturbations during unsupported sitting, exhibit a robust repertoire of direction specific postural adjustments (Hirschfeld and Forssberg 1994; Hadders-Algra et al. 1996a).

The standing position puts higher demands on the ability to maintain equilibrium than the sitting position; the surface of support is smaller and degrees of freedom added. But different standing positions challenge the system differently, e.g., standing *with* and *without support.* Biomechanically, during standing *without* support the translation of the surface of support will result in an inverted pendulum movement of the body, i.e., the whole body will sway around the ankle and, the torque around the

Figure 2. Different contextual constraints challenge the postural control system differently.

ankle therefore has to be controlled (Nashner 1976, 1977). When a adult person is holding on to a support, the biomechanical condition is different and the hands can be used to provide postural stability (Figure 2, Jeka and Lackner 1994; Metcalfe et al. 2004). The nervous system in adults reacts different to these two situations. When an adult person is standing *with hand support*, postural muscle activity will primarily be found in the arms and muscle activity of the legs will be low. When an adult person is standing *without support,* the postural adjustments will instead mainly be found in the muscles controlling the ankle torque (Cordo and Nashner 1982; Jeka and Lackner 1994). This task dependent gain control of the postural adjustments of the lower limbs has great impact on the interpretation of the postural muscle activity in children achieving independent standing. If the infant is not able to stand *without support* and is being assessed *with* support, absence of postural muscle activation in the legs could have two possible explanations. Either the infant is not able to produce adequate postural muscle activity in the lower limb muscles, or, there is a reduced gain of the postural leg muscle activity due to the extra arm support.

In standing position, Sveistrup and Woollacott (1996) have reported that direction specific adjustments are present, although not consistently before independent standing is achieved. They also reported that variation in postural muscle activity decreases with age and experience and that latencies get shorter with the experience of walking, primarily in muscles controlling the ankle (Sveistrup and Woollacott 1996; Woollacott and Burtner 1996). When children have substantial locomotor experience, at around the age of seven active hipflexion is used as a postural strategy (Roncesvalles et al. 2004). This strategy is similar to the 'hip strategy' used in adults during rather large perturbations, or when standing on a beam preventing ankle torque (Horak and Nashner 1986). During small perturbations adults activate muscles controlling the torque around the ankle, i.e., the 'ankle strategy'. Woollacott and co-workers have proposed that the development of postural adjustments starts with the control of the ankle and that gradually more muscle are added to the postural synergy. Assaiante and Amblard (1995) have proposed a different developmental course, the top-down organization. They stated that during childhood the frame of reference for postural control is moved in the opposite direction, from the head to the surface of support. This means that postural control for the head emerges before the control of the lower body. It is not until the age of around 10 years that postural adjustments begin to show similar consistency as in adults (Massion 1998; Forssberg and Nashner 1982; Berger et al. 1987; Woollacott et al. 1987; Roncesvalles et al. 2004).

1.2.2 Pre-determined networks and experience

In the past, two approaches on how to interpret the development of postural adjustments have been put forward (Forssberg 1999, Hadders-Algra 2000, Smith and Thelen 2003, Ulrich 1997). One underlines the innate organization of the basic features of postural adjustments. According to this view genetically pre-determined motor programmes for postural sensorimotor integration are functioning already during early development. A vast set of neural connections and networks process sensory information and give rise to a variety of postural adjustments, among them the complex and adult-like postural adjustment patterns. The other approach has been to emphasize the role of experience and learning to build up the organization of postural adjustments (Woollacott 1987). Although, the possibility of pre-determined connections is not ruled out, trial and error learning is the main focus.

It seems that any dissonance between these two approaches can be attributed to first, how variability in the young infant is interpreted and secondly the role of experience on the development of postural adjustments. Variability in postural adjustments can either be viewed as a multitude of pre-wired possible solutions or as an expression of chance connectivity. If accepting the pre-wired connectivity approach, it becomes reasonable to assume that the role of experience is to select and strengthen the adequate connections and to discard the inadequate ones. If, however accepting the idea that there is no predetermined connectivity, one could presume that experience is necessary in order to build neural connectivity. From both perspectives experience will enhance the development of adequate postural adjustments.

When interpreting the development of motor behaviour, one should consider the underlying neural mechanisms, the 'neural correlates' for motor behaviour. Our perspective embraces the idea that pre-determined networks together with experience underlie the development of postural adjustments. The basic anatomical infrastructure for motor control is established already prenatally. Thus, the newborn infant expresses a great variety in motor behaviours. However, the first year/years of postnatal life will involve tremendous changes within the nervous system, both expansive and regressive (Huttenlocher 1990; Eyre 2003; de Graaf-Peters and Hadders-Algra 2006). Axonal, dendritic and synaptic growth will cause expansion of the nervous system and the overproduction of synaptic contacts will be followed by synapse elimination (Changeux 1973; Huttenlocher 1990). Analogous to the NGST (Sporns and Edelman 1993), synapses producing inadequate motor patterns will be eliminated, while those producing adequate motor patterns will sustain (Figure 3, Forssberg 1999; Hadders-Algra 2000). Neural plasticity will also involve the shaping of supraspinal networks controlling movements, i.e., increase in cortical resolution of sensorimotor representations with increasing age (Chakrabarty and Martin 2000; Sanes and Donoghue 2000; Johansson 2004). Less synergistic and antagonistic muscle activity will be generated during movements (Illingworth 1975; Forssberg et al.

1991). The projection from cortex to the spinal cord will also undergo developmental changes, e.g., the withdrawal of exuberant ipsilateral corticospinal axons (Eyre 2003; Martin 2005), as will the motor neuron pool, e.g., the reciprocal inhibition of the antagonists during voluntary movements will emerge (Myklebust 1990). However, none of these changes will emerge in isolation, supraspinal activity will play a role in the development of networks controlling movements (Martin JH 2005). Thus, changes in the physical structures of the brain will be reflected in changes in its functioning (Kolb 1995), as von Hofsten (2004) puts it when discussion 'action' during infancy, this is 'a process with two foci, one in the central nervous system and one in the subject's dynamic interactions with the environment'.

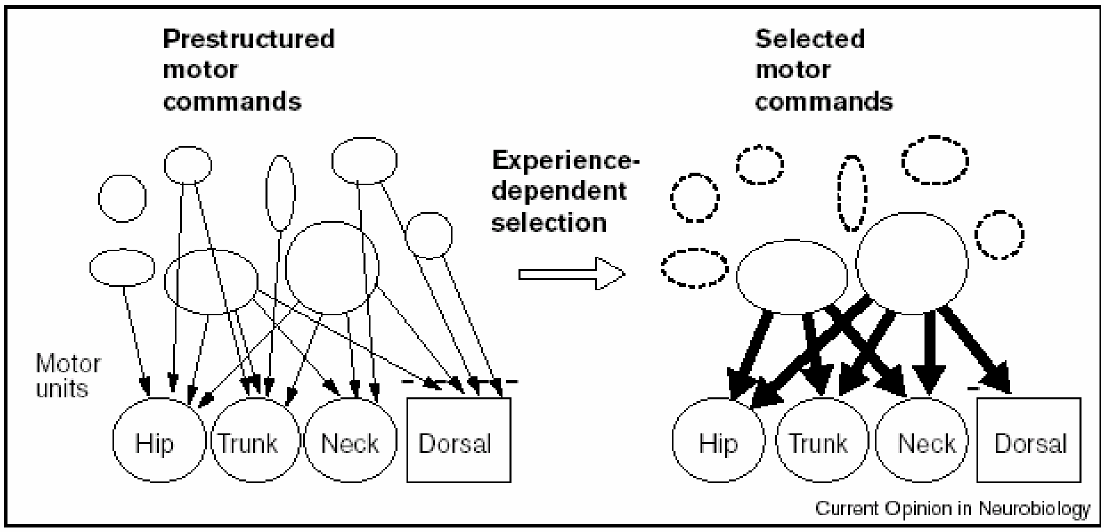

Figure 3. The developmental process of postural muscle activation patterns during infancy, according to the 'neuronal group selection theory'. From a large variation of muscle activation patterns, the most appropriate patterns are selected and strengthened. From Forssberg 1999.

1.3 Transition periods in motor development during infancy

Gross motor behaviour of the newborn marks the continuity of motor behaviour from fetal life into early postnatal life (Prechtl 1984). One example of such behaviour are the so called General Movements (GM, Hadders-Algra et al. 1992; Hadders-Algra 2001; Prechtl 2001; Hadders-Algra 2004). These are whole body movements, spontaneously generated, involving movements of neck, trunk, arms and legs. The quality of GMs, i.e., movement pattern, speed, size and force, change with age and the classification is done according to these qualitative properties. Typically developing full-term infants, exhibit the 'writhing', rather forceful quality, the characteristics of the movements change around the age of 2 months into a continuous flow of small, elegant so called 'fidgety' movements occurring irregularly over the whole body. GMs disappear around the age of 4 months as the goal directed motor behaviour emerges. Apart from the GMs, the movement repertoire of the young infant also includes a variety of evocable reactions which change over time and some will in typically developing infants become silent within the first months of postnatal life (McGraw 1945). Also, myotatic reflexes, i.e., tonic contraction of the muscles in response to a stretching force, due to stimulation of muscle proprioceptors (also called deep tendon reflex, stretch reflex) change with increasing age. In neonates Achilles tendon tapping, will evoke a muscle response not only in the soleus muscle but also in the tibialis anterior, due to the presence of functional excitatory connections from afferent neurons to both agonist and antagonist motor neuron pools (Myklebust 1990).

This reflex irradiation will persist through the period when independent walking is achieved and the reflex response will not take on adult properties until around 4-6 years of age. Another example of changing motor activation is the 'withdrawal reflex', evocable by painful stimulus under the sole of the foot, represents a type of multi joint movements involving flexor muscles i.e., a flexor synergy which bring the leg up and away from the stimulus including the dorsiflexion of the ankle and extension of the toes (Beintema 1968, Illingworth 1975). The extensor response in the toes will disappear as independent standing and plantigrade gait will develop. Synergistic muscle activity is present not only for protection from painful stimulus but also during voluntary movements. As motor skills develop muscle activity will gradually become more differentiated, i.e., less synergistic and antagonistic muscle activity will be generated (Illingworth 1975, Forssberg et al. 1991). Thus, during the first two years of life the infant will make tremendous achievements in motor development. Spontaneous movements will change and goal-directed movements will emerge, in parallel the infant will gain control over the head and trunk and the gross motor milestones will be achieved.

1.4 Cerebral Palsy

Cerebral palsy (CP) describes a group of disorders of the development of movement and posture, causing activity limitation, that are attributed to non-progressive disturbances that occurred in the developing fetal or infant brain. The motor disorders of cerebral palsy are often accompanied by disturbances of sensation, cognition, communication, perception, and/or behaviour, and/or by a seizure disorder (Bax et al. 2005). In the western world the prevalence of CP is 2,2-2,4 in 1000 live births (Hagberg et al. 1996, 2001). The lesion can occur during fetal or neonatal period and the cause may be several; brain malformations, hypoxic-ischaemic/haemorrhagic periventricular lesions and middle cerebral artery infarcts (Krägeloh-Mann 2004). The movement disorders associated with CP are spasticity, musculoskeletal malformations, dyskinesia (dystonia, athetosis, chorea, ataxia), retained transient infant reactions, paresis and central dyscoordination (Forssberg 1999). This means that CP a heterogeneous condition and spastic CP, which is characterized by at least two of; abnormal pattern of posture and/or movement, increased tone and/or pathological reflexes, can be classified as either bilateral or unilateral (SCPE 2000). Unilateral CP, which is traditionally named hemiplegic CP, constitutes about 33% of the CP group (Hagberg et al. 2001).

1.4.1 Voluntary and automatic motor control in children with CP

Voluntary motor behaviour in CP is accompanied by a variety of coordination issues (Forssberg 1999). Difficulties or inability to produce differentiated movements, e.g., of the fingers, is frequently seen (Bobath and Bobath 1975; Steenbergen et al. 1998a). Together with insufficiency in force generation during grasping and manipulation this will result in fine motor clumsiness (Eliasson et al. 1991; Steenbergen et al. 1998b). This dyscoordination could be attributed to disrupted sensorimotor development, which in combination with neural reorganization will give rise to sustained synergistic and additional antagonistic muscle activation patterns (Lawrence and Kuypers 1968 ; Passingham et al. 1978 ; Myklebust 1990 ; Leonard et al. 1990 ; Carr et al. 1993 ; Duque et al. 2003). Also impaired sensory processing might contribute to the motor deficits and often voluntary movements are performed at slow speed to enhance performance (Eliasson et al. 1991; Steenbergen et al. 1998; Thickbroom et al. 2001).

Studies on voluntary motor control in CP have mainly focused on hand function. Motor control of the ankle has been addressed in studies of automatized movements such as locomotion and postural adjustments, which are generated at a different level within the nervous system, i.e., subcortical networks. In a recent study by Tedroff and co-workers (2006), maximum voluntary contraction in leg muscles was assessed in different types of CP. Compared to a control group, children with CP more frequently activated a muscle other than the intended prime mover first, especially when the prime mover was a distal muscle. Children with hemiplegia for example, showed activation of tibialis anterior prior to the prime mover i.e., lateral gastrocnemius, during ankle plantar flexion.

Also automatic motor control, e.g., postural adjustments or locomotion, in CP is characterized by features reminding of disrupted sensorimotor development. Locomotion bears strong resemblances to infant stepping (Leonard et al. 1991a; Forssberg 1999). The EMG pattern of leg activity in typically developing children showed that a reciprocal muscle activity will emerge as the infants learn to walk independently, whereas in children with CP a pattern of co-contraction will sustain. Also postural adjustments show similar sequential and temporal organization as those of young children (Woollacott & Burtner 1996; Brogren et al. 1996; Woollacott et al. 1998). As reported for voluntary movements, synergistic and antagonistic muscle activity also characterizes postural adjustments in CP (Nashner et al. 1983; Woollacott et al. 1996; Brogren et al. 1996). Deficits in postural adjustments may appear as a result of hampered development of supraspinal regulatory mechanisms controlling CPG networks and the motor neuron pools (Myklebust 1990). It could also be due to a secondary maldevelopment of these networks or to sensory deficits. Myotatic reflex activity in children with CP following a tendon tap to a single muscle group (e.g., quadriceps femoris), will irradiate to muscles other than the stimulated (i.e., hamstring), and other muscles distant to the site of stimulation (Leonard et al. 1991b; Myklebust 1982).

Definitions

Voluntary motor activity: Conscious goal-directed movements for which the desired result is defined by an internal representation (Krakauer and Gehz 2000).

Automatic motor activity: Basic spatiotemporal movement patterns generated by subcortically located neuronal circuits, i.e., central pattern generators (Grillner 1985, Pearson and Gordon 2000).

1.5 Outlines of the thesis

The achievement of independent sitting and standing constitute gross motor milestones in the life of the young infant. However, we still know little about what is required in terms of postural adjustments to achieve these milestones. The background to this thesis reveals that postural adjustments have been thoroughly investigated in both adults and children. It also reveals that a well documented assessment is available, i.e., the movable surface of support paradigm. Already, we have information on how young children master the maintenance of equilibrium in different positions, once they are established. Already, we know that children with CP suffer from motor dyscoordination, including that of postural adjustments.

However, some conceptual issues are still to be addressed. First of all, to what degree is the control of posture genetically programmed? If direction specific postural adjustments are present during sitting at one month of age, one could assume that such muscle activity is genetically predetermined, that we are destined to control our body against gravity. Secondly, how primitive or well adapted are postural adjustments in young infants? If postural adjustments are present at early age, well before independent sitting and standing, have developed, what is the developmental course for postural adjustments? Thirdly, we do not know if infants are able to adapt postural adjustments according to contextual constraints. Finally, we do not know the relation between automatic motor control and voluntary motor control in children with CP. Can we gain further understanding for the underlying mechanisms of motor dyscoordination by studying both postural adjustments and voluntarily elicited movements?

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2 AIMS OF THE THESIS

The overall aim of the thesis was to explore mechanisms underlying the development of independent sitting and standing in typically developing infants and, to investigate correlations between voluntary and automatic motor control in children with Cerebral Palsy.

The specific aims were to

- investigate if direction specific postural adjustments are present in one month old infants, inexperienced to unsupported sitting — *Study I*
- describe the development of postural adjustments during sitting, prior the establishment of independent sitting — *Study II*
- describe the development of postural adjustments during standing, during the time in life when independent standing is established — *Study III*
- investigate if the performance of voluntary ankle movement can provide information relevant for the ankle movements during postural adjustments, in children with Cerebral Palsy — *Study IV*

3 MATERIAL AND METHODS

3.1 Subjects

The thesis covers 114 assessments of postural adjustments on the movable platform of infants and children from the age of one month to the age of 15 years. Muscle activity during dorsiflexion was assessed in 29 children, and eight children with CP were assessed with anatomical MR scans for the definition of brain lesions. Table 1 summarizes the distribution of subjects over the studies, subject category as well as the paradigm and acquisition type used.

Table 1

Study	n	Age	Paradigm	Subject category	Acquisition
I	8	1 month	Ext. perturbations, sitting	TD	EMG, kinematics
II	40	1-5 months	Ext. perturbations, sitting	TD	EMG
III	13	8-14 months	Ext. perturbations, standing	TD	EMG
IV	29	9-15 years	Ext. perturbations, standing	TD, CP	EMG
IV	29	9-15 years	Dorsiflexion	TD, CP	EMG
IV	8	9-15 years	Brain lesion definition	CP	MRI

3.1.1 Inclusion criteria and subject recruitment procedures

The infants of studies I-III, were recruited via paediatric nurses at health care clinics for healthy babies (in Swedish; Barnavårdscentral). To test the integrity of the motor development of the 1-5 months old infants, in Study I and II, general movements (GMs) were assessed and all children exhibited typical GMs. Infants recruited to Study III, were assessed with Alberta Infant Motor Scale, the Stand subscale (Piper and Darrah 1994). Children with CP (Study IV) were recruited via the Neuropeaditric Department of Astrid Lindgren Children’s Hospital and the Outpatient Clinics of Stockholm. Inclusion criteria were; hemiplegic CP, GMFCS I (Palisano et al. 1997), attendance to mainstream school, Selective Motor Control (SMC) score (Boyd and Graham 1999) of at least 1. The typically developing children of study IV had no history of motor problems or problems linked to motor development.

3.2 Apparatuses and procedures

3.2.1 Movable platform

External perturbations of the surface of support were induced to elicit postural muscle activity. The underlying principle for this paradigm is that if the equilibrium of the body is perturbed in one direction, the muscles on the opposite side of the body are activated to restore equilibrium. The perturbations we used, consisted of translations in forward or backward directions. We used a rectangular platform, 600x1200 mm, mounted on a metal frame 400 mm above floor level. The platform was driven by a servo motor which was programmed to translate at specific speeds and amplitudes. Onset of each translation was triggered manually by the experimenter, unpredictable to the subject, when the infants/children were focused and relaxed. In all studies the positions in which the subjects were tested, were standardized to head in midline, facing forward, arms not moving. This was done in order to perturb the subjects during a position which did not include any volitional movements which could be confounding to our results. Great care was taken to make the subjects feel comfortable. While testing infants (Study I, II, III) the parent was sitting facing the infant. Breaks were taken if needed for feeding or comfort. The older children (Study IV) were instructed to look into a mirror facing them and to stand as straight as possible with equal weight on both feet. This we could not control for and it could have been beneficial to have had additional force plate data. During standing for as many as 31 translations we noted that both typically developing children and children with CP, tended to want to put the weight on one leg. The children with CP tended to lean towards the unaffected leg and were therefore reminded repeatedly to stand on both feet. All assessments were video recorded for the selection of trials fulfilling the criteria for analyses.

The amplitude of the perturbations was set to 60 mm during both *fw* and *bw* translations, in all studies. In studies I and II, *fw* translations were presented at 120 mm/s and 180 mm/s and *bw* translations were presented at 180 mm/s and 333 mm/s. These speeds were chosen with regard to previous experience that these stimuli are well tolerated by infants (Hadders-Algra et al. 1996a). Also, for Study II the data was to be pooled with previously collected data on postural adjustments in infants (Hadders-Algra et al. 1996a) and the same data acquisition procedures as for that study were therefore undertaken. The higher platform velocity for *bw* translations for the sitting position were chosen due to different response thresholds for postural adjustments previously reported (Forssberg and Hirschfeld 1994; Hirschfeld and Forssberg 1994; Hadders-Algra et al. 1996). During the assessment of postural adjustments in standing we used slower velocities. These were determined through a pilot testing procedure of infants and children prior to data acquisition. For the standing position we did not include an a priori hypothesis that there would be differences in response rates during *fw* and *bw* translations. From a postural control perspective, e.g., differences in base of support, the two positions are fundamentally different and therefore we did not presume that different response thresholds would be found.

Infants were tested in three different positions, i.e., sitting *without support* Study I and II), standing *with support* (Study III) and standing *without support* (Study III and IV). As the infants of study I and II were not able to sit independently, the experimenter manually supported the trunk of the infants until 1-3 seconds before platform onset. The experimenter was holding the platform trigger in her hand and could control the onset of the translations and time it to the moments when the infants were placed in a relatively stable position. The same principle was applied to the infants in study III who were not yet able to stand *without support*, i.e., postural support was given until a few seconds before platform translation started, which was triggered by the experimenter. By using the moving surface of support paradigm in infants who were not able to sit (Study I, II) and stand (Study III) independently we have been working with an experimental design which has been methodologically difficult. The paradigm has previously been successfully used in primarily stabilized positions in both infants and young children, in both positions (Forssberg and Nashner 1982; Woollacott et al. 1987; Hirschfeld and Forssberg 1994; Hadders-Algra et al. 1996a). By providing the infants who were not able to sit or stand independently with the support from the experimenter's hands, one aspect of postural control was reduced, i.e., the infants did not have to align the body segments into a stable position, this was done by the experimenter. This procedure allowed us to target for the postural adjustments linked to the onset of the platform translation.

3.2.2 Postural muscle activity acquisition

Muscle activity was measured using surface electromyography (EMG), which provides a window into the nervous system (Enoka 1994). Bipolar electrodes with an interelectrode distance of 15 mm and an in-built 2,000 x preamplification (MYO 115, Liberty Technology, Hopkinton, MA, USA) were used. The muscles were defined according to function (Kendall and McCreary 1983), see Table 2. This means that we regard the postural control system in terms of a model consisting of agonists and antagonists. Agonists during *fw* translation of the platform and the subsequent elicited sway of the body *bw,* are ventral muscles. This means that the functional synergies for postural adjustments include muscles that can induce flexion in one joint and extension in another. These synergies are conceptually different from the ontogentically significant flexor and extensor synergies, which give rise to either consistent flexor or extensor movements in multiple joints (Illingworth 1975). Antagonists during *fw* translations are consequently muscles on the dorsal side of the body which counteract the agonistic muscle activity.

In studies I, II and III the electrodes were placed over the muscles of the right side of the body, in study IV the electrodes were placed bilaterally. The ground electrode was placed over the right lateral malleol. In table 2, the muscles recorded in the different studies are presented. The procedure for EMG electrode application of the infants started with the infant sitting in the caregivers lap, and the experimenter cleaning the skin locations. The electrodes were then taped to the skin using both double faced tape and medical tape. To prevent the infants from pulling the electrode cables, the electrode sites were then wrapped with a soft bandage. This was however not done over the neck. Offset recordings of the muscle activity was performed as the infants were sitting quietly in the caregivers lap.

Table 2

Muscle	Function	Abbreviations	Study
Sternocleidomastoideus	neck flexion	NF	I, II, III
Erector spinae, at C5-6 level	neck extension	NE	I, II, III
Rectus abdominis	trunk flexion	RA	I, II,
Erector spinae, at L3-4 level	lumbar extension	LE	I, II, III
Rectus femoris	hip flexion	RF	I, II, III, IV
Hamstrings	hip extension	HA	I, II, III, IV
Tibialis anterior	ankle dorsiflexion	TA	III, IV
Gastrocnemius, caput mediale	ankle plantar flexion	GA	III, IV

3.2.3 Postural data processing

Only trials meeting the aforementioned criteria for position and behavioural state were analysed. These were for all studies selected on the basis of the video-recordings. The signals from the platform and the EMG were sampled at 800 Hz, and stored in SC/ZOOM a dedicated signal analysis computer system (Department of Physiology, Umeå University, Sweden). A graphics terminal was used to manually define EMG events for each trial separately. EMG-recordings with artifacts were excluded from the analysis. EMG baseline activity was defined as the mean activity recorded 500 ms before trial onset. EMG-events occurring 30 ms after trial onset were included in the analysis. EMG bursts were defined when the muscle activity exceeded the baseline activity by 2 SD for a duration of at least 30 ms. In studies III and IV muscle activity occurring after 500 ms was not included in the analysis.

The first step in the EMG analysis consisted of the documentation of the muscle activation patterns by describing the presence of bursts and inhibition in the recorded muscles. The response rates for each child and each condition were calculated by dividing the number of trials with a response found with the total number of trials for that specific child during the present condition. The next step consisted of the analysis of EMG latencies. Latency was defined as the time interval between the onset of platform movement and the onset of an EMG response. For each subject the mean latency to response onset was calculated for each muscle and condition. Co-activity was considered to be present when muscle activation of the antagonist occurred within 100 ms after the onset of agonist activation.

3.2.4 Statistical analysis of postural data

Throughout the statistical analyses in all studies, a p-value less than 0.05 was considered to denote significant differences. We did not test for multiple comparisons, although we regard this to be a weakness, we have used statistical analyses commonly accepted in studies on postural control.

Differences in activation rates and latencies between ventral and dorsal muscles and between *fw* and *bw* translations were evaluated with the Wilcoxon Matched Pairs Test, in all studies. In study II, activation rates and mean latency values per infant were compared between ages using Kruskal-Wallis ANOVA by ranks test. In study III, differences between standing *with* and *without support* and differences in activation rates between ages, as well as between ages within conditions was were analysed with the Wilcoxon Matched Pairs Test. In study IV the Wilcoxon Matched Pairs Test was used to recognize differences also between the right and left leg as well as between groups.

3.2.5 Voluntary motor activity acquisition and processing

To assess muscle activity during ankle dorsiflexion, EMG data was collected during five trials of ankle dorsiflexion, i.e., the SMC assessment (Appendix I). The same EMG system as previously described was used. Activity from TA, GA, RF and HA were recorded bilaterally. The children were sitting with straight legs and they were asked to dorsiflex their right ankle to their full range of movement. Children with CP were asked to dorsiflex their affected leg. The goal was to complete a well controlled ankle dorsiflexion movement. The assessment was recorded on video. EMG bursts during active ankle dorsiflexion were identified visually from a graphic display. Muscle activity occurring within 1 second around the onset of the prime mover was regarded as muscle activity linked to the dorsiflexion, and number of muscles activated was counted. EMG bursts for ankle dorsiflexion were defined when the muscle activity exceeded the baseline activity by 2 SD. Spearman Rank correlation was used to evaluate the relation between number of muscles activated in the two tasks.

3.2.6 Biomechanical acquisition and processing

In Study I, kinematic data was recorded in synchrony with the EMG recordings. Previous studies on postural adjustments using kinematic recordings have beneficially added information on the consequences not only of the impact from the platform but also on the consequences of muscle activity and how the initial position is correlated with the response (Forssberg and Hirschfeld 1994; Hirschfeld and Forssberg 1994; Hadders-Algra et al. 1996a). In order to examine the biomechanical consequences of the translations, the kinematic data of the pelvis, bodysway and head were evaluated. The evaluation focused on 1) angular displacement from platform onset to the end of platform translation, 2) angular displacement from platform onset to the peak of platform acceleration, and 3) the rate of change in velocity from platform onset to platform acceleration peak. In addition, the linear displacement and the rate of change in velocity of the platform itself was analysed. In order to obtain information on the sitting position prior to platform onset, maximum angular values for forward and backward rotation during a one-second period prior to onset as well as the angular values at platform onset were determined.

Kinematic data was recorded by a 60 Hz Mac Reflex system in a six camera configuration for 3 seconds, starting 1 second prior to the perturbation. Reflective markers were placed on the head, on the processus spinosus at C7, on the spina iliaca anterior superior (SIAS) and on the trochanter major. Off-line data processing consisted of the calculation of the angle for the head movement (by a vector between markers for caput mandibulae and 1 cm in front of the angulus mandibulae), the pelvis rotation (by a vector between markers for SIAS and trochanter major) and for bodysway (by a vector between markers for C7 and the major trochanter), in relation to the horizontal axis.

Kinematic data were processed including tracking of markers and calculation of angles using standard trigonometry theorems applied to involved markers. Calculated angles were filtered with a Butterworth filter with a cut-off frequency of 6 Hz. The cut-off frequency was determined by running a Fourier analysis on angular data. Linear acceleration of the platform (d^2pos/dt^2) and changes in rate of angular velocity of pelvis and bodysway (d^2ang/dt^2) were calculated by numerical differentiation. Direction specific changes in rate of velocity imply both direction specific angular acceleration as well as non- direction specific angular deceleration. For the statistical processing of the kinematic data in study I, all trials were pooled. Differences in rates of change in angular velocity between pelvis and bodysway were calculated with the Paired *t*-test. Correlations between the rates of change in angular velocity and the number of direction specific muscles participating in the adjustment were calculated using the Pearson Product Moment Correlation.

Regretfully data acquisition was not easily compassed, due to technical inconsistency. The system used could not distinguish between markers at close distance from each other and few data was therefore obtained.

3.2.7 Acquisition and analysis of spontaneous motor behaviour

In Study II spontaneous motor behaviour was assessed and analysed in relation to the postural adjustments at the different ages tested. The purpose for this was to investigate if changes in postural adjustments also were reflected in changes of gross motor activities. Since postural control cannot be regarded as a separate entity, but as an inseparable part of postures or movements, we hypothesized that the development within one domain would mirror also the development in the other. Van der Fits et al. (1999), have previously reported that the accomplishment of successful goal directed reaching is accompanied by changes in postural adjustments. In order to analyse spontaneous motor behaviour, a video recording was made of 10 minutes in the supine position and balancing capacities in the sitting position. One investigator (ÅH) evaluated the video recordings off-line on the basis of the protocol provided in Appendix II. The evaluation provided information on the infant's development in terms of balancing capacity of head and trunk, goal-directed activity in the arms, and goal-directed motility of the trunk and pelvic region. To check the reliability of the video assessment, four randomly selected recordings at each age (4×5 recordings) were also scored by another investigator (EBC). Interobserver agreement expressed in Cohen's kappa varied from 0.71 to 1.00 (median 0.84), indicating a good or very good agreement (Landis and Koch 1977). Spearman Rank correlation was used to evaluate the relation between EMG activity and motor behaviour based on the video-analysis

3.2.8 Acquisition and analysis of standing capacity

In Study III, the infants' ability to stand was assessed with the stand subscale of the Alberta Infant Motor Scale (AIMS, Piper and Darrah 1994). Independent standing was attributed as a function to the infant when the item 'stands alone' was achieved.

3.2.9 Brain lesion definition

Anatomical images of the children's brains were collected for study IV. Both T1 and T2 sequences were used; T1; 3D-SPGR, T2; coronal flair and T2 axial.

4 RESULTS AND DISCUSSION

4.1 Direction specific postural adjustments are present at one month

Already at the age of one month, the infants were able to produce direction specific postural muscle activity, in the unsupported sitting position. Translations in the *bw* direction, evoked direction specific postural adjustments in 85% of the trials, and translations in the *fw* direction, in 72% of the trials, all levels taken into account. The postural adjustments were noted in all recorded muscles and particularly, direction specific postural adjustments were found in the neck muscles (Figure 4).

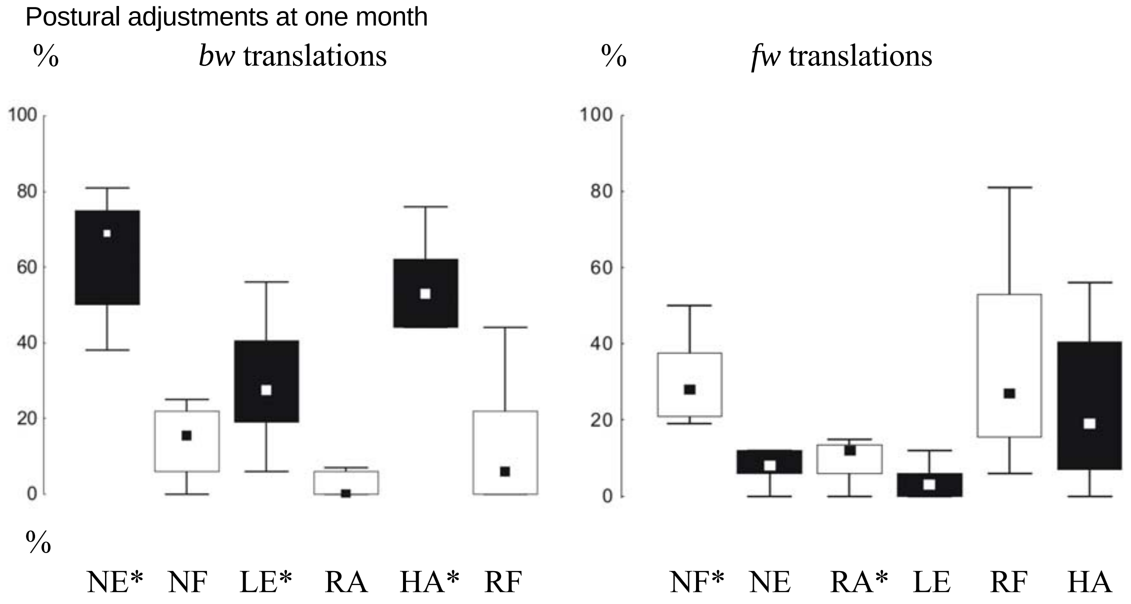

Figure 4. Muscle activity rates in agonistic and antagonistic muscles in one month old infants during sitting without support, during bw and fw translations. Asterisks indicate significant differences between dorsal and ventral muscles: Wilcoxon, *P<0.05. ■dorsal muscles □ventral muscles (Study I).

This finding is in agreement with earlier studies of our group. In 1994 Hirschfeld and Forssberg first proposed that postural adjustments develop in a predetermined way. In 5- to 7-month-old infants who were not able to sit independently, they found consistent direction specific postural adjustments during external perturbations in sitting position (Hirschfeld and Forssberg 1994). Later, also the presence of direction specific adjustments in non-sitting infants of 5–6 months was confirmed (Hadders-Algra et al. 1996a). Woollacott and co-workers, who also used the moving platform paradigm, were not able to find consistent direction specific postural activity in sitting infants aged 4–5 months, although they report of some direction specificity (Woollacott et al. 1987). However, the lack of direction specific activity within their group might be explained by the fact that the infants were not sitting freely while being perturbed, but were supported by an infant seat. It should be noted that platform velocities for *fw* and *bw* translations were not the same in our study. Backward translations were faster and this could explain the differences in ventral and dorsal muscle activity. Although different response thresholds for the two directions have been noted in infants (Hirschfeld and Forssberg 1994) we cannot rule out that the higher responses during *bw* translations as compared to *fw*, are due to these differences in velocities. Thus, it seems that the impact of the stimulus at this young age is important and could explain the high rates of adequate responses when testing infants in a freely sitting position. Harbourne and colleagues, who studied postural responses in non-sitting infants by means of a sudden release of trunk support in the sitting position, found 'directionally appropriate' responses in the infants aged 4–5 months, but not in those of 2–3 months (Harbourne et al. 1993). In contrast, Prechtl suggested that direction specific activity emerges at the age of about 10 weeks, i.e., 2-3 months of age since he found neck muscle activity during tilting perturbations in prone and supine position in some infants aged 4 days to 25 weeks (Prechtl 1989).

4.2 Acceleration triggers postural adjustments in the young infant

At one month, the biomechanical consequences of the translations in the *fw* direction during sitting were not as consistent as during translations in the *bw* direction. Forward translations did not always result in the direction specific *bw* pelvis rotation and the *bw* sway of the body. In about half of the trials the *fw* translations resulted in *non-direction* specific pelvis rotation and *non-direction* specific body sway, measured at the *end* of platform translation. Still the infants produced direction specific postural adjustments to a high degree, i.e., in 72% of the trials. We therefore analyzed the mechanical consequences at the *peak of platform acceleration*. During this initial phase of platform translation we found direction specific biomechanical behaviour of the pelvis and body sway, during both *fw* and *bw* translations. This means that the brisk start of the translation, affect the body and can give rise to sensory information of the direction of the translation. Angular displacement and the rate of change in velocity of the pelvis, were both larger than that of the body sway, during *fw* translations (angular displacement; $P<0.01$, rate of change in velocity; $P<0.001$).

The trigger mechanisms for postural adjustments have been intensely debated. In infants and children there has been a discussion on the contribution to the sensorimotor integration regarding different sensory modalities. Our results put emphasis on the proprioceptive qualities of the ingoing information on threats to equilibrium. In the sitting position, previous studies have indicated (Forssberg and Hirschfeld 1994; Hirschfeld and Forssberg 1994; Bloem et al. 2000; Dietz 1998) that proprioceptive information of body parts in the relative neighbourhood of the support surface plays a major role in the triggering. The startle response, a stereotype motor reaction, which can be evoked by vestibular stimuli, can be elicited in newborn babies. This means that sensorimotor programs can be triggered by the vestibular system from birth, however the primary role of the vestibular system in response triggering of postural adjustments was excluded in previous studies on the basis that the head and consequently the inner ear was not moving consistently with the external perturbations (Hadders-Algra et al. 1996a; Hirschfeld and Forssberg 1994). Despite the limited data on the behaviour of the head during platform perturbations in Study I, we suggested that the vestibular system is not the primary trigger of postural activity at the age of one month.

The visual system also provides information on the relationship between the head and body and the surrounding environment. Newborn infants are able to fixateobjects visually, and to follow moving objects with their eyes (von Hofsten 2004). When exposed to a moving surrounding visual field at close range (approximately 10 cm), newborn infants react to this by pressing the head in the opposite direction, which indicates the presence of sensorimotor coupling between visual input and postural head movements (Jouen et al. 2000). But whether their capacity to integrate rapid changes at a distance within the peripheral visual field, i.e., to perceive their motion through space in a room as of the present experimental setting is not clear. In fact, infants aged 4 months showed more often direction specific responses when they were deprived of visual input (Woollacott et al. 1987). The same study reported that at 2-3 years of age, visual input is still not required but influences the postural reactions. Multimodal sensorimotor integration for postural adjustments has been proposed to develop at around 5-7 years of age (Forssberg and Nashner 1982).

Although, the kinematic data in Study I, of infants aged one month is limited and should be interpreted with caution we suggest that cutaneous mechanoreceptors, which are known to be extremely sensitive to direction specific stretch (Johansson and Westling 1984, 1987; Edin 2001; Olausson et al. 2000), in the buttock region could pick up the impact of the platform on the lower parts of the infant's body. Possibly, the tactile information could be co-processed with the proprioceptive information of the pelvic region with the resulting information generating the direction specific adjustment (Edin 2001; Kavounoudias et al. 2001). Studies on the startle reaction have shown that the combination of information from several sensory modalities (vestibular, auditory and tactile), by far more easily elicit the startle response than unimodal stimulus (Yeomans et al. 2002). Cross-modal integration has been proposed to be rule rather than an exception (Shimojo and Shams 2001).

4.3 Variation characterizes postural adjustments at early age

Large variation was found in the direction specific postural adjustments in both the sitting and the two standing positions, at early age. Variation was noted in which muscle/muscles that were activated (Figure 5), in the number of muscles activated (Figure 6), as well as in the latencies to response onset (Figure 8). These results are in line with previous studies (Woollacott et al. 1987; Hadders-Algra et al. 1996a; Harbourne 1993). Variation characterizes motor behaviour in infants and young children (Touwen 1976, 1993; Connolly 1981; Haehl et al. 2000; Smith and Thelen 2003), and should be incorporated in theorizing from a developmental perspective (Connolly 1981). During spontaneous whole body movements, i.e., General Movements (GM), which are present in infants until voluntary movements emerge, variation denotes typical development (Prechtl 2001). Variable postural adjustments in the young infant can be considered as the motor output of neural activity from sets of existing neural connections (Hirschfeld and Forssberg 1994; Hadders-Algra 1996a, b). As response to stimulus one network configuration fires and triggers postural muscle activity. The next stimulus triggers another network configuration which evokes a different motor pattern.

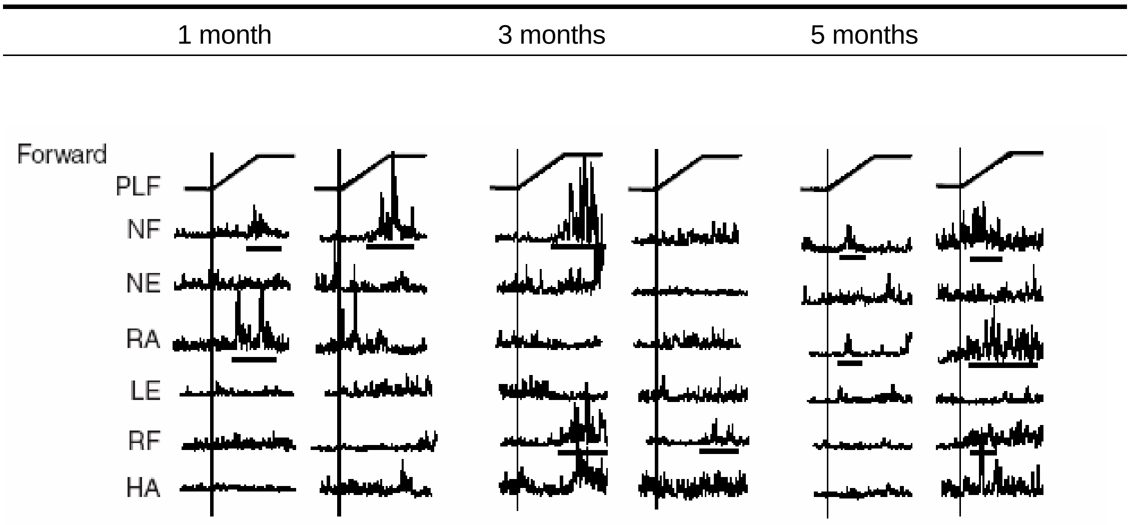

Figure 5. Examples of variable postural muscle activity during *fw* translations in three infants, aged 1, 3 and 5 months, during sitting without support. Two trials from each infant are presented (Study II).

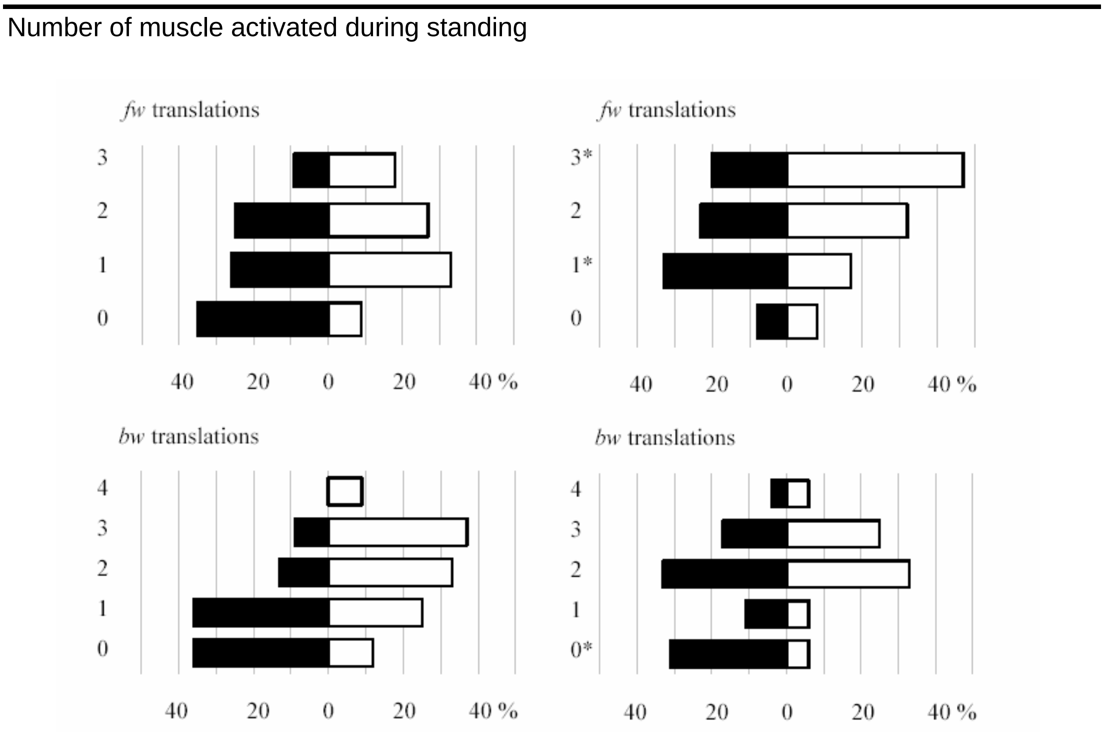

Figure 6. Variation in the number of muscles activated presented in % (median values) at 8 and 14 months, during standing ■ *with* and □ *without* support (Study III).

However, variation could also be viewed as an expression for the building of new connections through trial and error. In the dynamic systems approach little emphasis is put on the underlying neural mechanisms for motor development. Instead the activities and the observed trial-and-error behaviour of infants are in focus. From this perspective, motor behaviour is viewed as system without predetermined patterns which is self-organizing in accordance to the given constraints (Smith and Thelen 2003).

4.4 Modulation by selection with increasing age

With increasing age and experience we found that variation decreased in both sitting and standing positions. In sitting position, the 'complete' pattern became increasingly frequent with age (Figure 7). Already at one month of age the repertoire of direction specific adjustments included all three direction specific muscles. With increasing age, the activation rate of the 'complete' pattern first dropped at 3 months during both *fw* and *bw* translations. From 3 and 4 months onwards the rate gradually rose and at 5 months 6% of the trials resulted in the activation of all recorded direction specific muscles during *fw* translations, and in 12% during *bw* translations. In the results of study II, we included previously published data from Hadders-Algra et al. (1996a) in which the activation rates from infants aged 6 to 10 months were analyzed. Together these datasets give a total picture of the development of the complete patterns from the age of one month to 10 months.

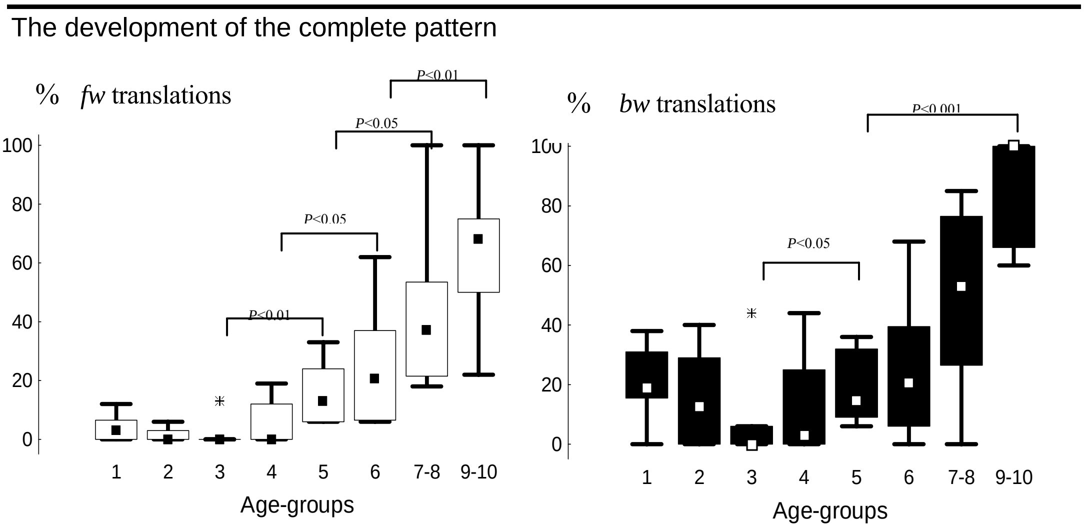

Figure 7. The activation rates for the 'complete pattern' in sitting, during which all recorded direction specific muscles were activated (Study II).

In standing, although we found that a three-muscle combination was more frequent with age we also noted the selection of specific muscle activity. In standing the modulation strived towards the more frequent and faster activation of ankle muscles with increasing age (Figure 8).

In accordance to NGST (Sporns and Edelman 1993), Forssberg in 1999 (and Hadders-Algra in 2000) proposed that the variation seen in postural adjustments during infancy and early childhood constitutes the basic postural behaviour from which appropriate postural adjustments will be selected (Hadders-Algra 1996a, b). From the large repertoire of muscle combinations, which also includes the muscle activation pattern present in adults, the most functional pattern of postural adjustments will be selected and strengthened. During movements the infant is provided with sensory information from proprioception which gives feedback on the consequences of the movements (Prechtl 2001). It has been suggested that the nervous system utilizes such spontaneous neural activity to shape and strengthen sensorimotor coordination (Sporns and Edelman 1993; Khazipov 2004; Forssberg 1999; Hadders-Algra 2000). The application of NGST on the development of postural adjustments means that from a rich repertoire of postural adjustments the most appropriate adjustments are strengthened through a selection process (Forssberg 1999; Hadders-Algra 2000; van Heijst et al. 2000).

During the acquisition phases of independent sitting and standing we found that the selection was expressed in two ways, i.e., the selection of the complete pattern and that of context dependent patterns. Particularly for the sitting position the 'complete pattern' increased with age. The sitting position is one of the first independent antigravity positions to be acquired. It emerges as early as from around six months of age (Piper and Darrah 1994). The engagement of the whole body in the response patterns could reflect a first selection phase (Touwen 1993; Assaiante and Amblard 1995). With increasing experience, postural adjustments will become more fine-tuned to the specific constraints of the situation (Hirschfeld and Forssberg 1994; Hadders-Algra et al. 1996a). This reshaping of the direction specific postural adjustments can be attributed a secondary selection phase (Touwen 1993; Hirschfeld and Forssberg 1994; Hadders-Algra et al. 1996a). In the standing position the three-muscle combination, i. e., muscles of neck, upper and lower leg, also increased with age, however the temporal organization of muscle activity also revealed context dependent patterns. The increased activity in muscles controlling the ankle joint in the older children could thus reflect the secondary selection phase, a fine tuning of the postural activity.

4.5 Postural adjustments are context dependent at early age

Our data show that infants exhibit different postural adjustment patterns according to the contextual constraints. The biomechanical constraints of the positions, that of sitting and those of standing *with* and *without* support all differ from each other. The sitting position offers a broad base of support whereas during standing *without* support the projection of COM must fall within a much more narrow area. This leads to muscle activity controlling the torque around the ankle (Nashner 1976, 1977). During standing holding on to a support, additional support via the hand is added to the stabilizing properties of that particular position (Jeka and Lackner 1982). According to Massion and co-authors (2004), postural control has two main functions; antigravity control and controlling the relationship between perception and action. Together they shape the internal representation of the body's configuration, or body scheme (Gurfinkel 1993), and its relationship to the external world (Massion 1998, Massion et al. 2004). The differences in postural adjustments between the two standing positions imply that infants early begin to build internal representation of the body and explore its interaction to the external world as they are exposed to a new standing condition. The low rates of direction appropriate postural adjustments reported in young infants in sitting position could reflect that muscle activity is scaled in that particular situation (Woollacott et al. 1987; Harbourne et al. 1993). Although the infants can distinguish and adjust to the two different standing positions before they can stand independently, the refinement of the postural adjustments and the building of internal representations of the body and the environment will continue for years to come (Forssberg et al. 1992; Massion 1998; Roncesvalles et al. 2004).

In our data, from both sitting and standing positions we found evidence for the top-down developmental sequence for postural adjustments. In sitting position neck muscles were generally the most frequently activated muscles before the age of five months. With increasing age the trunk and leg muscles were more often activated. In standing position, there was predominantly direction specific agonist/antagonist activation in the proximal muscles at the younger ages. With age the distal muscles were more frequently activated, while proximal remained. That motor control develops in a cephalo-caudal or top-down order has long been imbedded in the theoretical framework of the neuromuscular maturation of the infant (McGraw 1945). From mastering the lifting and balancing of the head in lying positions, the infant will continue to develop control of the body in antigravity positions and become increasingly mobile (Darrah and Piper 1994). Assaiante and Amblard (1995) formulated an ontogenetic model for the sensorimotor organisation of postural control. This model relies on two principles, the stable reference frame and the gradual mastering of various degrees of freedom. The reference frame during quiet standing is the feet, during the carrying of a glass of water the reference frame is moved to the glass, because this is what needs to be kept in a stable position in order not to spill any of the water. Assaiante and Amblard argued that with ontogeny the reference frame moves from top towards bottom, i.e., from the importance to control of the head in space to the control the torque around the ankles. This implies that the frame of reference changes with the task.

4.6 Development of postural adjustments is non-linear

It has repeatedly been reported that motor development is not a linear process (McGraw 1945; Prechtl 1984; Thelen and Spencer 1998). We found oscillations in our data at particular ages. First, around three months, there was a decrease in direction specific postural adjustments. From this age postural adjustments started to correlate to spontaneous motor behaviour. This coincides with changes in the EMG pattern for GMs, i.e., decrease in tonic background activity and the reduction of the amplitude and duration of phasic EMG bursts (Hadders-Algra et al. 1992). It also coincides with decreased H-reflex excitability (Hakamada 1988). The ‘neural correlates’ for such changes in muscle activation could hence be changes within the motor neuron pools (Ijkema-Paassen and Gramsbergen 2005), increased supraspinal modulation of spinal networks (Myklebust 1990; Leonard et al. 1991b), the withdrawal of ipsilateral corticospinal axons (Eyre 2003). It could also reflect that muscle activity per se is important for the development of the sensorimotor pathways (Khazipov et al 2004).

In standing changes were particularly noted between the ages of 10 and 14 months. Not only, were the ankle muscles more often included in the response with increasing age, but also, they were recruited with shorter latencies (Figure 8). At the same time the activation of neck muscles stayed approximately the same. This coincides with a change in leg muscle activation patterns in infants learning to walk (Leonard 1991a). Before the development of independent walking, the EMG activity of young children exhibit co-contraction and short-latency burst. As children gain independent walking, the muscle activity becomes reciprocal. We did not find any significant correlations of muscle activity to the standing capacity, as measured by the stand subscale of Alberta Infant Motor Scale. However, the emergence of independent standing and walking and an increased ability to integrate sensory information have previously been reported to influence postural adjustments (Forssberg and Nashner 1982; Woollacott and Burtner 1996; Sundermier and Woollacott 1998; Woollacott et al. 1998; Barela et al. 1999).

Latencies to response onset during standing

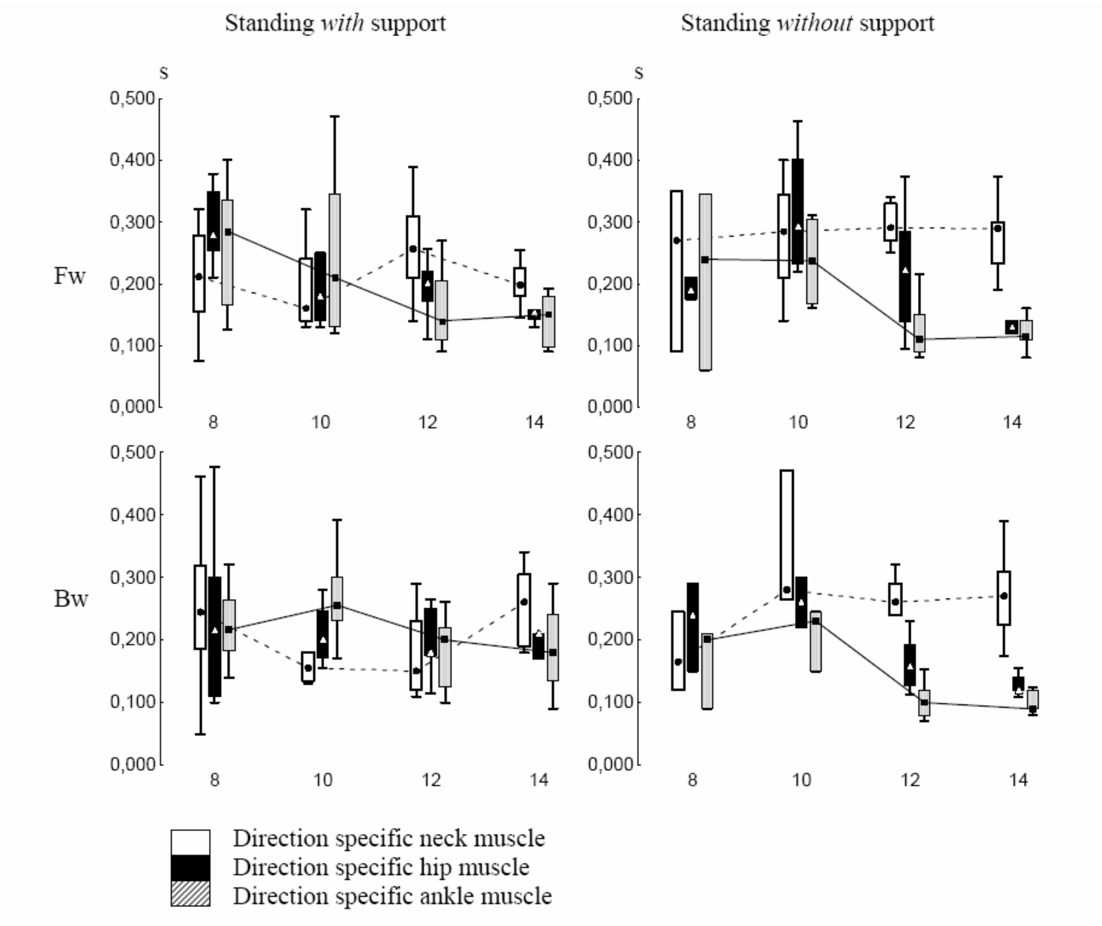

Figure 8. The development of direction specific latencies to response onset. The direction specific muscles during *fw* translations are NF, RF and TA, during *bw* translations; NE, HA and GA. Boxes show 25-75% of the data, whiskers show non-outlier ranges (Study III).

4.7 Motor control in children with CP

Externally triggered postural adjustments, i.e., the small adjustments that may be required to reassure or to regain the well balanced position, are part of the global maintenance of equilibrium. To put these postural adjustments in the perspective of motor activities we explored postural adjustments in relation to voluntary ankle dorsiflexion (Study IV). It has been proposed that the performance on the SMC scale (Boyd and Graham 1999) could serve as a predictor of motor function in children with CP (Østensjø et al. 2003). Since the control of the ankle is important for postural adjustments during standing the idea was to test if this assessment could provide information relevant also for the control of the ankle during a postural task. We found a tendency for a positive correlation of the number of muscles activated during the two tasks. However, we also noted that in some children the activation of many muscles during voluntary dorsiflexion did not mean the activation of many muscles during the postural assessment. One child for example activated seven muscles during active dorsiflexion, during the postural task antagonistic activity was only noted in 33% of the trials. This means that the testing of voluntary motor control as done with the SMC could give some information on automatized motor control, however, not to full satisfaction. Although it is likely that a common mechanism, such as deficient regulation of spinal networks would affect both types of motor control, our results show does not have to be the case. Consequently, the testing of both types of motor control is needed in order to reveal the full clinical picture of motor control in children with CP.

We choose to count the number of muscle activated during dorsiflexion regardless of sequencing. Tedroff et al. (2006) who tested maximum voluntary contraction in leg muscles in children with CP reported 22 different muscle activation sequences for dorsiflexion. They recorded muscle activity from one leg, i.e., four muscles. We recorded activity from both legs, i.e., eight muscles, leaving us with a multitude in possible muscle activation sequences. Some of the children exhibited mirror movements, and we therefore restricted our analysis to counting the number of muscles activated not taking the sequencing into account. Mirror movements in children with hemiplegic CP are commonly found (Kuhtz-Buschbeck et al. 2000), but the SMC scale does not test for this. However, the importance of mirror movements of the legs in relation to gross motor activities has not been thoroughly investigated. Mirror movements during manual activities are not related to the degree of hemiplegia, and these can be suppressed to some extent by voluntary effort (Kuhtz-Buschbeck et al. 2000). The simultaneous rating of mirror movements (Woods and Teuber 1978) while assessing dorsiflexion with the SMC scale, could be done to gain further insight on this.

4.8 Limitations and future research

This thesis contributes with information on the early development of postural adjustments but it also leaves some questions that are still open.

Data collection of infant motor behaviour, is accompanied with practical and logistic difficulties. We have had to deal with some specific problems such as low numbers of participants, particularly in Study III and, few data from the kinematic assessment in Study I. Consequently it would be beneficial if the results from these studies could be reproduced. Also, to out rule that the postural adjustments were triggered by anything else than the impact from the platform in the non-sitting (Studies I, II) and non-standing (Studies III) infant, the additional testing of postural adjustments to natural perturbations as Harbourne and colleagues (1993) has done could also be beneficial.

In Study I we stated that tactile input in young infants can trigger the postural response. It would therefore be interesting to investigate the sensitivity of stretch of the skin in young infants.

Study III leaves us with one major concern; it would be of great importance to test more non-standing infants in the unsupported standing condition to get enough data to make proper statistical analyses.

Study IV, could be considered as a first attempt to put the role of reactional postural adjustments into the perspective of volitional action in children with CP. It would be most beneficial to investigate the clinical relevance for impaired postural control and, to investigate the effects of training. The last question has been addressed by Woollacott and collegues (2005) in a pilot study and it would be interesting to test the effect of different types of training on both postural adjustments and every day life.

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Appendix I

Selective Motor Control scale (Boyd and Graham, 1999).

Grade	Definition
0	No movement when asked to dorsiflex
1	Limited dorsiflexion using mainly m. extensor hallucis longus and/or m. extensor digitorum longus
2	Dorsiflexion using m. extensor hallucis longus, m. extensor digitorum longus and some m tibialis anterior activity
3	Dorsiflexion achieved using mainly m. tibialis anterior, but accompanied by hip and/or knee flexion
4	Isolated selective dorsiflexion achieved, through available range, using a balance of m. tibialis anterior activity without hip and knee flexion

Appendix II

Evaluation of spontaneous motor behaviour in supine position and balancing capacity in sitting position (based partly on Touwen [1976])

Balancing capacity of head and trunk
Head position in the supine position
0 = cannot keep head in midline
1 = can keep head to a limited extent in midline
2 = can keep head adequately in midline
Symmetrical abduction posture shoulders as a postural strategy
0 = absent
1 = occasionally present
2 = frequently present
Head balance in sitting position
0 = no head balance
1 = limited head balance, can keep head up for a few seconds
2 = moderate head control, balances head with some wobbling movements
3 = adequate head control
Balance of the trunk in sitting position
0 = no balancing capacity of the trunk
1 = is able to balance upper part of the body, i.e. needs substantial support while sitting
2 = can almost sit independently, needs a little external support
3 = can sit independently
Goal-directed motility of arms/ Hands to the midline/mouth
0 = absent
1 = occasionally present
2 = frequently present
Goal-directed motility of trunk and pelvic region / Backward pelvis tilt
0 = no posterior pelvis tilt
1 = occasional posterior pelvis tilt (buttocks in general on support surface)
2 = tilts pelvis frequently, but buttocks major part of the time on support surface
3 = tilts pelvis frequently, buttocks major part of the time from the support surface
Hands touching lower parts of legs
0 = absent
1 = present, touches knees
2 = present, grasps feet
Turning into prone position
0 = no rolling or turning attempts
1 = rolls to side
2 = turns into prone position