# ABSTRACT

Title of Dissertation: THE DEVELOPMENT OF ADAPTIVE SENSORIMOTOR CONTROL IN INFANT UPRIGHT POSTURE

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Postural control has been suggested as an important factor for early motor development, however, little is known about how infants acquire the ability to control their upright posture in changing environments and differing tasks. This dissertation addresses these issues in the first two years of life when infants learn to sit, stand, and walk. Three specific aims will be addressed: 1) to characterize the development of unperturbed infant upright postural sway; 2) to establish the influence of static somatosensory information on infant postural sway; and 3) to characterize the dynamic relationship between the infant's posture and sensory information. Three studies were conducted.

The first study longitudinally examined infants' quiet stance and the influence of static touch in the 9 months following walk onset. With increasing walking experience, infants' upright postural sway developed toward lower frequency and slower velocity without changing the amount of sway. Additional touch information attenuated postural sway and decreased the sway velocity without affecting the frequency characteristics. We concluded that early postural development may involve increasing the use of sensory information to tune sensorimotor relationships that enhance estimating self-motion in the environment. The second study longitudinally characterized infants' unperturbed sitting postural sway and the influence of static touch. A temporary disruption of infant sitting posture was observed around walk onset. Light touch contact attenuated sitting postural sway only at this transition when infants' posture became unstable. These results suggest a sensorimotor re-calibration process in infant postural control to accommodate the newly emerging bipedal behavior of independent walking. The third study systematically examined the adaptive visual-postural dynamics, specifically the frequency- and amplitude-dependent features, in a cross-sectional sample of infants as they develop from sitting to standing and walking. The results revealed that infants as young as sitting onset were able to control their sitting posture responding to an oscillating visual stimulus as well as to re-weight the visual information as the stimulus amplitude changes. However, newly sitting infants, compared to experienced walkers, were more responsive but variable when the stimulus amplitude was small. We conclude from these three studies that infant postural development involves a complementary process between improving postural control of self-motion and an increasing sensitivity to environmental motion.

# THE DEVELOPMENT OF ADAPTIVE SENSORIMOTOR CONTROL IN INFANT UPRIGHT POSTURE

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# Chapter 1

# Introduction

Postural control is an essential element for sensorimotor performance and has been suggested as an important factor in the development of motor skills during infancy (Bertenthal & Clifton, 1998). However, infants' postural control is nascent at birth. It is not until around six months of age that the infant is able to control the head and trunk in sitting and another six months before he/she can maintain balance on two feet and achieve bipedal locomotion. While there is much descriptive documentation on the chronologies of infant postural development (Bayley, 1993; Gesell, 1946; McGraw, 1943; Piper & Darrah, 1994), little is known about the processes that underlie these developmental changes.

Early theories characterized postural control as a static state resulting from the summation of reflexes that act on the body to compensate for gravitational forces (Horak & Macpherson, 1996; Shumway-Cook & Woollacott, 2001). Contemporary conceptualizations view postural control as the results of dynamic, complex interactions among the neuromuscular system, its surrounding environment, and the task constraints (Bertenthal & Clifton, 1998; Horak & Macpherson, 1996). Human postural sway represents a system that continuously adapts to the internal and external perturbations (Oie, Kiemel, & Jeka, 2002) rather than a simple unfolding of reflex chains. Recently, adult upright posture has been characterized as a combination of postural estimation and feedback control processes (Oie et al., 2002; van der Kooij, Jacobs, Koopman, & van der Helm, 2001). Estimation is the process in which sensory information from multiple sources is combined to give continuously updated estimates of body dynamics. Feedback control is the process whereby motor commands, based upon the current estimates of body dynamics, are sent to the musculature to maintain the upright posture. Successfully controlling the multi-segmented body across various postural tasks (e.g., sitting, walking, and running) in an ever-changing environment requires adaptive and reliable sensorimotor relationships that provide the basis for postural estimates and the generation of appropriate motor responses (Kuo, 2005; Oie et al., 2002).

Many models have been proposed to explain how adult upright posture is controlled. In most models, sensory information from multiple sources including visual, vestibular, and somatosensory, plays a critical role in postural control. Adult upright posture is influenced by the properties of the sensory information (Dijkstra, Schoner, Giese, & Gielen, 1994; Jeka, Oie, & Kiemel, 2000; Peterka, 2000; Peterka & Benolken, 1995) as well as the interactions among multiple sensors (Kiemel, Oie, & Jeka, 2002; Oie et al., 2002; Peterka & Benolken, 1995). For example, the entrainment of adult upright posture to a moving visual environment has been shown to be dependent on the frequency and amplitude of the visual stimulus (Dijkstra et al., 1994; Peterka & Benolken, 1995) and could be modified by the properties of somatosensory information that was provided simultaneously (Oie et al., 2002). Postural control depends on multiple sources of sensory information. Adaptive postural control requires the ability to re-weight the sensory information from these multiple sources (Kiemel et al., 2002; Oie et al., 2002). This sensory re-weighting process provides the basis for updating the postural estimates and generating appropriate motor commands to adapt to the changing sensory environment and task demands. From this adaptive sensorimotor control perspective, postural development would be hypothesized to involve the calibration of these sensorimotor relationships.

There is little evidence about how adaptive postural control develops in infancy; a time when postural behavior changes dramatically. Much of the research on the development of postural control in infants has examined age-related changes in the muscle responses to a mechanical perturbation of the support surface (e.g., Hadders-Algra, 2005; Hedberg, Carlberg, Forssberg, & Hadders-Algra, 2005; Sveistrup & Woollacott, 1996). The conclusion from such studies is that the organization of postural adjustments has an innate origin and that postural development is a process of neuromuscular maturation. Far fewer studies have examined the perception-action relationships in the development of infants' upright posture. Research has revealed that infants, as young as newborn, are able to show direction-appropriate postural responses to a visual flow stimulus (Jouen, 1990; Jouen, Lepecq, Gapenne, & Bertenthal, 2000). With increasing age, the infant's postural response to a discrete visual stimulus becomes more direction-consistent and magnitude-appropriate (Butterworth & Hicks, 1977; Lee & Aronson, 1974). The discrete stimulus, however, does not capture the dynamic relationship between the postural system and the continuously changing sensory information receiving from the body and its surrounding.

Recent research has begun to probe infants' postural responses to a continuous sensory stimulus. For example, seated infants are able to couple to an oscillating visual stimulus (e.g., moving room) although the results are equivocal as to how this visual-postural relationship changes with the sensory properties (frequency) and whether there are experience- or age-related changes in this coupling relationship (Barela, Godoi, Freitas, & Polastri, 2000; Bertenthal, Boker, & Xu, 2000; Bertenthal, Rose, & Bai, 1997). One reason there are equivocal results may be due to the use of large stimulus amplitudes that reduce postural responsiveness to the stimulation (Peterka & Benolken, 1995). These conflicting results also may be due to the use of inconsistent optic flow velocities; a property that has been suggested as critical to adult postural control (Jeka, Kiemel, Creath, Horak, & Peterka, 2004; Kiemel et al., 2002). Further, the visual stimulus frequencies employed in these infant postural studies (Barela et al., 2000; Bertenthal et al., 2000; Bertenthal et al., 1997) were adopted from adult research and may not be appropriate for the frequency range of infants' postural sway that is known to be higher than adults' sway (Metcalfe et al., 2005a).

If we are to understand how the sensorimotor relationships adapt to the properties of sensory information during development, it is important first to understand infants' quiet unperturbed posture. Only one study has examined the development of infants' quiet stance and characterized postural development as a reduction in the rate constant, indicating a frequency decrease in infants' postural sway (Metcalfe et al., 2005a). With increasing experience in upright stance, infants use somatosensory information from the hand lightly touching a contact surface for prospective control of upright posture (Barela, Jeka, & Clark, 1999) and to modify the parameters (e.g., stiffness) of the control system. When lightly touching a gently oscillating somatosensory drive, infants showed temporal stability in the sensorimotor relationships at the onset of walking that strengthened with increasing walking experience (Metcalfe et al., 2005b). Metcalfe and colleagues suggested that postural development is a continuous sensorimotor calibration process which allows infants to use sensory information to better estimate their body dynamics and to issue motor commands that lead to flexible and stable stance control.

### *Dissertation Purpose and Specific Aims*

The purpose of this dissertation was to systemically study the development of sensorimotor control in the period when infants' postural behavior undergoes dramatic changes; that is, in the first two years of life when infants learn to sit, stand, and walk. To understand this development, the first step is to describe the age- and experience-related changes in infant posture. This dissertation is the first research to characterize the development of infants' unperturbed postural control in sitting and standing, the two most significant postural milestones during infancy. This dissertation also examined the sensorimotor relationship in infant posture and how it adapts to changing sensory stimuli during the developmental period when infants learn to sit, stand, and walk.

This dissertation focused on three specific aims:

*Specific Aim #1: To characterize the development of independent, unperturbed upright posture as infants develop postural control sufficient to sit, stand, and walk.*

Postural development in childhood has been characterized by changes in the temporal, spatial, and frequency properties of unperturbed postural sway (Kirshenbaum, Riach, & Starkes, 2001; Riach & Hayes, 1987). Previous research suggested that the development of infant standing posture involves frequency changes rather than a consistent attenuation of postural sway (Metcalfe et al., 2005a). In this dissertation, infants' unperturbed postural sway in sitting and standing is fully characterized in the temporal-spatial and frequency domain during the development of sitting, standing, and walking.

*Hypothesis 1*: With increasing experience in upright posture, infants will decrease the rate-related properties of postural sway, i.e., frequency and velocity. As shown in previous research, infant upright posture would not show developmental changes in the spatial characteristics, e.g. variance and area (Metcalfe et al., 2005a). The results for this hypothesis are reported in chapter three for standing and chapter four for sitting.

*Specific Aim #2. To establish the influence of static somatosensory information from light touch contact on infants' independent, unperturbed upright posture as infants develop postural control sufficient to sit, stand, and walk.*

Research has consistently found a reduction of postural sway when providing additional sensory information. While it is suggested that sensory information does not affect the control process in adult posture, infants may use the sensory information to modify the control parameters (stiffness or damping) of the developing postural system that reflects in the rate-related characteristics of postural sway (Metcalfe et al., 2005a; Metcalfe & Clark, 2000). This dissertation examined the influence of static somatosensory information obtained from the hand lightly touching a contact surface on infants' sitting and standing posture as the infant acquires the skills of sitting, standing, and walking. The influences of stationary touch contact on infant posture were fully examined with temporal-spatial as well as frequency domain measures.

*Hypothesis 2:* Touching a stationary contact surface will reduce infants' sitting and standing postural sway that can be measured by temporal-spatial variables (e.g., sway variance, amplitude, and area). In addition, infants will show changes in the rate-related measures of postural sway, including frequency and velocity. The results for this hypothesis are reported in chapter three for standing and chapter four for sitting.

*Specific Aim #3. To characterize the sensorimotor relationship of infant postural control and its relation to the sensory properties as infants develop postural control sufficient to sit, stand, and walk.*

The sensorimotor coupling relationship of adult posture responding to dynamic sensory stimuli (visual or somatosensory) shows frequency- and amplitude-dependent properties that reflect in the strength and temporal relations of the coupling (Dijkstra et al., 1994; Jeka, Schoner, Dijkstra, Ribeiro, & Lackner, 1997; Oie et al., 2002; Peterka & Benolken, 1995). Infants entrain their upright postural sway to dynamic somatosensory (Metcalfe et al., 2005b) and visual stimuli (Barela et al., 2000; Bertenthal et al., 2000; Bertenthal et al., 1997). However, it is unclear whether this coupling relationship is adaptive to different sensory properties, i.e. frequency and amplitude, and whether it changes during infancy. The third study in this dissertation examined infants' sitting posture while responding to dynamic visual inputs and how this sensorimotor relationship adapts to sensory properties (frequency and amplitude) during the period when infants develop to sit, stand, and walk.

Two hypotheses were tested and the results are reported in chapter five.

*Hypothesis 3a:* Infants' postural entrainment to the sensory stimulus will show frequency-dependent characteristics, measured by the strength and temporal relations of the entrainment, at the onset of sitting. With increasing sitting experience, the frequency-dependent pattern of the sensorimotor coupling will become more consistent as measured by the temporal relationship.

*Hypothesis 3b:* Infants' postural entrainment to the visual stimuli will not show amplitude-dependent changes at the onset of sitting. As upright postural experience increases, the infant's postural response will scale to changes in stimulus amplitude and become more consistent.

### *Dissertation Organization*

This dissertation is organized in six chapters. In the next chapter, the literature on the following topics is reviewed: theoretical perspectives and research paradigms on postural control; adult postural control in upright stance; and, perspectives employed in understanding infant postural development including neuromaturational, normative, postural synergy, and sensorimotor control perspectives. Chapter three reports an experiment that examined the development of infants' quiet standing posture in the first year of independent walking. Postural sway of infants' upright stance with or without somatosensory influence from touching a stationary contact surface was characterized. Chapter four describes the experiment and results on the development of infants' postural control in sitting. More specifically, this study examined how a new acquired postural behavior (i.e., walking) affects a previously established posture (i.e., sitting). Chapter five illustrates the third experiment which examined the development of infants' sensorimotor control of sitting posture. In this experiment, infants' ability to re-weight the visual information and adapt their sitting posture to the sensory properties (both frequency and amplitude) was examined. The final chapter includes a summary and general discussion of the results from all three experiments in this dissertation on the development of infant sensorimotor postural control. Recommendations for future research are also proposed in chapter six.

# Chapter 2

# A Review of the Literature

In this chapter, literatures related to our understanding about infant postural development will be reviewed. Before discussing the background literature on the development of posture, the first part of this chapter will examine postural control in general.

## *Posture: An Overview*

Posture is a fundamental component in our daily activities. It provides a stable basis for the body to execute automatic or goal-directed movements. Postural control serves two important functional goals: postural orientation and postural equilibrium (Horak & Macpherson, 1996). Postural orientation is the relative position of the body segments with respect to each other, i.e., alignment of the trunk over the legs, head over the trunk, etc, as well as to the environment, i.e., the alignment of the body to the support surface or to the gravitational vertical. Humans tend to assume a particular postural orientation according to the task at hand. In most cases, this means that the head and trunk are kept aligned with respect to the gravito-inertial and support surface. Postural equilibrium is the state when all forces acting on the body are balanced so that the body remains in its stable position (static) or is in motion (dynamic). These forces include external forces due to the gravity and to interactions with the surrounding environment, and internal forces from the body's movement. The resultant of the external forces acts at the center of mass (CM), the point at which the entire mass of the body is balanced

(Winter, 1995). The central nervous system (CNS) needs to estimate and coordinate all the external and internal forces to produce appropriate muscle torques and thereby to control the position of the CM and maintain equilibrium.

Maintaining equilibrium in certain postural orientations, even in quiet stance, is not an effortless task since the body is never motionless. Postural control involves coordinating a multi-segmented body in which the position of the CM can change dramatically when the body configuration changes. To maintain static equilibrium, such as in quiet upright stance, the horizontal projection of CM position needs to lie within the base of support. The larger the base of support, the more the CM can move without loosing its equilibrium. For dynamic postural tasks, such as locomotion, the CM is never within the base of support but is continuously regulated to maintain the equilibrium (Horak & Macpherson, 1996). For the multi-segmented body, transformation from muscle contraction to forces to control the movement of the CM is complex. In the past century, numerous studies have focused on how the CNS controls human upright posture in adult upright stance.

## *Postural Control in Adult Upright Stance*

Since last century, there have been several important theoretical conceptualizations to explain human posture. In this section, these conceptualizations, including reflexive control perspective, postural synergy, and sensorimotor perspective, are discussed.

### *Reflexive Control Perspective*

Early research on human postural control was strongly influenced by Sherrington's reflexive control theory that viewed reflexes as the foundation for all behaviors (Sherrington, 1906). Complex behaviors were viewed as resulting from a chain of reflexes that were triggered by a sensory stimulus. In the early 20th century, posture was regarded as a static state which was assembled from the summation of all reflexes acting in response to gravitational force acting on the body (Magnus, 1924). The CNS was thought to control the motor system through reflexes from the higher, middle, and lower centers in a top-down hierarchical manner. The function of the higher level CNS centers was to inhibit the lower level reflexes. Therefore, the lower level reflexes would not appear in adults unless the higher CNS center was damaged. This approach led to much of the early research on postural control being done in humans or animals with selective CNS lesions. Systemically examining the animal's postural reflex activities with various CNS lesions, Magnus identified the reflexes that worked cooperatively to maintain posture in various animals (Magnus, 1924). These early studies of postural control focused mainly on examining reflexes, righting, and equilibrium reactions with regard to the CNS function. This reflexive control perspective had a significant impact on clinical intervention which emphasized inhibiting the lower level reflexes and facilitating higher level ones (Bobath, 1970). From this perspective, posture was defined as a static body position that was independently controlled by pre-wired reflexes generated to support the body against the gravity (Reed, 1989).

However, postural control includes not only antigravity function in the static conditions but also orientation of the body segments with each other and to the environment (Horak & Macpherson, 1996; Massion, 1998). The goal of orientation is to form an interface between perception and action so that the postural control system can produce appropriate responses adaptively in various conditions (Massion, 1998). Postural control is a multi-dimensional process that involves many parallel and hierarchical mechanisms, including peripheral sensory reception from the environment and the body, central sensorimotor interpretation and transformation, motor response selection and planning, and motor response execution (Horak & Macpherson, 1996). In addition to reflexes, many factors, e.g., body biomechanics and sensory environment, affect the postural control needed for goal-directed movements.

### *Postural Synergy Perspective*

To control the posture of the multi-segmented body, the CNS faces the problem of dealing with the many degrees of freedom (DOF) from the muscles and joints. To solve the DOF problem in motor control, Bernstein (1967) proposed that a group of muscles that act together in a coordinated sequence (a synergy) can be modulated by sensory information to achieve functional goals. Postural adjustments are achieved by coordinated and sequential muscle activations that are called postural synergies (Horak & Macpherson, 1996). These synergies are characterized as a series of muscle activation that are triggered by the sensory inputs from the peripheral sensors and are coordinated with a specific timing sequence and amplitude. The ordering and amplitude can be modulated to achieve the overall goal of postural function in a given task.

The perspective of the CNS controlling posture through sensory-triggered postural synergies has developed from a research paradigm using a platform perturbation which was first introduced by Nashner (1971; 1976). This paradigm has been one of the most frequently employed paradigms in the study of posture. In these studies, participants stand upright on a platform that can be suddenly moved (upward/downward tilt or forward/backward translation) and their postural responses are measured via electromyography (EMG) of related muscles. Studies have found that when the support surface is suddenly moved, direction-specific postural responses are evoked rapidly (70~100ms) to prevent loss of balance (Horak & Macpherson, 1996). These muscle activities are temporally organized and can be modified by the perturbation stimulus (Horak, Diener, & Nashner, 1989), initial position, prior experience (Horak et al., 1989), task demands (Horak & Nashner, 1986). For example, when the stimulus is predictable, the postural responses are scaled to the anticipated perturbation velocity and amplitude (Diener, Horak, & Nashner, 1988; Horak et al., 1989). The postural responses (100ms) would be suppressed when the participant was instructed to step soon after the support surface began to move, (Burleigh, Horak, & Malouin, 1994) but increased when vision was stabilized with respect to the head during the platform perturbation (Nashner & Berthoz, 1978). These results suggest that adaptive postural behavior involves integration of the central set from the prior experience and the task demands and the information received from multiple sensors. The CNS controls posture through flexible synergies that can be fine-tuned to various task demands (Horak & Nashner, 1986; Massion, Alexandrov, & Frolov, 2004).

Although the postural synergy perspective and the perturbation paradigm have provided important information about postural control system, several aspects of postural control system cannot be fully understood due to the limitations of this research paradigm. Postural synergies responding to a platform movement are a relatively static behavior resulting from a discrete perturbation event. Human upright posture, however, represents a sensorimotor control system that is continuously adapting to subtle internal and external perturbation (Collins & De Luca, 1993; Kiemel et al., 2002). It involves complex and dynamic interactions between the neuromuscular system and its surrounding environment and the task constraints to adjust to these internal and external perturbations to postural orientation and equilibrium (Horak & Macpherson, 1996; Reed, 1989). Postural control requires a continuous interaction between sensory inputs and neuromuscular activations. The platform perturbation paradigm examines postural adjustments after the postural system is perturbed by a discrete mechanical stimulus. It does not tell us how the continuous and dynamic sensorimotor interaction is controlled by the nervous system. To understand postural function, it is necessary to understand both the perturbation and the continuous relationships between sensory information and postural action.

### *Sensorimotor Control Perspective*

For postural control, sensory information comes primarily from three systems: vision, vestibular, and somatosensory (Horak & Macpherson, 1996). Each sensory system receives information from specific stimuli: the visual system detects the relative position and motion of the head to the environment; the vestibular system detects the velocity of the head motion; and, the somatosensory system provides the information about the body configuration and motion and its relation to the environment (Horak & Nashner, 1986). Redundant information from multiple sensory systems is important to detect changes in conditions, to resolve sensory ambiguities, and therefore to ensure successful postural control (Bertenthal & Clifton, 1998; Horak & Macpherson, 1996). Postural function requires sensorimotor organization to produce coordinated movements of multiple body segments in the ever changing environment. To understand postural control, it is necessary to know how the CNS processes the sensorimotor relationships between the multi-segmented body and the sensory information from multiple senses to produce appropriate and adaptive postural behaviors.

Recent research has focused on understanding the sensorimotor dynamics of postural control system. Studies have examined adults' quiet upright posture with or without manipulation of sensory environment and sought to understand the underlying mechanisms of sensorimotor control (Dijkstra et al., 1994; Jeka et al., 2000; Jeka et al., 1997; Schoner, 1991; van Asten, Gielen, & van der Denier Gon, 1988). Human posture, even quiet upright stance, is never motionless. Sensory information provides information about the body, the environment, and their relationships for the CNS to produce appropriate postural responses. The sensory consequences of the postural responses then serve as feedback for postural control. Perception and action are not separated but mutually dependent in postural functioning. This concept of sensorimotor (or perception-action) control has formed a theoretical and experimental framework for the study of human postural control. In this section, the perception-action approach on adults' postural control will be discussed using studies of adult postural sway with or without sensory manipulation.

### *Postural sway in adult quiet stance*

In contrast to the reflex and postural synergy perspectives, some researchers have sought to characterize postural control in upright stance. Studying postural sway during upright stance has a long history. In the 19th century when Karl von Vierordt used a paintbrush attached to the head to record the trajectories of body sway. Nowadays postural sway is usually measured at the feet using the trajectory of center of pressure (CP) or as an estimated measure of the body's center of mass (CM).

The human body is never motionless when standing upright. Many studies have focused on describing the summary statistics of postural sway and how the postural sway variables (e.g., sway path, area, variance, etc.) change in various conditions (Prieto, Myklebust, Hoffmann, Lovett, & Myklebust, 1996). It has commonly shown that, when providing additional sensory information (vision or touch), adult postural sway would decrease (Ashmead & McCarty, 1991; Clapp & Wing, 1999; Jeka & Lackner, 1994; Kiemel et al., 2002; Prieto et al., 1996). Using frequency analysis, adults' upright posture can be characterized as low-frequency oscillations with the postural sway mostly concentrated in the frequency range below 1.5 Hz regardless the sensory conditions (Ashmead & McCarty, 1991; Prieto et al., 1996; Zatsiorsky & Duarte, 1999). In addition, postural sway changes with age (Prieto et al., 1996), disease (Bronstein, Hood, Gretsy, & Panagi, 1990), and task demands (Woollacott & Shumway-Cook, 2002). These summary statistic measures are easy to use and computationally undemanding for clinical use (Chiari, Cappello, Lenzi, & Della, 2000). Although they described useful information about human postural sway, most of them provided little about the underlying mechanism of the control processes.

Several models have been proposed to explain the sensorimotor control of human posture. For example, Collins & DeLuca applied stabilogram diffusion analysis technique and suggested a postural control model that involves both open- and close-loop (feedforward and feedback) control processes (Collins & DeLuca, 1993). However, Perterka suggested that a feedback model with a PID (proportional, integral, and derivative) controller is sufficient to represent data of human upright postural sway (Peterka, 2000). Some suggest that postural control is a complex sensorimotor feedback control process (van der Kooij, 1999, 2001, Mergner, 2003, Morasso, 1999), while others suggest models that rely on internal representations of postural system that are constructed from previous sensorimotor experiences (Morasso, Baratto, Capra, & Spada, 1999).

Among the various studies and postural control models, it has been consistently suggested that adults' upright postural sway can be characterized by two major components: a slow drift component and a fast oscillation component (Collins & De Luca, 1993; Dijkstra et al., 1994; Kiemel et al., 2002; Zatsiorsky & Duarte, 1999). The slow component dominates the amount of sway and is often attributed to the central commands that set the desired equilibrium point while the fast component is seen as corrective reactions around the reference point (Collins & De Luca, 1993; Dijkstra et al., 1994; Kiemel et al., 2002; Zatsiorsky & Duarte, 1999). This combination of slow and fast components has been further explained as two control processes of human postural system: state estimation and feedback control (Kiemel et al., 2002; Kuo, 2005; van der Kooij et al., 2001). The state estimation process uses an internal model of sensory and body dynamics to process sensory information and to form an estimate of the current and future postural state. The state estimate is then used to specify appropriate muscular responses to achieve the desired postural orientation and equilibrium (Kuo, 2005). Recently, researchers have shown that mathematical models including both a state estimator and feedback controller, compared to simple control-theory models, can better represent adults' postural sway under selected sensory conditions (Kiemel et al., 2002;

Kuo, 2005). It is further suggested that, for young adults' quiet stance, the imperfect sensory processing and state estimation, rather than the execution of muscular responses, are the primary sources of postural sway, even in a simple quiet stance task (Kiemel et al., 2002). To form estimates of a postural state from the received sensory information from multiple sensors and to register appropriate motor commands to muscular system, an internal model that mimics the dynamics between motor responses and the sensory inputs is assumed (Kawato & Wolpert, 1998; Wolpert, Ghahramani, & Jordan, 1995). This internal model (sensorimotor relationships) is also used to predict, from the motor commands, the sensory consequences from further feedback to update the state estimate (Kuo, 2005). This internal model is acquired and modified in the CNS and can be calibrated through sensorimotor experiences to achieve postural control function adaptive to various sensory conditions (Kawato & Wolpert, 1998; van der Kooij et al., 2001).

### *Dynamic sensorimotor relationships of postural control*

The sensorimotor dynamics is complex and is important for the understanding of how the CNS controls postural behavior. Visual, vestibular, and somatosensory systems provide information about body position and motion of the body and it's relation to the external world. On the other hand, movements of the body bring sensory consequences in one or more sensory systems. Sensory and motor systems are not separable but continuously interacting with each other. One way to understand the dynamic sensorimotor relationships in postural control is to examine the postural behavior in a given sensory condition and see how it adapts to the changes in the sensory environment.

Among the three major sensory systems, vision is the most investigated domain using a moving room paradigm, which was first demonstrated in a seminal paper by Lee

& Aronson (1974). In the 1970s, Gibson pointed out that vision not only provides information extrinsic to the body but also provides feedback about an organism's own movements relative to the external world (Gibson, 1966). Inspired by Gibson's idea, Lee & Aronson (1974) manipulated optic flow information by physically moving the surrounding walls of the room where infants stood in. Their results revealed that newly walking infants showed direction-specific postural sway when standing on a fixed support surface while the walls of a room moving forward or backward.

Instead of discrete visual perturbation in the first study in infants, their following work examined adult postural responses to a continuous visual input created by sinusoidal or irregular movements of the room (Lee & Lishman, 1975). Their results showed that adults' body were consistent with the direction of the continuous optic flow caused by the moving room. In addition to direction-specific postural sway, recent research has shown that, in adults, the postural responses to the visual information reflect the temporal features of the visual stimuli. Specifically, visual flow information presented at low frequencies is shown to induce adult postural sway at the frequency of visual input (Dijkstra et al., 1994; Jeka et al., 2000; Lestienne, Soechting, & Berthoz, 1977; Peterka, 2002). Further, when the visual stimuli are oscillating at frequencies near the adult's natural frequency of sway (i.e., ≈ 0.2 Hz), the postural sway is best entrained to the visual stimuli (Dijkstra et al., 1994; Jeka et al., 2000). However, when the stimulus frequency is less than 0.2 Hz, body sway leads the stimulus motion; and as the driving frequencies increased beyond the adult's natural sway frequency, sway increasingly lags behind the driving frequency and postural response decreases.

In addition to the temporal specificity of postural coupling to sensory stimulus, the sensorimotor relationships of postural control also depend on the spatial features of the sensory information. Research has shown that, within a certain range, the postural response is proportional to the amplitude of the sensory driving stimulus. However, when the amplitude exceeds a certain value, postural sway is no longer responsive to the driving stimulus and indeed decreases with increasing stimulus amplitude (Peterka, 2002; Peterka & Benolken, 1995). This decrease in the postural response to large visual stimuli is referred to as sensory re-weighting. Sensory re-weighting does not only occur within the same sensor (intra-modality) but also between different sensors (inter-modality). In a study in which both somatosensory and visual information were manipulated, Jeka and his colleagues found that postural coupling to the visual stimulus increased when the amplitude of the visual stimulus remained the same but the somatosensory stimulus became larger, and vice versa (Oie et al., 2002).

Extending the moving room paradigm from vision to somatosensory inputs, Jeka and his colleagues (1998a; 2000; Jeka et al., 1997; Oie et al., 2002) examined adult postural sway while standing with the right hand lightly touching an oscillating contact surface. Similar to the visual moving room studies, adults' postural responses to a continuous somatosensory stimulus also showed frequency-dependent (Jeka, Oie, Schoner, Dijkstra, & Henson, 1998a; Jeka et al., 1997) and amplitude-dependent features (Oie et al., 2002). Further, it was found that the sensorimotor relationships vary not only by the parameters (frequency and amplitude) of the given sensory stimulus, but also by the other available sensory information. In their studies with simultaneous visual and somatosensory stimuli, Jeka found that the entrainment of adults' postural responses to visual information would increase when the amplitude of the somatosensory input increased (Oie et al., 2002). This adaptability of sensorimotor relationships to the changes of available sensory information is called as sensory re-weighting.

The ability to 're-weight' sensory information for postural control is a critical component of the adaptive sensorimotor control required to maintain upright posture in an ever-changing world (Horak & Macpherson, 1996; Oie et al., 2002; Peterka & Benolken, 1995). Under normal conditions, the visual, somatosensory, and vestibular systems provide information about the body's spatial orientation and movement. When the environment changes (e.g., going from a lighted to dark room), the system needs to detect and adapt to this change. Further, if the sensory information is unreliable or misleading, this information may need to be ignored or attenuated. For example, if you close your eyes (stimulus amplitude zero), postural stability is maintained by re-weighting so as to not rely on visual, but on vestibular and somatosensory information. Each of the sensors does not operate as an individual sensorimotor channel. Rather, they are integrated and weighted by the nervous system based on an internal model of the sensorimotor dynamics for postural control that forms postural estimates and produces appropriate postural responses to achieve the required postural orientation and equilibrium (Horak & Macpherson, 1996).

In summary, the contemporary conceptualization of adult postural function is a complex and dynamic sensorimotor control process that may involve estimation and feedback control processes. Sensory information from multiple sources is used, based on an internal model of the sensorimotor dynamics of the postural system, to form postural estimates that specify body position and motion in the environment and generate appropriate responses.

## *Development of Infant Postural Control*

The development of postural behavior is an important and significant component in early motor development. Dramatic changes of postural behavior occur in the first two years of life as infants gradually develop the ability to control their body in the upright position. At birth, newborn infants have only minimal control of their head. In the next year, infants improve dramatically in controlling their posture (Bayley, 1993; Piper & Darrah, 1994). By two months of age, they can control the head at midline in the supine position and, about one month later, can further raise the head up against gravitational forces while prone on their bellies. Usually by 6-7 months, they achieve the first upright posture, sitting, in which they need to control two linked body segments- the head and the trunk. It is not until around their first birthday when the infants are able to maintain balance of their multi-segmented body on two feet and walk forward, and another six to nine months later before the energetically different and postural-demanding bipedal gait of running is achieved (Bayley, 1993; Piper & Darrah, 1994). With their advances in postural control, infants are able to not only control the body segments against the gravity but also perform other motor tasks at the same time without losing balance.

Indeed, the development of postural control is critical to the development of many motor skills, such as reaching and walking, during infancy (Bertenthal & Clifton, 1998). For example, the development of reaching in 5- to 8-month-olds is related to infants' ability to control their sitting posture (Rochat, 1992; Rochat & Goubet, 1995). Postural control is also suggested as a rate-limiter for the acquisition and refinement of independent walking (Clark & Phillips, 1993; Ledebt & Bril, 2000). To understand infant motor development, it is important to understand how infants develop to control their posture. Despite its important role in early motor development, however, little is known about how infant postural control develops in the early years of life. In this section, I will review what we know about postural development based on different theoretical perspectives.

### *Neuromaturation Perspective*

Unlike adult postural control, the study of postural development did not draw much attention until the 1930s when the field of motor development started (Clark & Whitall, 1989). Traditional views of postural development focused on its association with a predictable sequence of motor behaviors. These behaviors, called motor milestones, often occur in a sequential order around certain ages with some variations. For example, some of the major milestones for infant postural development include lifting head in prone position around 2 months, sitting unsupported around 6 months, pull-to-stand around 9 months, standing unsupported around 11 months, independent walking around 12 months, and running around 18 months (Bayley, 1993; McGraw, 1943; Piper & Darrah, 1994). Early theoretical perspective of motor development in the 1930s placed great importance on the maturation of nervous system and has been referred as neuromaturation theory (Clark & Whitall, 1989). Based on this theory, the sequential appearance of the postural milestones during development reflects the process of CNS maturation.

Neuromaturation theory of motor development emerged in the 1930s, led by Gesell and McGraw. Using a co-twin control study, Gesell suggested that the development of basic motor skills is determined by internal (genetic) rather than external (environmental) factors (Gesell & Thompson, 1929). He described the emergence of behaviors in the first few years of life and constructed a "developmental norm" for the sequential schedule of behavioral milestones (Gesell, 1946). Influenced by recapitulation theory, he suggested that the sequential milestones reflect the neural maturation process which is determined by the biological and evolutionary history. He formulated the law of developmental direction as from head to foot and from proximal to distal. Specifically, he portrayed a "spiral hierarchy" hypothesis in which reciprocal inhibition at the CNS was used to explain the pattern changes of infant crawling (Gesell, 1939). New behaviors emerge from the central neural mechanisms with no external influence from the environment. Similar to Gesell, McGraw also attributed infant postural development to CNS maturation. In 1932, McGraw used still pictures to describe infants' postural behaviors as they evolve from reflexive to matured and equilibrium patterns (McGraw, 1932). She established a developmental norm for infants' progression of posture and locomotion in the upright position. Associating her results with the changes of neural configuration of cerebral cortex, McGraw concluded that the development of motor behavior reflect the advancing maturation of the CNS. Postural development is a gradual process of growth that occurs in a cephalo-caudal direction (McGraw, 1932; 1943; 1946). However, unlike Gesell who focused mostly on reporting the "product" of development-sequential milestones, McGraw further investigated the underlying process for the observed behaviors. She described in detail infant postural and locomotion behaviors and explained the process with the maturation of cortical control (McGraw, 1932; McGraw, 1941). Although McGraw explained infants' behavioral changes as resulting from CNS maturation, she also noted that learning and environment play important roles for the individual variations in motor development (McGraw, 1946).

### *Normative Perspective*

The neuromaturation theory has played a significant role in the study of motor development, including postural development. Since Gesell (1946) and McGraw (1932), many motor assessment tools have been created using normative norms to evaluate infants' functional skills that require postural control and to detect infants at risk for developmental problems (Bayley, 1935; 1993; Piper & Darrah, 1994; e.g., Shirley, 1933). In these developmental norms, postural development is viewed as the sequential behavioral changes, such as sitting, standing, and walking, simply resulting from CNS maturation. From the mid-1940s to 1970, postural development was studied with description of the emerging sequences and movement patterns of the postural milestones (Clark & Whitall, 1989). Indeed, these developmental norms of posture milestone are still used nowadays especially in clinical practice. The use of normative norms to access postural development assumes that postural behaviors emerge sequentially at certain ages. During this period with normative perspective, research focused on describing age-related changes of postural behavior during the developmental course. Postural development was viewed as the emergence of the sequential postural milestones with the assumption that certain behaviors would appear at certain ages due to neuromaturation.

In addition to describing the milestones of postural behavior, some other research used the normative perspective and focused on examining the neural organization of postural development. With strong influence from neuromaturation theory and the neurobiological studies in animals and patients (e.g., Magnus, 1924), it was believed that postural development depends on the CNS maturation. With advancing CNS maturation, the higher level cortical function inhibits and integrates lower level CNS results in the observed appearance and disappearance of various reflexes during infancy and childhood (Bobath, 1965). Many neurological assessment scales (e.g., Andre-Thomas, Chesni, & Saint-Anne Dargassi, 1960; Milani-Comparetti & Gidoni, 1967; Prechtl & Beintema, 1964) were constructed to examine the presence and time courses of reflexes, righting, and equilibrium reactions. For example, it was believed that Asymmetric Tonic Neck Reflex (ATNR) appears around 1 month and then disappears around 4 months of age in normal infants while the Labyrinthine Right Reflex (LRR) appears around 3 months of age and remains in life (Milani-Comparetti & Gidoni, 1967). In children with CNS lesions, such as cerebral palsy, the higher level reactions may not appear and therefore the primitive reflexes are not inhibited. Reflex examination was used mostly clinically to assess neurological functions and therapeutic treatment emphasized on facilitating higher level reactions and inhibiting lower level reflexes (e.g., Andre-Thomas et al., 1960; Bobath, 1965; Milani-Comparetti & Gidoni, 1967; Prechtl & Beintema, 1964).

Although the normative norms provide important information about the age-related behavioral changes of postural development, they address only the product but not the underlying process of postural development. To understand motor development, it is necessary to understand both the product and the process (Clark & Whitall, 1989). The product of postural development is the observed postural behavioral changes while the process is the underlying mechanisms of these changes. The neuromaturation perspective only considers the CNS advances as the factor for postural development but ignores other non-neural systems (such as sensory and musculo-skeletal) and their interactions that are also critical for postural control and development (Bertenthal & Clifton, 1998).

Recent theoretical perspectives have viewed motor development as a complex process that involves multiple systems and their interactions in the environment rather than automatically emerging from the maturation of the CNS. It is now believed that postural development results from complex interactions of the changing cognitive, musculoskeletal, nervous, and sensory systems in the environment. New research approaches on postural development are inspired by a systems perspective of motor development (Bertenthal & Clifton, 1998; Shumway-Cook & Woollacott, 2001; Thelen & Smith, 1994). Many theoretical models have been proposed using different perspectives to explain the development of infant posture. For example, McCollum & Leen (1989) used an inverted pendulum model and predicted that, considering the constraints on infants' body anthropometrics, infant postural development could be characterized as increasing time constant of their body sway which leads to a shift of their postural responses from hip to ankle strategies. Examining the coordination between the body segments, Assaiante (1998) also suggested that infant postural development involves changes in their postural strategies. Among the various studies, one of the most used approaches is using a "postural synergy perspective" to examine the neural organization of the sensory-triggered postural responses in infants and children.

### *Postural Synergy Perspective*

In adults, it has been shown that temporally organized postural synergies can be triggered following perturbations (titling or translation) of the support surface (Horak et al., 1989; Nashner, 1976). Many studies used the platform perturbation paradigm to investigate whether these postural synergies exist in infants and how they may change during development. It is assumed that postural development involves changes of the neuromotor control for producing postural synergies. Research found that infants at 15-18 months of age were able to show distal-to-proximal muscle activation patterns, similar to adults but more variable, in stance position (Forssberg & Nashner, 1982; Shumway-Cook & Woollacott, 1985). Examining the changes of infants' postural synergies during the developmental course from sitting to independent walking, Woollacott and her colleagues reported that as infants had more experience in sitting or standing, their postural responses to the moving platform showed a gradual addition of muscle activations and increased consistency of the response amplitude and latency in the given posture (Sveistrup & Woollacott, 1996; Woollacott, Debu, & Mowatt, 1987). It was suggested that the developmental principles for postural adjustments in standing is the same as in sitting, but timing is different. The recruitment of muscle activation develops in a top-down direction from neck to truck for sitting while the muscle activation patterns change in a bottom-up direction from ankle to thigh to trunk for standing (Shumway-Cook & Woollacott, 2001; Sveistrup & Woollacott, 1996).

Indeed, as early as 1 months of age, infants were shown to have direction-specific postural adjustments, and sometimes with adult-like complete muscle patterns, when the sitting support surface suddenly moving forward or backward (Hedberg, Forssberg, & Hadders-Algra, 2004). These results were interpreted as an evidence of innate origin of the basic level of postural adjustment organization and suggested that the development of postural adjustments does not simply progress with gradual addition of appropriate muscles to the synergies (Hedberg et al., 2005; Hedberg et al., 2004). The development of postural adjustments involves not only the muscle recruitment but also refinement of the relative and absolute timing of the muscle activations in the postural synergies. Infant postural development can be characterized with changing variability of the postural adjustment toward increasing functional adaptability to various conditions and tasks (Hadders-Algra, 2005; Hadders-Algra, Brogren, & Forssberg, 1996; Hedberg et al., 2005; van der Fits, Otten, Klip, van Eykern, & Hadders-Algra, 1999). The amount of postural experience in a given task is important to the development of infants' postural adjustments to the platform perturbation. Eight month-old infants who have much experience in sitting but not in standing showed matured muscle responses in seated position. However, they did not show adult-like muscle patters until they had been in standing position for weeks and started to walk independently (Sveistrup & Woollacott, 1996; Woollacott et al., 1987). These results indicate that the development of infant postural control may require specific experience that allows infants to learn to control their posture in various tasks and conditions.

Infants' postural synergies responding to a support surface perturbation have been shown to be modified by the available sensory conditions. Sundermier and Woollacott reported that the availability of vision enhances newly walking infants' muscle responses to a support surface translation but this vision effect did not exist in pre-walking infants (Sundermier & Woollacott, 1998). When the visual surround was fixed during the platform perturbation, infants were not able to resolve the sensory conflict and did not show long latency muscle activity in their postural synergies (Shumway-Cook & Woollacott, 1985). However, young infants were not able to adapt their postural synergies to various sensory conditions as well as older children and adults and showed more variable muscles responses (Forssberg & Nashner, 1982). These results support the idea that infants' postural adjustment develops toward increasing functional adaptability to various conditions and tasks (Hadders-Algra, 2005).

### *Sensorimotor Control Perspective*

Current theoretical perspectives on motor development have viewed the integration between perception and action as necessary for the regulation of coordinated movements (Bertenthal & Clifton, 1998; von Hofsten, 2004). Postural function involves complex and dynamic interactions between the motor system and multiple sources of sensory information (Horak & Macpherson, 1996). Postural development requires integrating the changes in sensory and motor systems as well as the sensorimotor relationships (Bertenthal & Clifton, 1998; Reed, 1989; Shumway-Cook & Woollacott, 2001). Although the platform perturbation paradigm was originally designed to examine the sensory-triggered postural responses, the moving support surface elicits not only sensory but also mechanical perturbation. Postural control involves not only antigravity functions but also forming an interface between perception and action (Massion, 1998). To understand postural development, it is necessary to understand how sensory influences infants' postural control as they gradually gain the control of their body motion.

#### *Infants' postural responses to discrete sensory stimulus*

Along with the platform perturbation studies, another research paradigm designed to examine the sensory influence in postural control is a "moving room paradigm". As described in the earlier section, this paradigm is to examine postural behaviors responding to optic flow created by movements of the surrounding walls and therefore involves only sensory but not mechanical perturbation. The moving room paradigm was first introduced by Lee & Aronson (Lee & Aronson, 1974) who qualitatively coded the direction and amplitude of infants' body movements responding to the moving room. Their results showed that infants who were just beginning to stand independently had direction-specific postural responses (sway or stagger) to the forward/backward movements of the walls. Later studies replicated these results and showed that optical flow in the peripheral visual field could induce direction-specific postural sway (Bertenthal & Bai, 1989; Stoffregen, Schmuckler, & Gibson, 1987).

To understand whether this optic flow induced postural response exist in infants before they are able to stand, , Butterworth (1977) examined pre-standing infants in the sitting posture and showed that infants' postural responses to the visual stimulus decreased after they gained more experience in the sitting position. Indeed, as young as newborn infants were able to show direction-appropriate postural reactions to optic flow inputs. When 3-day old infants were presented with optic flow stimulus, direction-specific postural responses were shown by the pressure changes recorded underneath the head (Jouen et al., 2000). Moreover, these newborn infants showed postural responses scaled to the velocity of the optic flow. These results suggest that the basic forms of sensorimotor relationships between vision and postural action may exist early at birth. Postural development may involve improving the integration between the motor responses and the sensory information to produce appropriate postural function.

Although the perturbation paradigms (platform or moving room) have provided important information about postural development, they examine postural responses resulting from a discrete perturbation event. Posture is a complex and dynamic sensorimotor control process in which sensory and motor systems interact continuously to achieve appropriate behavior adaptively to various sensory environment and tasks (Bertenthal & Clifton, 1998; Horak & Macpherson, 1996). Postural function includes not only muscles reactions to discrete external perturbations (sensory or mechanical) but also continuous integrations between the sensory and motor systems to perform actions adaptive to the environment and tasks. To understand infant postural development, it is important to understand the dynamic sensorimotor relationships of infant posture and how it changes with increasing experience or age during the developmental course.

Since neonates are able to show adult-like postural muscle activations (Hedberg et al., 2004) and postural responses to optic flow information (Jouen, 1990; Jouen et al., 2000), the rate-limiting factor for postural development may not be action or perception per se. Rather, the development of sensorimotor relationships, also called perception-action coupling in previous studies, may be an important key to understand how infants develop to achieve coordinated and adaptive postural behaviors. In order to ensure a stable posture with their changing sensory and motor systems, infants need to continuously calibrate and update their sensorimotor relationships of postural control through the developmental course. How does this sensorimotor calibration process as infants develop to control their posture in the upright? To answer this question, it is necessary first to characterize infants' continuous postural function and the sensorimotor relationships of the behavior. In the following sections, studies that may contribute to our understandings of the dynamic, continuous sensorimotor control of infant posture will be reviewed and discussed.

### *Infants' unperturbed independent upright posture*

Unlike the numerous literatures on adult quiet posture, only two studies, to my knowledge, have examined infants' unperturbed independent standing posture. Ashmead and McCarty (1991) applied spectral analysis on the postural sway in 12-14-month olds and found that infants swayed more than adults even that the infants stood with two feet while the adults stood on one foot or in tandem stance. Examining the frequency distribution of the sway, both infants and adults showed their postural sway concentrated in the low frequency spectrum (below 1.5 Hz). Although the frequency distribution seemed to be similar between infants and adults in their report, the comparison between infants and adults cannot be drawn due to the low spectral resolution (0.25 Hz) and the different standing tasks being tested. Unfortunately, infants' unperturbed postural sway was neither fully characterized nor compared to adult posture in Ashmead and McCarty's study. The limitation of their research design with only one cross-sectional group also prevents our further understanding of infant postural development. Our previous study examined longitudinally infants' standing posture in the first 9 months following the onset of independent walking (Metcalfe et al., 2005a). Using stabilogram-diffusion analysis to characterize the temporal structure of infants' unperturbed postural sway, our results revealed that infants did not show magnitude attenuation of their postural sway variance through the period of investigation. Rather, the rate at which their postural sway decayed to maximum variance decreased after they gained more walking experience. It is suggested that, with increasing walking experience, infants learn to use sensory information to form postural estimate and thus rely less on fast feedback correction. The reduction of rate constant is indicative for the developmental changes in the frequency domain of infant's unperturbed posture. With the method emphasized on stabilogram-diffusion analysis, however, it is unknown whether the development of infants' unperturbed posture reflects in the temporal, spatial, and spectral characteristics of the postural sway. To understand the sensorimotor control of infant postural development, it is necessary to fully characterize infants' unperturbed posture and how it changes during the developmental course.

Although research on infant postural control is limited, several studies have reported the developmental changes of children's upright posture. The development of children's postural control have been shown as a reduction of the overall variance (Newell, Slobounov, Slobounova, & Molenaar, 1997; Riach & Hayes, 1987) as well as changes of the rate-related characteristics (Kirshenbaum et al., 2001; Riach & Hayes, 1987; Riach & Starkes, 1994) of their postural sway with increasing age. With increasing age, children swayed slower (Kirshenbaum et al., 2001; Riach & Starkes, 1994) and the spectral frequency of their postural sway shifted toward low frequency range (Riach & Hayes, 1987). The power spectral analysis showed that the principal energy of children's postural sway was mostly concentrated in the range below 0.8 Hz but that young children showed some power in the 0.8~2.0 Hz range (Riach & Hayes, 1987). Applying the estimation and feedback control model (Kiemel et al., 2002; Kuo, 2005; van der Kooij et al., 2001), these results again support the idea that postural development involves an increase of using sensory information to form postural estimate and to plan for appropriate postural responses and therefore decreasing the reliance on feedback corrective process.

### *The influence of static sensory information on infant upright posture*

To understand the sensory influence on postural control, one way is to examine postural changes after removing one or more sensory information. Although it has been consistently shown that sensory information helps stabilize adults' upright posture, research evidence suggests that the sensory influence of postural control may differ during development. While older children, like adults, swayed more when eyes closed comparing to eyes opened, young children showed less postural sway when eyes closed (Newell et al., 1997; Riach & Hayes, 1987). Similarly, Ashmead and McCarty (1991) found that, unlike adults who sway more in the dark than in the light, infants did not seem to be affected by the availability of the visual information. These results indicate that postural development may involve changes of using sensory information, specifically vision in these studies, to control their posture.

Unlike vision, our previous studies revealed that infants were able to reduce their postural sway variance when touch was available (Metcalfe et al., 2005a; Metcalfe & Clark, 2000). Further, the additional somatosensory information allowed infants to decrease the rate constant of their postural sway during the early months of independent walking (Metcalfe et al., 2005a). These results suggest that infants may use sensory information to modify the parameters of their postural control system (i.e., stiffness and damping). This interpretation is also supported by another study in which, when touching a stationary contact surface, infants showed lower correlations between the body segments which might be due to reduced stiffness (Metcalfe & Clark, 2000). On the other hand, the change of rate constant of infants' postural sway with additional sensory information or increasing walking experience could be due to enhancements of using sensory information to form postural estimate and thus reduce the reliance of fast corrective behaviors. Supporting evidence for prospective use of sensory information to form postural estimate also comes from a study which examined the temporal relationship between touch force and infants' postural sway (Barela et al., 1999). Infants with few standing experience used touch to react to the postural deviation for regaining their stability. After having few months of walking experience, infants showed their use of touch leading their postural deviation. In summary, infant postural development may involve improvements in the use of sensory information to form postural estimate as well as changes of the parameters of the control system.

One of the important and significant features of postural development during infancy is the increasing ability to maintain balance in various positions from sitting, standing, to walking. In the limited literature on the development of infants' unperturbed posture, all studies focused on the standing posture after they are able to stand or walk. Sitting is the first upright posture in which infants need to maintain equilibrium of the multi-segmented body against the gravity, with appropriate orientation to the external environment. However, it is unknown how infants' upright posture is controlled in sitting position before they can stand with support and how it may change after infants develop the ability to maintain balance in the upright stance. Sitting and standing are two behaviors that pose very different postural demands. Not only the body segments to be controlled and the base of support are different but also the sources of sensory information differ between these two postural tasks. For example, the somatosensory information from the ankle may not be critical while seated but plays a significant role for the control of upright stance. As the infant develops to sit, stand, and walk, the internal model which represents the sensorimotor dynamics of the postural system needs to be changed to fulfill various task demands. How does the internal model of postural control change developmentally to achieve adaptive postural behavior in various tasks? To answer this question, it is important first to understand how infants control their upright posture in both sitting and standing positions and how postural control system may change during the transition from one behavior to another. Despite the very limited studies on infants' unperturbed upright posture, several studies have emphasized on the dynamic sensorimotor relationships and examined infants' postural behavior in sitting and standing with continuous and dynamic sensory inputs.

### *Dynamic sensorimotor relationships of infant posture*

The study of the dynamic and continuous sensorimotor relationships of postural control has mostly done with the moving room paradigm. Early research that used this paradigm to study infant posture focused on infants' responses to a discrete visual stimulus (e.g., Bertenthal & Bai, 1989; Butterworth & Hicks, 1977; Lee & Aronson, 1974). The results on these studies qualitatively showed infants' responsiveness to the visual stimulus but provided little about the sensorimotor dynamics of infants' postural control. To understand the development of postural function, it is necessary to study how infants use the sensory information to modulate their postural behavior. The first developmental study that examined infant posture in a continuous sensory condition was done by Delorme and his colleagues (Delorme, Frigon, & Lagace, 1989) who examined the frequency of infants' postural sway in an oscillating moving room. In their study, infants with various standing ability and walking experiences, aged from 7 months to 4 years) were tested in supported standing posture while the room was oscillating at a specific frequency. Infants’ postural sway was measured indirectly from a force platform. Their results found that infants, after achieving independent stance, were able to modulate their postural behavior and showed the peak sway frequency identical to the driving frequency of the moving room. With only one frequency tested, however, it is unknown whether infants’ postural entrainment to the optic flow shows adult-like frequency-dependent feature (Dijkstra et al., 1994; Jeka et al., 2000).

To understand whether infants’ postural behavior depends on the sensory properties (i.e., frequency and amplitude), Bertenthal and his colleagues (1997) conducted a study to examine 5-13 month-old  infants’ sitting posture in a moving room that was oscillating at various frequencies (0.3 & 0.6 Hz) and amplitudes (9 and 18cm). Their results showed that infants, even before they could sit independently, were able to entrain their sitting posture to the moving room motion and this visuo-postural entrainment significant improved between age 5 and 9 months. Further, infants’ postural responses to the optic flow inputs scaled to the frequency or amplitude of the room motion. As the frequency or amplitude of the room motion increased, infants’ postural entrainment increased. In a later study, Bertenthal further tested a wilder frequency range and demonstrated that 9-month olds, similar to adults, showed frequency-dependency visual-postural relationships in sitting (Bertenthal et al., 2000). Infants showed a significant decline of the sway coherence as a function of visual frequency from 0.2 to 0.8 Hz, and adult-like temporal relationship in which postural sway lagged behind the optic flow as the frequency increased. The equivocal results on the visual frequency effect between their two studies were explained as due to using different measures (CP vs. head and CM). From the two studies, Bertenthal concluded that infants’ postural control system is not fundamentally different from adult system but the postural responses to visual inputs become more consistent with experience during development.

Unlike adult research, the visual motion used in Bertenthal and his colleagues' studies is large (9 and 18 cm in Bertenthal et al., 1997 ; 0.4~3.2 cm in Jeka et al., 2000). The large visual motion may be a "perturbation" to the system, to which the infant may demonstrate responsiveness. In fact, when Barela and colleagues (Barela et al., 2000) tested infants' sitting posture with smaller visual inputs (2.26 and 5.65 cm), they did not find developmental changes with increasing sitting experience. Opposite to Bertenthal's findings, Barela reported infants' postural coherence to the visual inputs improved as the visual frequency increased but no difference in the phasing relationships. Another explanation for these conflicting findings, also, may be found in the different stimulus velocities employed as this property has been suggested as critical to adults' postural control (Jeka et al., 2004; Kiemel et al., 2002). Further, the stimulus frequencies employed by Bertenthal and Barela were adopted from adult research and may not represent the true range of infants' postural sway frequency which might change during the developmental course (Metcalfe et al., 2005a).

Adopting the moving room paradigm with somatosensory inputs, our previous study longitudinally examined the coupling relationship between infants' standing posture and a driving somatosensory stimulus that oscillated laterally at 0.3 Hz. The results showed that the dynamic coupling between infants' standing posture and somatosensory information exists before the onset of walking. With more walking experience, this coupling relationship becomes more temporally consistent. These findings suggested that infants are better able to estimate their body position relative to the environment as they gain experience in the upright. Postural development involves fine tuning of sensorimotor relationships which helps adequately estimate body position in space and thus facilitates refined control over temporal aspects of postural sway. It is unknown, however, whether this somatosensory-postural relationship has frequency-dependent property or whether it exists before the infant is able to stand, i.e. in sitting posture.

In conclusion, recent research evidence from limited studies on infant unperturbed posture and the sensory influences has suggested that postural development may involve a fine tuning of the sensorimotor relationships of the postural control system and thus facilitating the ability to form precise postural estimate and to produce appropriate postural responses. However, the lack of systematic investigation on the development infant postural control prevents our understanding of how this sensorimotor tuning process may occur during the developmental course. If we are to understand infant postural development, the first step is to understand infant unperturbed posture and to examine how it may be influenced by sensory information during the developmental course. In the next two sections, I will report two experimental projects in which infants' unperturbed posture in sitting and standing was longitudinally studied.

# Chapter 3

# Development of Infants' Unperturbed Standing Posture

# Development of Infant Upright Posture: Sway Less or Sway Differently?[1]

*Abstract*

Postural control has been suggested as an important factor for early motor development; however, compared to adults, little is known about how infants control their unperturbed upright posture. A significant gap in our understanding is a characterization of infants' unperturbed, independent standing. We, therefore, began by first longitudinally characterizing infants' quiet stance in the 9 months following the onset of independent walking. Second, we examined the influence of sensory information, light touch contact, on their postural control. Nine typically developing infants were tested monthly as they stood on a small pedestal either independently or with the right hand lightly touching a stationary contact surface. Center of pressure excursions were recorded and characterized by distance-related, velocity, and frequency domain measures. The results indicated that, with increasing walk age, infants' postural sway changed its rate-related characteristics toward lower frequency, slower and less variable velocity oscillations without changing the spatial characteristics of sway. Additional touch contact stabilized infants' postural sway as indexed by decreases in sway position variance, amplitude, and area as well as changing frequency and velocity features of the sway.

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Taken together, these results suggest that instead of swaying less, infants sway differently with increasing upright experience. These differences suggest that early development of upright postural control may involve a refinement of sensorimotor dynamics that enhances estimation of self-motion for controlling upright stance.

*Key words: Posture, Development, Infant, Somatosensory, Standing*

## *Introduction*

Postural control is an essential ability in developing motor skills needed for daily living activities (Bertenthal & Clifton, 1998). To control the multi-segmented body over its support base requires an accurate and reliable relationship between sensation and action that is adaptive to an ever changing environment and task demands. This relationship is not yet fully developed at birth. Indeed, it takes infants almost a year to stand independently and many years thereafter to develop adult-like postural control. While the sensorimotor control of posture has been extensively studied in adults (cf. Horak & Macpherson, 1996), surprisingly little is known about infant upright postural control in the first two years of life. Early research provided chronologies of postural milestones such as when infants sit, stand, and walk (Gesell, 1946; McGraw, 1932; Shirley, 1933). Later, studies explored how infants use sensory information in the development of their postural control by recording their responses to discrete sensory and mechanical perturbations (Forssberg & Nashner, 1982; Lee & Aronson, 1974; Sveistrup & Woollacott, 1996) or how their posture is coupled to sensory information (mostly visual) (Barela et al., 2000; Bertenthal et al., 2000; Bertenthal et al., 1997; Metcalfe et al., 2005b). Unlike the research on adult postural control, however, no studies have fully characterized quiet, unperturbed stance in infants in the first months after they stand independently. If we are to understand how infants develop and refine their sensorimotor control over postural behaviors, it is necessary to first understand the development of infants' unperturbed, independent upright posture. Therefore, the purpose of the present study was to address this significant gap in our knowledge by analyzing infants' quiet, unperturbed stance from the onset of walking and thereafter for a period of time that will allow us to precisely characterize the aspects of postural sway which undergo change as typically developing infants gain upright postural and locomotion experience.

Human upright posture is never motionless. Contemporary conceptualizations view postural sway as the result of dynamic and complex processes in which the postural control system is continuously adapting to a range of internal and external perturbations (Horak & Macpherson, 1996; Kiemel et al., 2002). Adults' quiet stance has been characterized in many studies and models have been proposed to explain the sensorimotor control of the human postural system. From this research, adults' upright posture is consistently described as a low-frequency motor behavior with two major components: a slow drift component and a fast damped-oscillatory component, with the former accounting for the majority of postural sway variance (Collins & De Luca, 1993; Dijkstra, 2000; Kiemel et al., 2002; Zatsiorsky & Duarte, 1999). Using different approaches, studies have attempted to link these two components to underlying physiological control mechanisms. For example, the fast component is usually explained by the control dynamics of an inverted pendulum (e.g., Johansson, Magnusson, & Akesson, 1988) while the slow dynamics are attributed to errors in postural state estimation (Kiemel, Oie, & Jeka, 2006; Kiemel et al., 2002). In addition to the rate-related features (i.e., in the frequency domain), research has also found that the amount of adults' postural sway increased with aging (Prieto et al., 1996), diseases (Bronstein et al., 1990), or challenging tasks (Woollacott & Shumway-Cook, 2002). On the other hand, postural sway could be attenuated by providing additional sensory information (somatosensory or vision) (Jeka & Lackner, 1994; Jeka et al., 2000; Prieto et al., 1996).

Little is known about how the dynamics of human postural control develop in the early stages of life span. While toddlers were shown to gradually increase the upper body stability during upright locomation (Ledebt & Bril, 2000), our previous study using stabilogram-diffusion analysis suggested no developmental change in the sway variance of infants' upright stance across the first year of independent walking (Metcalfe et al., 2005a). Instead, the rate constant at which infants' postural sway decayed to maximum variance decreased as they gained more walking experience, suggesting that infants' posture relied more on the slow dynamics process resulting from the errors of state estimation. Rate-related information (i.e., velocity and frequency) from the sensory environment has been suggested as critical for human postural behavior (Dijkstra et al., 1994; Jeka et al., 2004; Kiemel et al., 2006) . Changing the rate-related characteristic of infants' postural sway may enhance the integration of sensory information in the postural control system. Therefore, the rate-related features of quiet postural sway may provide important information about the sensorimotor control of human posture during infancy.

In a study of 12~14-month-old infants, investigators found that infants' postural sway, like adults', was concentrated mostly in the low end (below 1.5 Hz) of the frequency spectrum (Ashmead & McCarty, 1991). Due to the low spectral resolution (0.25 Hz) of this study and its cross-sectional research design, it is unknown whether the frequency distribution of infants' postural sway was different from adults' or changed developmentally. In 2~14 year old children, enhanced postural control has been described as exhibiting decreased variance (Newell et al., 1997; Riach & Hayes, 1987), velocity (Riach & Starkes, 1994) and frequency of postural sway (Riach & Hayes, 1987). These results are consistent with the notion that postural development involves changes in rate-related features of the postural behavior that enhance the integration of sensory information in the postural control system. What remains unknown is whether the developmental processes of changing rate properties of postural control start as early as infancy when dramatic changes in infants' standing behavior are observed.

It is often seen that newly standing/walking infants hold onto furniture to help balance their body in the upright position. Research revealed that 13-14 months old infants tended to hold onto an external supporting object when standing on a narrow surface (Stoffregen, Adolph, Thelen, Gorday, & Sheng, 1997). Additional somatosensory cues from the hand lightly touching a static contact surface has been shown to attenuate the body sway during upright stance in young adults (Jeka & Lackner, 1994) as well as in infants during the first year of independent walking (Metcalfe & Clark, 2000). Touch also provides a window to study how infants use the sensory information to help control their unsteady upright posture at earlier developmental epochs. In a previous study in which infants stood with the hand touching a contact surface, Barela and colleagues examined the temporal relationship between touch force and infants' postural sway (Barela et al., 1999). At the developmental milestone of pull-to-stand, the force that infants applied to the contact surface through the hand lagged temporally behind their postural sway, indicating the use of touch forces mechanically. After a few months of independently walking, the temporally relationship changed so that applied forces through the hand led body sway, suggesting that infants used touch for prospective postural control. However, without a full characterization of the postural behavior, it remains unclear how the dynamics of infants' upright postural sway may be influenced by the additional touch contact.

Our purpose in this study was, first, to fully characterize the development of infant posture in "hands-free", quiet upright stance by examining changes in both spatial and temporal (i.e., rate-related) features of the infants' postural sway over the first year of independent walking. Second, we investigated how lightly touching a contact surface may influence the dynamics of infants' postural sway during upright stance. Our overall goal is to provide a foundation for the development of infant postural control so that future research can be extended to better understand the sensorimotor control of infants' upright posture.

## *Method*

### *Participants*

Nine infants (6 males and 3 females; 5 Caucasian, 1 African-American, and 3 Asian) were recruited from the surrounding areas of the University of Maryland, College Park. All infants were born full-term without birth complications or any history of developmental delay. At 6, 9, and 12 months of age, infants were assessed with the Bayley Scales of Infant Development (Bayley, 1993) to verify that their development was within normal limits. Infants entered the study when they were able to sit independently (mean age = 6.3 ± 0.7 months) and were tested monthly until they had been walking independent for 9 months (mean age at walk onset = 11.8 ± 1.7 months). Walk onset was defined as the day that the infant took 3 continuous independent steps. For the purpose of this investigation, infants were only assessed at the ages when they could maintain independent upright stance (i.e., "hands free"); specifically from walk onset onward. All infants were paid a modest compensation per testing session and each infant's parent or guardian provided written informed consent prior to inclusion in the longitudinal study. To provide a reference group for comparison, five healthy adults (2 females and 3 males) were also included in this study. These adults (mean age = 29.8 ± 8.2 years) were unpaid volunteers who provided written informed consent. All experimental procedures were approved by the Institutional Review Board at the University of Maryland, College Park.

*Apparatus and Procedure*

Figure 3.1 illustrates the experimental set-up for infants, wherein each participant stood on a pedestal mounted on a force platform in parallel stance with eyes open, either independently (no-touch) or with his/her right hand lightly touching a stationary surface (touch). Similarly, adults stood on a pedestal in a position analogous to the infants. Data were acquired remotely with a customized LabView$^{TM}$ program. All signals were sampled at 50.33 Hz in real time and synchronized to a manual trigger at trial onset.

Figure 3.1. An infant stands independently on a pedestal in the no-touch condition. An experimenter sits in front of the infant to keep his/her attention in the task. In the touch condition, the infant's hand lightly touches the bar which is pictured here to the infant's right.

*Touch apparatus*

For the infants, the contact surface was a customized touch bar which was a 4.4 cm diameter convex surface formed by the top half of a 45.7 cm long PVC tube. The touch bar was positioned to the right of the infant at approximately the iliac crest level in the touch condition. The purpose of this convex surface was to be "touchable" without being "graspable" by the infants. The contact surface was attached atop two support columns, each instrumented with force transducers (Interface MB-10; Scottsdale, AZ) for resolving applied hand vertical forces. For the adults, the contact surface was a 5-cm diameter circular metal plate mounted on a tripod and positioned to the right and forward of each participant at the iliac crest level. The touch apparatus for the adults was identical to those used in previous experiments (Jeka, Ribeiro, Oie, & Lackner, 1998b). Previous studies have consistently reported that infants (Barela et al., 1999; Metcalfe et al., 2005b; Metcalfe et al., 2005a) and adults (Jeka et al., 1998a; Jeka et al., 1998b) applied small vertical forces, around 3.8 N and < 1 N respectively, during quiet stance with the right hand touching the touch apparatus.

*Postural sway recording*

Center of pressure excursions in medial-lateral ($CP_{ML}$) and anterior-posterior ($CP_{AP}$) directions were calculated from ground reaction forces measured by a force platform (Kistler 9261A). Three-dimensional upper trunk and approximate center of mass displacements were sampled using a Logitech 6-dimensional position tracking system (VR Depot; Boony Doon, CA). The present analysis focused on the results of CP sway trajectories.

*Procedures*

After entering the laboratory, the infant was given a brief period of acclimation to the laboratory (e.g., playing with toys, interacting with the experimenters). The testing area was constructed as an approximately 2.1 × 5.1 $m^2$ room formed by black curtains that reduced distractions from the surrounding laboratory environment. Following the acclimation period, the infant was introduced to a small pedestal (10 cm deep x 20 cm long x 11 cm tall) affixed to the force platform. The purpose of the pedestal was to discourage the infant from moving their feet during testing. The infant's shoes were removed and, once placed on the pedestal, the position of the touch apparatus was adjusted to the appropriate height and the Logitech trackers were affixed.

During the testing session, the infant completed 5 conditions including: independent stance (no-touch), touching a static surface (touch), and 3 conditions of touching an oscillating surface (frequencies = 0.1, 0.3, 0.5 Hz; amplitudes = 1.6, 0.59, and 0.36 cm, respectively). Three trials were collected in each condition and all trials lasted 60 s except for the 0.1 Hz trials which were 90 s. The 15 trials were presented in a randomized order except that an independent stance trial never occurred within the first 5 trials. This decision was based on our previous experience with this paradigm which has shown that infants tend not to participate in touch conditions when independent stance trials are presented first. For this study was to examine the development of unperturbed, quiet upright stance, the analyses focused only on the conditions in which the infants: 1) stood independently; or, 2) touched the static surface. The data of the 3 dynamic touch conditions are presented elsewhere for the discussion on how infants' upright posture responds to a dynamic somatosensory stimulus (Metcalfe et al. 2005b).

To facilitate participation, an experimenter sat in front of the infant and attempted to maintain his/her attention with toys or books. The parent or guardian was always present and helped position the infant for each trial as well as prevent any possible falls. One to three short breaks were taken between trials when needed and the total testing session lasted for 25-50 minutes depending on the infant's cooperation. All infant testing sessions were displayed on a remote monitor and video taped with a standard sVHS recorder (Panasonic AG-7350) for online observation of trials during acquisition as well as later behavioral coding. The videotape records were synchronized with the analog data using an event synchronization unit (PEAK Performance Technologies; Englewood, CO) and time-stamped with a SMPTE code generator (Horita RM-50 II; Mission Veijo, CA). Following completion of all experimental conditions, the infant's height and weight were measured.

Experimental equipment and procedures for adults were the same as for the infants with some exceptions. Adult participants stood on a block (19 cm deep x 40.5 cm long x 29.5 cm tall) that was analogous to that used for the infants, but scaled to the adult's larger body size. During the testing session, the participant completed 4 conditions including: independent stance, touching a stationary surface, touching an oscillating surface similar to the infants (frequency = 0.3 Hz; amplitude = 0.59 cm), and touching an oscillating surface in which the amplitude of oscillation halved at 30 s (0.3 cm) and then stopped at 60 s during the trial. Two trials were collected in each condition and all trials lasted for 30 s except for the decreasing-amplitude trials which were 90 s. The 8 trials were presented in randomized order. For this analysis we focused only on the two conditions in which the adult participant stood either independently or with the hand touching a static surface. Details of adult testing procedures are presented elsewhere (Metcalfe et al. 2005b).

### *Data Reduction and Analysis*

#### *Behavioral coding*

Following infant data acquisition, videotapes were reviewed independently by two trained coders for valid segments of quiet posture. Criteria for valid segments included: (1) standing independently from the experimenter or parent; (2) no vigorous head, arm, or trunk movement; (3) no falling, bouncing movement, or foot displacement; (4) appropriate touch for the experimental condition, that is continuously touching but not grabbing the touch bar in the static touch condition and hands completely free in the no-touch condition; and, (5) at least a 10-second segment that met the previous criteria. Only those segments identified as acceptable by two coders were used for subsequent data analyses. Adult data were not video coded, as these participants were able to complete the task in the specified duration without actions that invalidated trial segments.

After behavioral coding for infants, the length of each standing segment varied, ranging from 10 (shortest accepted duration) to 60 (whole trial) seconds. Two measures of stance duration were computed: mean segment time (MST) and total stance time (TST). MST was calculated as the averaged duration across all segments while TST was the sum of all segment durations of each infant within one testing session.

*Postural sway measures*

All data and signal processing was performed using customized programs written in MATLAB (Version 6.12, Mathworks Inc., Natick, MA). Raw signals of $CP_{ML}$ and $CP_{AP}$ time series with the mean removed were low-pass filtered using a recursive 2nd-order Butterworth filter ($f_{cut\text{-}off}$ = 5 Hz). Resultant CP ($CP_R$) data were calculated from $CP_{ML}$ and $CP_{AP}$ to characterize infants' postural sway. To fully describe infants' standing posture, we included three groups of measures derived from $CP_R$ displacements: distance-related, velocity, and frequency measures.

Distance-related measures included sway amplitude, area, and position variability. Sway amplitude was computed as a mean of the absolute values of $CP_R$ displacement. It is a directionless measurement of how far the body moves away from the mean position. Sway area is a statistically-based estimate of a confidence ellipse that encloses approximately 90% of the points on the CP trajectories (Prieto et al., 1996). Position variability was calculated as the standard deviation of $CP_R$ displacements and represents the average deviation from the center-upright position. For each infant postural data segment, sway velocity is derived from $CP_R$ displacements. Two measures, mean velocity and velocity variability, were computed as the average and standard deviation of sway velocity. For frequency measure, power spectrum density of $CP_R$ time series was computed using multi-taper method with 8 tapers to characterize the frequency distribution of infants' standing posture. Total power was calculated as the integrated area of the power spectrum from 0 to 5 Hz. To describe the distribution of postural sway across frequencies, spectral bandwidth was determined as the frequency range that starts from 0 Hz and accumulated 50% power of the frequency spectrum. This measure represents the breadth of the frequency distribution accounting for fluctuations in infants' postural sway. Presented in Figure 3.2 are examples of CP excursion during one trial segment and its corresponding amplitude spectrum from an infant at 1 and 8 months post-walking and a young adult.

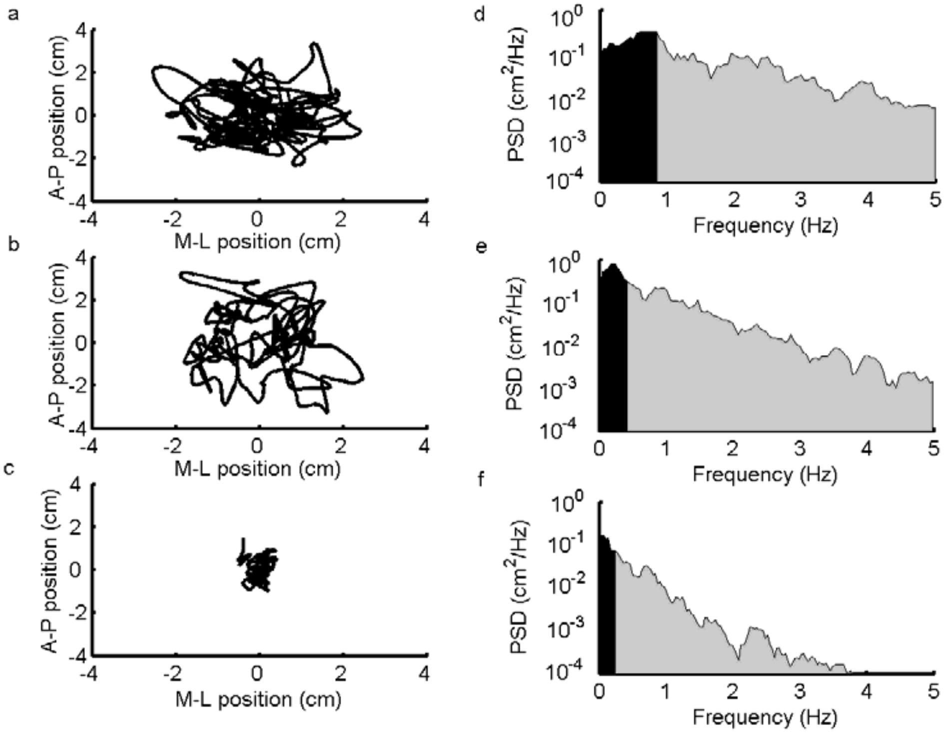

Figure 3.2. Exemplar of CP trajectories and amplitude spectrum for (a) & (d) an infant at one month post-walking; (b) & (e) the same infant at 8 months post-walking; and, (c) & (f) an adult. The black area represents the spectral bandwidth in which 50% power of the frequency spectrum was accumulated.

### *Statistical Analysis*

To longitudinally characterize infants' upright posture, infants' postural data across the 9 months post-walking were analyzed to examine the influence of walk age and touch. Walk Age (days elapsed after walk onset) was used to normalize all data to each individual infant's developmental level. For each dependent measure, hypothesis testing was conducted on averages, weighted by the segment length, within each infant and Walk Age. Mixed-model regression analysis was used to determine the influence of Touch and Walk Age on each dependent measure. This method was selected because it differentially accounts for fixed (e.g. experimental manipulations) and random (e.g. within-subject) sources of variation as well as provides tools to assess variance heterogeneity and to control for correlated measures. It also allows for random patterns of missing cells and thus, is well-suited for analysis of longitudinal data where missing data typically occur. In the statistical model, random-effects were specified as Infant as well as Infant × Walk Age and Infant × Touch interactions, to control for within-subject effects. During the regression procedures, a method similar to backwards selection was used to determine which fixed-effects parameters (Walk Age, Touch and their interaction) were most strongly related to the dependent variables.

For the comparison between infants and young adults, mixed model two-way ANOVA (2 Group × 2 Touch conditions) with Touch as the within-subject effect was used to determine whether infants after 9 months of walking were different from the adult group. All statistical analyses were performed with the Statistical Analysis Software (SAS) program (Release 8.01, SAS Institute Inc., Cary NC, USA). A $p$ value equal to or less than 0.05 was defined as statistically significant.

## *Results*

After behavioral coding, the mean segment time (MST) across walk ages and touch conditions was 28.2 ± 17.5 s. No significant effect was found in Walk Age, Touch, or their interaction (all $p > 0.1$). The total stance time (TST) was significantly influenced by Walk Age ($p < 0.01$) as well as the interaction effect of Walk Age × Touch ($p < 0.05$). Further examination revealed that TST significantly lengthened with increasing Walk Age, from 50.6 s to 112.5 s with a rate of 0.18 s/day, only in the no-touch condition (Bonferroni adjusted $p < 0.01$) but not in the touch condition (adjusted $p > 0.1$).

The mean and standard deviations of all postural measures within each Walk Age level (months elapsed after walk onset) are presented in Table 3.1.

### *Distance-related Postural Measures*

In the first 9 months of independent walking, infants showed no developmental changes with increasing Walk Age in the distance-related measures of their standing postural sway (all $p > 0.1$, Figure 3.3). However, when the infant touched a stationary surface, the amount of sway decreased 8.30% in position variability, 15.46% in amplitude, and 31.67% in area compared to the no-touch condition. The observed attenuation was realized as a significant effect of Touch on the dependent measures of sway variability ($F(1,69.4) = 6.04$, $p <0.05$), amplitude ($F(1,69.6) = 23.66$, $p<0.0001$), and area ($F(1,69.7) = 25.39$, $p<0.0001$). No significant Walk Age × Touch interaction was found.

Compared to young adults, infants at 9-month post-walking showed significantly higher sway variability, amplitude, and larger area (all $p <0.001$). Touch significantly attenuated the distance-related measures of postural sway in both 9-month post-walking infants and young adults (all *p* <0.005).

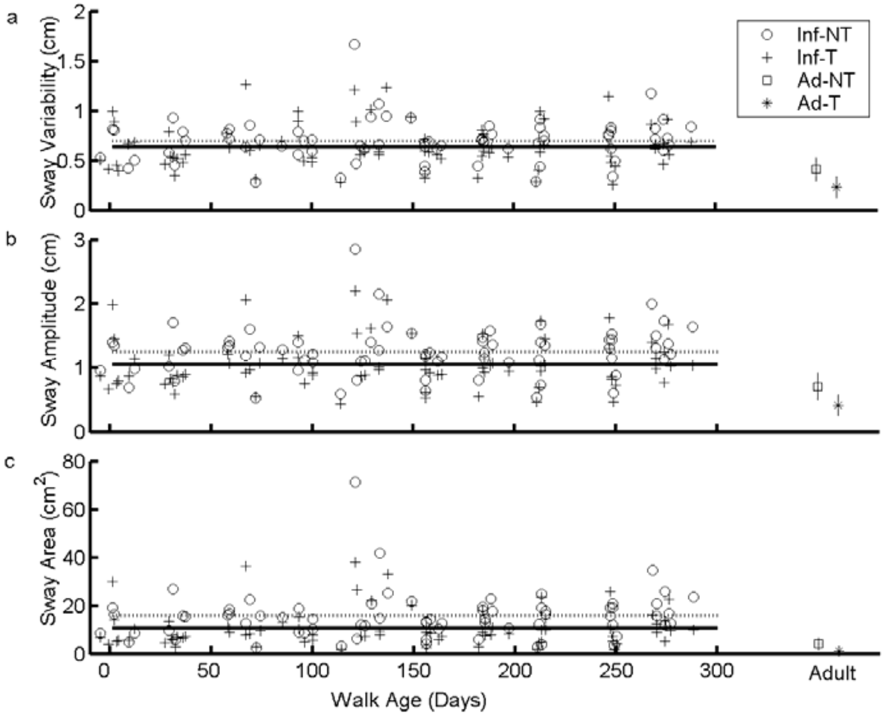

Figure 3.3. Variability (a), Amplitude (b), and Area of 90% ellipse (c) of CPR sway in infants across Walk Age and adults in touch (T) and no-touch (NT) conditions. Regression estimates of infant postural data were indicated by solid line for T and dotted line for NT condition.

Table 3.1. $CP_R$ based postural sway measures of unperturbed upright stance in infants across the first 9 months of independent walking and young adults.

| Walk age (Months) | Sway variability (cm) | | Sway amplitude (cm) | | Sway area ($cm^2$) | | Mean velocity (cm/s) | | Velocity variability (cm/s) | | Spectral bandwidth (Hz) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NT | T | NT | T | NT | T | NT | T | NT | T | NT | T |
| 0 | 0.62±0.18 | 0.63±0.22 | 1.08±0.30 | 1.07±0.45 | 11.59±5.99 | 10.22±8.64 | 7.01±2.70 | 6.16±2.93 | 4.59±1.39 | 4.15±1.73 | 0.71±0.11 | 0.61±0.17 |
| 1 | 0.69±0.19 | 0.53±0.13 | 1.22±0.34 | 0.85±0.17 | 14.79±8.07 | 6.80±2.98 | 7.87±3.21 | 5.79±1.55 | 4.98±1.80 | 4.10±0.82 | 0.70±0.23 | 0.67±0.19 |
| 2 | 0.68±0.19 | 0.69±0.27 | 1.25±0.34 | 1.12±0.43 | 14.96±6.23 | 12.01±10.14 | 7.29±1.78 | 6.52±1.40 | 4.58±1.12 | 4.34±1.03 | 0.64±0.97 | 0.52±0.15 |
| 3 | 0.67±0.08 | 0.68±0.22 | 1.18±0.16 | 1.06±0.27 | 12.66±4.00 | 9.56±4.11 | 6.96±1.01 | 6.32±0.54 | 4.38±0.70 | 4.08±0.22 | 0.58±0.03 | 0.52±0.22 |
| 4 | 0.82±0.40 | 0.77±0.33 | 1.43±0.70 | 1.29±0.60 | 22.98±21.52 | 17.09±13.17 | 7.45±2.99 | 6.47±2.48 | 5.00±1.90 | 4.34±1.38 | 0.53±0.12 | 0.51±0.17 |
| 5 | 0.63±0.16 | 0.58±0.19 | 1.11±0.28 | 0.94±0.32 | 11.99±5.43 | 8.54±5.52 | 5.66±2.17 | 4.74±2.50 | 3.84±0.88 | 3.20±1.13 | 0.50±0.11 | 0.40±0.10 |
| 6 | 0.68±0.12 | 0.60±0.15 | 1.27±0.25 | 1.03±0.27 | 15.25±5.37 | 9.65±4.34 | 5.68±1.77 | 4.37±1.84 | 3.92±0.77 | 3.06±0.84 | 0.55±0.09 | 0.38±0.09 |
| 7 | 0.66±0.22 | 0.64±0.26 | 1.17±0.41 | 1.05±0.43 | 13.89±8.15 | 9.98±7.33 | 5.39±1.39 | 4.84±1.63 | 3.83±0.86 | 3.58±1.10 | 0.47±0.13 | 0.42±0.13 |
| 8 | 0.66±0.18 | 0.58±0.30 | 1.19±0.34 | 0.99±0.47 | 14.02±6.62 | 9.13±8.79 | 4.97±1.43 | 3.95±1.65 | 3.63±0.98 | 2.98±1.34 | 0.46±0.05 | 0.43±0.13 |
| 9 | 0.81±0.18 | 0.68±0.15 | 1.49±0.29 | 1.16±0.28 | 20.32±7.62 | 12.35±5.27 | 5.50±1.37 | 4.63±1.70 | 3.86±0.67 | 3.92±1.32 | 0.45±0.10 | 0.44±0.12 |
| Adults | 0.42±0.11 | 0.23±0.11 | 0.71±0.21 | 0.41±0.17 | 4.08±2.69 | 1.33±1.16 | 1.48±0.43 | 1.06±0.40 | 1.07±0.31 | 0.76±0.30 | 0.31±0.07 | 0.34±0.12 |

Walk age was presented as months elapsed after walk onset.

The values shown are the mean ± standard deviation among infants for each walk age level.

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### *Postural Sway Velocity*

The velocity of infants' postural sway was significantly influenced by Walk Age and Touch (Figure 3.4). With increasing Walk Age, infants showed a linear decrease of their postural sway speed (0.009 cm/s per day, F(1,69.6) = 14.46, $p<0.001$) and its variability (0.004 cm/s per day, F(1,73.8) = 7.16, $p<0.01$). When touching a stationary surface, infants' postural sway was slower (F(1,30.6) = 49.27, $p<0.0001$) and less variable (F(1,16.1) = 14.30, $p<0.005$) compared to the no-touch condition. No Walk Age × Touch effect was revealed in the velocity measures.

Compared to young adults, infants at 9-month post-walking showed faster (F(1,11) = 35.01, $p<0.001$) and more variable (F(1,11) = 63.66, $p<0.0001$) in their postural sway velocity. However, neither Touch nor Group × Touch interaction showed significant influences on the postural sway velocity of young adults and infants at 9-month post-walking (both $p>0.05$).

### *Postural Sway Frequency*

The frequency distribution of infant postural sway significantly changed with increasing Walk Age and Touch (Figure 3.5). Spectral bandwidth, which is mathematically equivalent to the median frequency, showed a significant decrease with increasing Walk Age (F(1,66.1) = 45.42, $p<0.0001$) and Touch (F(1,67.7) = 12.33, $p<0.001$). No significant Walk Age × Touch interaction was found. During the period of investigation, infants' mean body height increased from 75.59 cm at walk onset to 85.18 cm at 9 months post-walking. To consider that the decrease in spectral bandwidth in developing infants may be due to an increase in body height, linear Mixed-Model regression model was reapplied including body height as a covariate. The results revealed that, after considering body height, Walk Age remained a significant factor in the decrease of spectral bandwidth in the first 9 months of independent walking (F(1,25.3) = 32.27, *p*<0.0001). From walk onset to 9-month post-walking, the spectral bandwidth of infants' postural sway decreased from 0.6~0.7 Hz to 0.4~0.5 Hz. After walking for 9 months, infants continued to show higher spectral bandwidth for postural sway than young adults (F(1,11) = 6.04, *p*<0.05). However, no significant Touch or Group × Touch interaction effect on the spectral bandwidth was found for infants at 9-month post-walking and young adults.

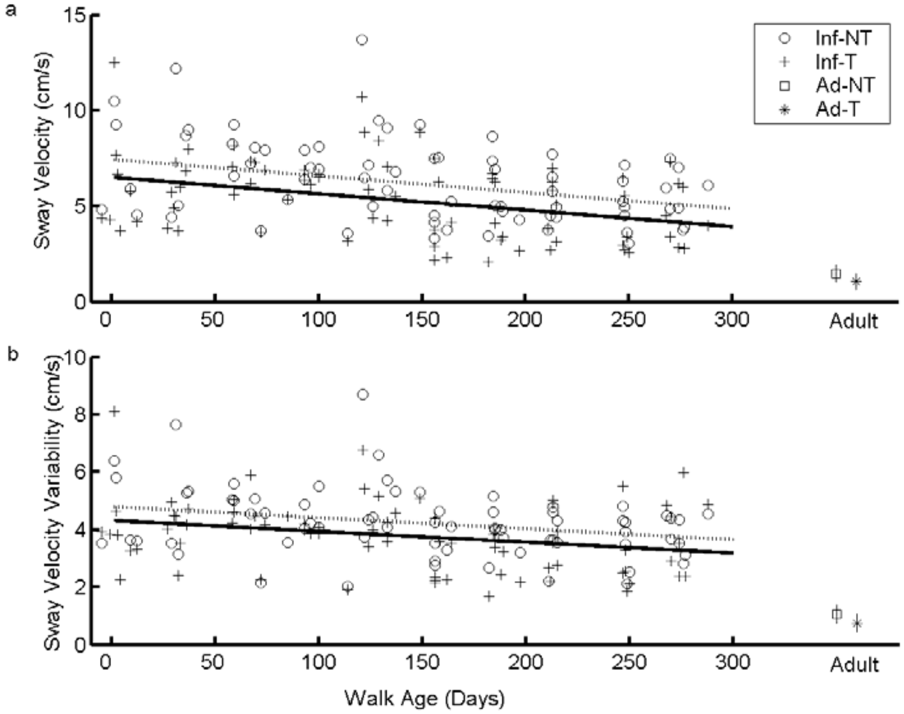

Figure 3.4. Mean (a) and Variability (b) of CPR sway velocity in infants across Walk Age and adults in touch (T) and no-touch (NT) conditions. Regression estimates of infant postural data were indicated by solid line for T and dotted line for NT condition.

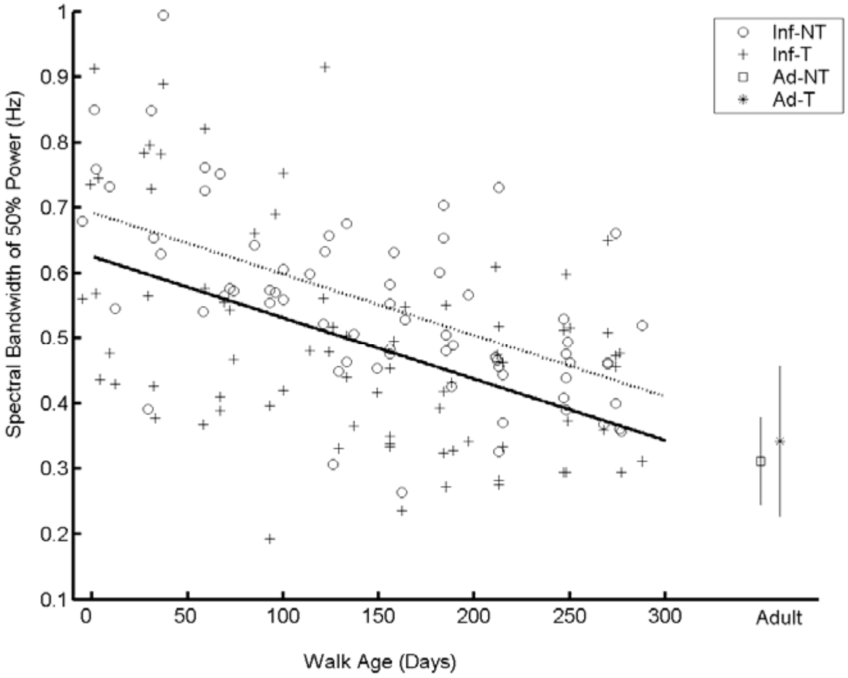

Figure 3.5. Spectral bandwidth within which 50% power of CPR frequency spectrum in infants across Walk Age and adults in touch (T) and no-touch (NT) conditions. Regression estimates of infant postural data were indicated by solid line for T and dotted line for NT condition.

While the spectral bandwidth decreased with increasing Walk Age, the position variance of infants' postural sway remained the same. To directly test whether the decreased spectral bandwidth was due to increasing postural sway in the relatively low frequency range, spectral power accumulated within 0~0.5 Hz was calculated. Mixed model regression analysis revealed that, with increasing Walk Age, infants increased postural sway in the low frequency range (F(1,119) = 5.34, *p*<0.05). The power accumulated within 0~0.5 Hz was not significantly influenced by Touch or Walk Age × Touch interaction (both *p*>0.05).

## *Discussion*

In the present study, we sought to provide fundamental information regarding postural development in infants' upright stance. Our results suggest that early development of upright postural control involves changes in the rate-related characteristics rather than a progressive attenuation of postural sway. More specifically, along with increasing walking experience, infants' upright postural sway develops toward a lower frequency, a slower and less variable velocity. What changes in the development of standing posture is more a question of "how" rather than "how much" the infant sways. Additional light touch contact from the hand helped stabilize infants' upright posture by attenuating the sway magnitude and also changed the dynamics (i.e., velocity and frequency) of the sway.

### *Development of Unperturbed Upright Stance*

Surprisingly, infants did not consistently sway less in upright stance as they mastered bipedal walking. Our findings of no significant sway magnitude attenuation as infants gain more experience in upright standing and walking is contrary to previous studies that showed age- or experience-related decrease in sway variability in older children (i.e., 2~14 years old) (Riach & Hayes, 1987) and infants during the transition to independent walking (Barela et al., 1999). The discrepancy between the present research and previous studies may be due to the longer stance duration required in the present study. Barela et al used 10-second segments, while we used segments that were up to 60 seconds long (mean = 28.2s). Longer stance duration allows better characterization of infants' postural behavior. Indeed, we suggest that the lack of consistent attenuation of postural sway in early development may be unique in infancy. Two mechanisms have been hypothesized to explain the existence of postural sway: one is exploratory and the other is performatory (Reed, 1982; Riley, Wong, Mitra, & Turvey, 1997). Exploratory postural sway creates sensory information for the system to explore sensorimotor relationships for postural control system; whereas performatory postural sway uses sensory information to control posture. For infants who have presumably not yet formed a reliable and stable sensorimotor relationship for postural control, it is important to explore the postural state space so as to experience varied sensorimotor interactions. Postural sway of a newly walking infant may be functional in gathering sensory information that would enhance the calibration of the sensorimotor relationship for postural control and help postural estimation for producing appropriate responses. The interaction of enhanced stability and increased exploration may result in no observable change in the overall magnitude of sway. Therefore, the lack of a decrease in sway magnitude could be an important feature for the developmental process ongoing within newly walking infants. As infants showed more postural sway than young adults in the present study and age-related changes were reported in children in previous studies (Riach & Hayes, 1987), we suggest that the developmental change of postural sway attenuation may be observed in a larger time scale (i.e. year).

Similar to previous studies in adults (Zatsiorsky & Duarte, 1999), children (Riach & Hayes, 1987), and toddlers (Ashmead & McCarty, 1991), infants' standing postural sway in their first 9 months of independent walking exhibited low-frequency oscillations. During the first 9 months of independent walking, infants progressively increased the dominance of their postural sway in the lower end of the frequency spectrum. The decrease in sway frequency in developing infants might result from two sources:

mechanical and control mechanisms. Rapid anthropometrical changes in infants' second year may serve as a mechanical basis for the observed frequency changes. Using a theoretical inverted pendulum model, McCollum & Leen (1989) predicted that postural development could be characterized as a decrease in sway frequency based on the constraints of infants' body anthropometrics. In their equations, lower sway frequency was expected from the increasing body height of the growing infant. Our results revealed, however, after increased body height was accounted for statistically, Walk Age remained a significant factor for frequency changes in infants' standing posture. Therefore, while the observed changes in sway frequency in early postural development may partially be explained by the growth-induced mechanical factors, our evidence indicates that there is more to the story, namely, changes in the control system underlying more mature upright stance. We argue that the development of infants' upright posture may involve changes in sensorimotor control mechanisms as well as anthropomorphic changes associated with growth processes that lead to different postural behaviors.

The increase of infants' postural sway in the lower end of the frequency spectrum suggest that infants' postural system may develop so as to rely more on the estimation process and less on the fast corrective corrections. Walking provides dynamic sensorimotor experiences and enables the infant to refine the sensorimotor relationship that allows utilizing the sensory information to estimate the body position and motion in the environment. Thus, infants are better able to predict the outcomes of their own actions and to prevent excessive corrective actions. This developmental change from reactive to prospective postural control has also been suggested in a previous study in which infants changed the use of touch forces through the hand touching a contact surface to assist control of standing posture during the transition to independent walking (Barela et al., 1999). Prospective control with postural estimations allows infants to plan for appropriate compensatory corrections and, therefore, avoid losing balance while performing various motor tasks, such as walking. The increased dominance of incorporating sensory information in forming postural estimates during early postural development is also supported by the decrease in the sway velocity across walk ages. During the first year of independent standing and walking, infants' postural sway develops from ballistic toward more sensory-guided actions. Slower sway allows the infant to better use sensory feedback in adjusting their postural actions and thus to prevent excessive movements. With standing and walking in the upright posture, infants may learn to better incorporate sensory information in the postural control system and refine the sensorimotor relationship. This developmental process of sensorimotor integration may last into childhood as the decrease in postural sway velocity has also been shown in children between 4 to 13 years of age (Kirshenbaum et al., 2001; Riach & Starkes, 1994). Taken together, our results in the rate-related characteristics (i.e., frequency and velocity) of infants' postural sway in quiet stance support the idea that early postural development involves a refinement of sensorimotor dynamics that enhances utilizing sensory information in estimating self-motion in the environment.

Interestingly, developmental changes in infants' upright posture were not found in mean amplitude or position variance but, rather, in the mean sway speed and its variability. Velocity measure, comparing to position measures, is shown to reflect more consistent results for adults' postural behaviors in various sensory conditions (Kiemel et al., 2006). We suggest that sway velocity is also a more sensitive measure for detecting developmental changes in infants' postural behavior in quiet stance. Further, velocity information of sensory inputs is shown to be more critical than position or acceleration information for the control of quiet stance in adults (Jeka et al., 2004; Kiemel et al., 2006; Kiemel et al., 2002). Postural sway creates sensory feedback. Changing postural sway velocity alters the critical information of the sensory feedback. Further, changing sway velocity during the developmental course may tune the motor system so as to enhance the integration between perception and action. Our results may suggest an important mechanism underlying the development of sensorimotor integration.

### *Influence of Static Touch Contact*

Although the amount of infants' postural sway did not change with increasing upright experience, it was attenuated when infants lightly touched a stationary contact surface. This finding is consistent with previous research in adults (Jeka & Lackner, 1994; Jeka & Lackner, 1995), children (Riach & Hayes, 1987), and infants (Metcalfe et al., 2005a; Metcalfe & Clark, 2000). Sway variability has been related to the effectiveness of the postural control system (Prieto et al., 1996) and it has been consistently suggested that additional sensory information (vision or touch) helps stabilize posture (Jeka & Lackner, 1994; Kiemel et al., 2002; Metcalfe et al., 2005a; Metcalfe & Clark, 2000; Riach & Hayes, 1987).

In addition to attenuating the amount of sway, touch contact also led to decreases in the sway velocity and its variability. It has been shown that degrading somatosensory inputs resulted in increases in the magnitude as well as velocity of adults' postural sway (Jeka et al., 2004). Touching a contact surface provides information about body position and velocity from configurations of the hand to the body. This somatosensory information can further be used in estimating the current postural state and in guiding future postural responses (Jeka & Lackner, 1994; Kiemel et al., 2002). Our frequency measures further showed that, as the infant touched a stationary contact surface, the sway frequency decreased without significant changes in the amount of sway in the lower end of spectrum (0~0.5 Hz). These results suggest that light touch contact helps the formation of the postural state and therefore attenuates the amount of corrective actions. Additional touch contact from the hand stabilizes infants' standing posture not only by attenuating the magnitude of their sway but also by changing the dynamics of the sway; that is, the frequency and velocity characteristics of the postural behaviors.

## *Conclusion*

Our present study showed that early development of upright postural control after learning to walk is not featured as a progressive reduction of postural sway. Instead, early postural development may involve fine tuning the dynamics of the sensorimotor system for postural control through enhancing the use of sensory information to form postural estimates and to generate appropriate responses. Walking provides dynamic and rich sensorimotor experience in the upright position and therefore may enhance the development of infants' postural control. Lightly touching a stationary contact surface stabilizes infants' standing posture by attenuating the magnitude of their sway as well as changing the dynamics of the sway.

# Chapter 4

## Development of Infants' Unperturbed Sitting Posture

## Two Steps Forward and One Back: Learning to Walk Affects Infants' Sitting Posture[2]

*Abstract*

The transition from sitting to walking is a major motor milestone for the developing postural system. This study examined whether this transition to walking impacts the previously established posture (i.e., sitting). Nine infants were examined monthly from sitting onset until 9 months post-walking. Infants sat on a saddle-shape chair either independently or with their right hand touching a stationary contact surface. Postural sway was measured by sway amplitude, variability, area, and velocity of the center of pressure trajectory. The results showed that for all the postural measures in the no-touch condition, a peak before or at walk onset was observed in all the infants. At the transition age, when peak sway occurred, infants' postural sway measures were significantly greater than at any other age. Further, infants' postural sway was attenuated by touch only at this transition. We suggest that this transient disruption in sitting posture results from a process involving re-calibration of an internal model for the sensorimotor control of posture so as to accommodate the newly emerging bipedal behavior of independent walking.

*Keywords: Posture; Infant; Walking; Transition; Sensorimotor; Re-calibration*

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## *Introduction*

Infants first demonstrate sitting independently at six months of age and walking independently at one year (Bayley, 1993; Piper & Darrah, 1994). For the developing postural system, these two behaviors pose very different postural demands. In sitting, the infant's head, trunk and arms are balanced over a very broad base of support with the center of mass close to the base. Once the infant rises to stand, the base narrows (over the two small feet), the number of body segments to be controlled increases (now including the thigh and shank), and the center of mass is considerably higher; all of which increase the postural challenge. The postural dynamics become even more complex for walking as the multi-segmented body moves over its changing base of support. In adults, upright postural control has recently been characterized as a combination of estimation and control (Kiemel et al., 2002; van der Kooij et al., 2001). Estimation, in this context, is the process in which sensory information from multiple sources is combined to give continuously updated estimates of body position and velocity (i.e., dynamics). Complementary to estimation is the process of control whereby motor commands, based upon the current estimates of body dynamics, are sent to the musculature to maintain the upright posture. From this perspective, the developmental transition from sitting to walking would be conceptualized as a re-calibration of the relationship between estimation and control. Based on this characterization, we surmise that as infants explore upright stance and prepare to walk independently a re-calibration between estimation and control, if such a control scheme is generalized across qualitatively different postures, would be manifested in an observable disruption of already established postures. Thus, we examine here infants' sitting posture as walking emerges.

A growing body of evidence suggests that an important component of developmental transitions into new behaviors is a re-calibration of the sensorimotor system. Several groups have shown that with increasing age or sitting experience, the temporal relationship between infants' postural responses and sensory stimuli becomes more adult-like: including visual (Bertenthal et al., 1997), haptic (Barela et al., 1999), and proprioceptive stimuli (Hadders-Algra et al., 1996; Hadders-Algra, Brogren, & Forssberg, 1998; Woollacott et al., 1987). We have argued previously that such results suggest an improving internal model (Metcalfe et al., 2005a). This internal model mimics the sensory and body dynamics for postural control and allows estimation of the postural state as well as generation of motor commands for desired postural responses (Kawato & Wolpert, 1998; van der Kooij et al., 2001). With more postural experience, infants are better able to estimate their body dynamics and thus issue motor commands that lead to increasingly flexible and stable upright stance control.

Presently, the evidence is sparse on how an internal model may change when infants learn a new postural behavior. Recent evidence from our work on the development of walking and posture suggests that there is a re-calibration of the sensorimotor system (i.e., the internal model) for quiet standing as walking experience increases (Metcalfe et al., 2005b). A longitudinal analysis of the infants' upright postural responses to a gently oscillating somatosensory stimulus from walk onset to 9 months post-walking revealed an improving temporal relationship. We suggest that these data indicate a continuous refinement in tuning between the postural system and sensory information as infants have more dynamic experience in the upright, i.e., walking. However, would we expect the same continuity in sensorimotor tuning when the transition is between two less similar postural tasks, i.e., sitting and walking? Some have argued, for example, that there is no transfer of learning between one motor milestone to another (Adolph, 1997; 2000).

Evidence in support of a transfer between one postural task and another comes from a series of experiments by Corbetta and colleagues (Corbetta & Bojczyk, 2002; Corbetta & Thelen, 1996). Infants begin to reach with two hands around four months of age and then, within few months, progress to one-handed reaching. However, a reversal in the reaching pattern occurs when infants learn to walk. Specifically, Corbetta and colleagues observed that sitting infants transiently returned to two-handed reaching during the transition to independent walking. They interpreted this observation as indicative of a neuromotor re-organization for the control of the arms. Alternatively, one could speculate that the re-emergence of the previous reaching pattern was due to a re-organization of the sensorimotor relationship (i.e., internal model) for postural control during this transition period with an indirect effect on their arm control. It is not possible to confirm this notion from the data presented in the Corbetta studies, because postural sway was not measured. However, their results would be consistent with disruptions in the internal model resulting from the emergence of walking.

Thus, the purpose of this study was to examine whether infants' sitting postural control changes during the transition to independent walking. We longitudinally assessed infants' postural sway with the hypothesis that the transition to bipedal locomotion will be associated with changes in sitting posture. Such a result, if the hypothesis were confirmed, would be positive for the notion of re-calibration or tuning of a generalized internal representation that is involved in postural sway dynamics. We further examined the influence of somatosensory information on postural sway by providing a stationary contact surface to the sitting infants. It would be expected that this type of information may further reveal characteristics of the sensorimotor recalibration.

## *Method*

This study was part of a larger longitudinal experiment designed to investigate the development of perception-action relationships of infants' postural control. The current analysis focuses on characterizing the effect of walking on infants' unperturbed sitting posture and therefore, our presentation focuses on the details relevant to the specific questions involved in this study.

### *Participants*

Nine infants (6 males and 3 females; 5 Caucasian, 1 African-American, and 3 Asian) were recruited from the surrounding areas of the University of Maryland, College Park. All infants were born full-term without birth complications or any history of developmental delay. Infants entered the study when they were able to sit independently (mean age = 6.3 ± 0.7 months) and were tested monthly until they had walked independently for nine months (mean age at walk onset = 11.8 ± 1.7 months). Walk onset was defined as when the infant could walk for three continuous steps without falling. Walk age was defined as the duration (in months) from walk onset to the testing date; a negative walk age indicates a test before, a positive walk age indicates a test after walk onset. At chronological ages 6, 9, and 12 months, infants were assessed with Bayley Scales of Infant Development (Bayley, 1993) to verify that their development was within the normal range. Each infant's parents gave written informed consent prior to inclusion in the longitudinal study. For each testing session, the infant's parents received a small remuneration. In addition to infants, six healthy adults (2 females and 4 males) were also tested in a similar experimental protocol so as to provide important reference data. These adults (mean age = 22.9 ± 3.9 years) were unpaid volunteers who had also provided written informed consent prior to the experiment. All experimental procedures were approved by the Institutional Review Board at the University of Maryland, College Park. For the purpose of this study, data analysis only included the testing sessions when the infants could sit independently on a saddle-shape chair; given individual variation in postural stability, this time ranged from 2 to 4 months before walk onset and then continued onward for all infants.

### *Apparatus*

Figure 4.1 illustrates the experimental set-up for the touch condition in which the infant sat on a customized saddle-shaped chair with eyes opened and with the right hand touching a stationary surface. In the no-touch condition, the infant's hands were free, without touching the contact surface. Similarly, adults sat on a saddle-shaped pedestal in a position analogous to the infants, but scaled in height and width to account for their larger body size. Both the infant and adult chairs were firmly affixed to a force platform. All data were acquired with a customized LabView$^{TM}$ program using a National Instruments A/D Board with all signals synchronized and sampled at 50.33 Hz in real time.

#### *Touch apparatus*

For the infants, a customized instrumented touch bar was mounted on a support frame and positioned to the right of the infant. The contact surface was the top half of a

4.4 cm diameter × 45.7 cm long PVC convex surface, which was designed to be "touchable" without being "graspable" by the infant. This contact surface was supported by two columns, each instrumented with force transducers (Interface MB-10; Scottsdale, AZ) for registering hand forces applied vertically. The touch apparatus could be adjusted to the appropriate height for each infant in each testing session. For the adults, the contact surface was a 5-cm diameter circular metal plate mounted on a tripod and positioned to the right and forward of the participant at approximately the iliac crest. Both the touch apparatus and servo control system for the infants and adults were identical to those used in previous experiments (Metcalfe et al., 2005b).

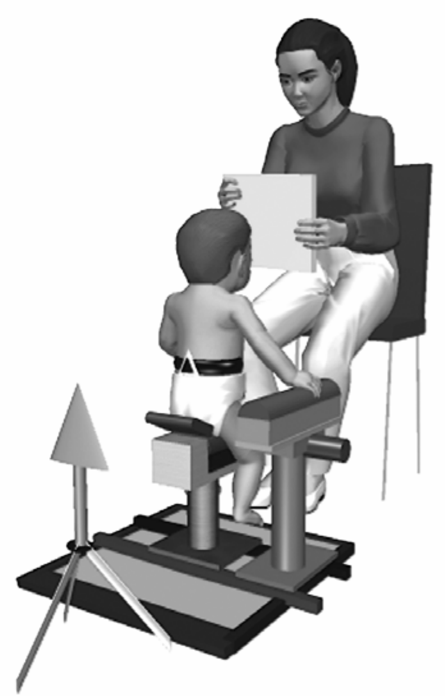


Figure 4.1. An infant sat on a saddle-shape chair affixed onto a force platform in the touch condition. An experimenter sat in front of the infant to keep his/her attention on the task.

#### *Postural sway measurement*

Center of pressure in the medial-lateral ($CP_{ML}$) and anterior-posterior ($CP_{AP}$) directions were calculated from ground reaction forces measured by a force platform (Kistler 9261A). A Logitech$^{TM}$ 6-dimensional position tracking system (VR Depot; Boony Doon, CA) was used to measure the infant's approximate center of mass (CM) sway, however, the results reported here focus only on the CP sway trajectories.

#### *Video*

All infant testing sessions were videotaped with a standard sVHS recorder (Panasonic AG-7350) for later behavioral coding. The videotape records were synchronized with the analog data using an event synchronization unit (PEAK Performance Technologies; Englewood, CO) and time-stamped with a SMPTE code generator (Horita RM-50 II; Mission Veijo, CA).

### *Procedures*

After entering the laboratory, the infant was allowed a brief period of acclimation to the environment and the experimenters. The testing area was an approximately 2.1 × 5.1 meters room formed by heavy black curtains that were intended to reduce distractions from the laboratory. Following the acclimation period, the infant was placed on the chair and the position of the touch apparatus was adjusted to the height of the infant's iliac crest and the Logitech trackers were affixed. To facilitate participation, an experimenter was positioned in front of the infant attempting to maintain his/her attention with toys or books. The parent or guardian was always present and helped position the infant for each trial as well as prevent any possible falls.

During the testing session, the infant completed the following five conditions: 1) independent sitting (no-touch), 2) touching a static surface (touch), and 3-5) three conditions of touching an oscillating surface (frequencies = 0.1, 0.3, 0.5 Hz; amplitudes = 1.6, 0.59, and 0.36 cm, respectively). Three trials were collected in each condition and all trials lasted 60 s, with the exception of 90 s for 0.1 Hz trials. The 15 trials were presented in a randomized order except that independent sitting condition never occurred within the first 5 trials. This exception was based on previous experience with this paradigm which has shown that infants tend not to participate in touch conditions when independent sitting trials are presented first. One to three short breaks were provided between trials. In the present study, we focus only on the conditions in which the infants 1) sat independently or 2) sat with the right hand touching the static surface. The three oscillating touch conditions form the basis for another report.

Experimental equipment and procedures for adults were the same as for the infants except for the body-scaled chair/contact surface arrangement. Again, this analysis focused only on the two conditions for which a comparison was to be drawn; in particular, those conditions in which the adult participant either sat independently or with the right hand touching the static surface.

### *Data Reduction and Analysis*

#### *Behavior coding and signal processing*

Following data acquisition, two trained coders independently reviewed all the infant trials to identify segments of quiet sitting. The criteria for valid segments included: (1) sitting independently from the experimenter or parent/caregiver, (2) no vigorous head, arm, or trunk movement, (3) no falling or bouncing movement, (4) appropriate touch for the experimental condition, i.e., continuously touching, but not grabbing, the touch bar in the static touch condition, and hands completely free in the no-touch condition, and (5) at least a 10-second segment that met all other criteria as stated above. Small head/trunk (i.e. turning) and limb movements (i.e. pointing) were accepted. The start and end times of the segments were coded to the nearest second and only those data segments independently coded as acceptable by two coders were used for subsequent data analyses. After behavioral coding, the length of each sitting segment varied from 10 (minimum acceptable duration) to 60 (whole trial) seconds. Two measures of sitting duration were computed: mean segment time (MST) and total sitting time (TST). MST was calculated as the averaged duration across all segments of each infant within each testing session. TST was the sum of all segment durations of each infant within each testing session. Adult data were not coded, as these participants were able to sit quietly for the specified duration.

Raw signals of $CP_{ML}$ and $CP_{AP}$ time series were mean-detrended and low pass filtered using a recursive 2nd-order Butterworth filter ($f_{cut\text{-}off} = 5$ Hz). All data extraction and signal processing were performed using custom programs written in MATLAB (Version 6.5.0, Mathworks Inc., Natick, MA).

*Postural sway measures*

Resultant CP ($CP_R$) data were derived from $CP_{ML}$ and $CP_{AP}$. Distance-related measures including sway variability, amplitude, area, and velocity, were calculated from the $CP_R$ position data to characterize infants' postural sway. Sway variability was calculated as the standard deviation of $CP_R$ displacement and represents the average distance from the center-upright position. Sway amplitude is the mean of the absolute values of $CP_R$ displacement, and is a directionless measurement of how far the body sways away from the mean position. Sway area is a statistically based estimate of a confidence ellipse that encloses approximately 90% of the points on the CP trajectories (Eq. 1& 2) (Prieto et al., 1996). Sway velocity is the average velocity of the $CP_R$ displacement that was calculated as total path length divided by the segment duration.

$$S_{MLAP} = 1/N \sum_{n=1}^{N} CP_{ML}[n]\,CP_{AP}[n] \text{ ------------- Eq. 1}$$

($S_{MLAP}$: covariance of $CP_{ML}$ and $CP_{AP}$; N: the number of $CP_R$ data points)

$$\text{Area} = 2\pi F_{0.1[2,N\text{-}2]}\,[S^2{}_{ML}S^2{}_{AP}\quad S^2{}_{ML\,AP}]^{1/2} \text{ ---- Eq. 2}$$

(For a large size of data points (N>120), $F_{0.1[2,N\text{-}2]}$ is 2.313.)

*Statistical Analysis*

Only infants' postural data were entered into statistical analysis; data obtained from the adult participants were processed in a similar manner but were only employed to provide a reference point for contextualizing the infant results. Statistical analyses of infant data were accomplished using two-way (walk age × touch) repeated-measures ANOVAs to examine the effect of walking experience on infants' sitting postural sway. Appropriate post-hoc comparisons using Tukey's procedure were performed on any significant differences found across walk age. The ANOVAs were constructed using a linear mixed-model so as to differentially account for fixed (e.g. experimental manipulations) and random (e.g. within- and between-subject) sources of variation as well as to account for random patterns of missing cells which are common in the analysis of longitudinal data. All statistical analyses were performed with the Statistical Analysis

Software (SAS) program (Release 8.01, SAS Institute Inc., Cary NC, USA). A *p* value, after Bonferroni adjustment, of less then 0.05 was defined as statistically significant.

## *Results*

### *Individual Profiles of Infants' Sitting Posture*

The purpose of this study was to examine the effect of walking on the development of infant sitting posture. Following data reduction and prior to statistical analysis, we examined the individual profiles of all dependent measures of postural sway across walk age for each infant. All measures in the no-touch condition, including sway variability (Fig 4.2A), amplitude (Fig 4.2B), area (Fig 4.2C), and velocity (Fig 4.2D), revealed a peak around the age of walk onset in all infants. To assess the significance of this pattern, a "transition age" was identified, by visual inspection, as the walk age at which this peak occurred. For most infants, all four dependent measures showed the peak postural sway occurring at the same walk age. For infant number 7, however, no clear peaks were identified around the age of walk onset except in sway velocity. Therefore, the transition age for this infant was defined as when the sway velocity was the highest. Table 4.1 delineates the correspondence between walk age and chronological age (in months) at the transition for each individual infant. On average, this transition age varied from 3 months before to the month of walk onset; it is noteworthy that the peak was never identified following the onset of independent walking. Finally, to explicitly test the relationship between the dependent measures of postural sway and this transition age relative to walk onset, we aligned all data to this "transition age" - thus creating a transition-normalized walk age. All subsequent analyses (separate two-way repeated-measures ANOVAs) were based on the relationship between each dependent measure, the two touch conditions and across the normalized walk age (-1 to 9 months from the transition age).

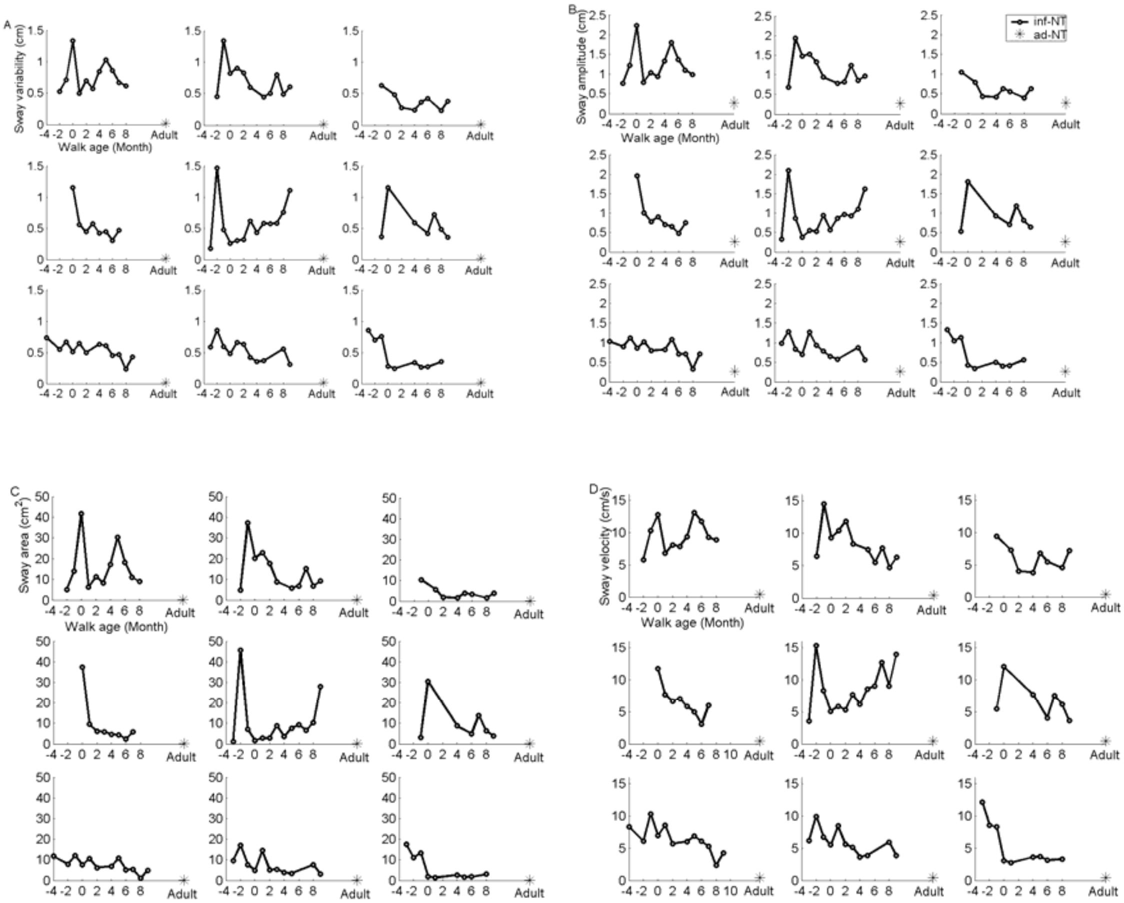


Figure 4.2. Individual profiles for infants' $CP_R$ sway (A) variability (cm), (B) amplitude (cm), (C) area of 90% ellipse ($cm^2$), and (D) velocity (cm/s) across walk ages in the no-touch condition. Adults' averaged postural sway was presented for comparison reference. (○: infant no-touch, ✳: adult no-touch).

Table 4.1. Corresponding walk age and chronological age (in months) for each infant at the transition when postural sway measures peaked.

| Infant Number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| Walk age at the transition | 0 | -1 | -1 | 0 | -2 | 0 | -1 | -2 | -3 |
| Chronological age at the transition | 12 | 10 | 10 | 9 | 11 | 11 | 12 | 10 | 12 |

### *Effect of Walk Onset on Infant Sitting Posture*

After aligning all infants to the transition age, a significant increase in postural sway at this transition age was shown for all postural measures (Fig 4.3). Repeated-measures ANOVAs revealed significant main effects for normalized walk age, touch condition, as well as a normalized walk age by touch interaction effect for sway variability, amplitude, area, and velocity (all $p < 0.05$, Table 4.2). Post-hoc analyses revealed that when infants sat independently without touching a contact surface, their postural sway at the transition age was significantly larger than at other normalized walk ages (all $p < 0.05$, Bonferroni adjusted). With exception of the significant increase at the transition age, infants did not show significant changes in their postural sway from -1 to 9 months normalized walk age (all $p < 0.05$, Bonferroni adjusted). For the touch effect, infants' postural sway was attenuated by touching a contact surface only at the transition age ($p < 0.05$, Bonferroni adjusted) but not at other ages (all adjusted $p > 0.05$).

### *Duration of Infant Quiet Sitting Posture*

The duration of quiet sitting across eleven months studied did not change either for mean segment time (MST) or total sitting time (TST) (both $p > 0.05$). However, infants significantly increased their sitting duration when touching a stationary contact surface. Overall, MST increased from 23.02 ± 11.44 s to 28.59 ± 13.75 s and TST increased from 78.94 ± 52.62 s to 101.67 ± 43.06 s from no-touch to touch condition (both $p < 0.05$). The normalized walk age by touch interaction was not significant for either MST or TST (both $p > 0.05$).

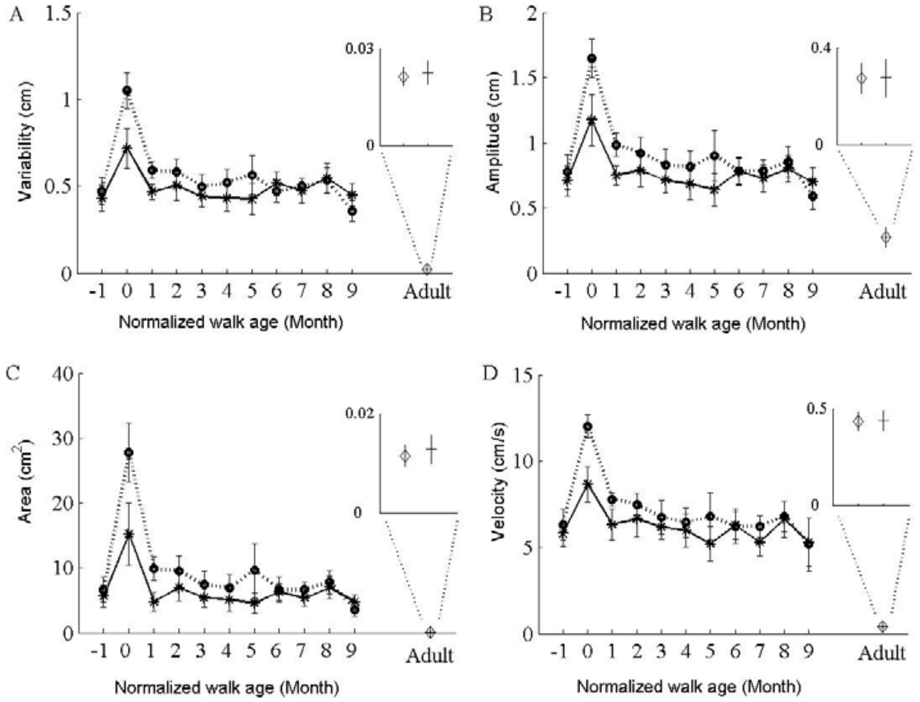


Figure 4.3. $CP_R$ sway (A) variability (cm), (B) amplitude (cm), (C) area of 90% ellipse (cm$^2$), and (D) velocity (cm/s) across normalized walk ages and touch conditions. Infants' postural sway was presented as Mean ± S.E.. Adults' averaged postural sway was presented for comparison reference. (○ : infant no-touch, ✳: infant touch, ◊ : adult no-touch, + : adult touch) (Note: Difference in scale between infants and adults.).

Table 4.2. Statistical results of the repeated-measures ANOVAs for all postural measures in infants across normalized walk ages and touch conditions.

| $CP_R$ sway | Normalized walk age | | Touch | | Normalized walk age x Touch | |
|---|---|---|---|---|---|---|
| | DF | F Value | DF | F Value | DF | F Value |
| Variability | 10, 65.3 | $5.47^{c}$ | 1, 7.39 | $17.82^{b}$ | 10, 64.7 | $3.60^{c}$ |
| Amplitude | 10, 65.2 | $4.99^{c}$ | 1, 7.90 | $44.57^{c}$ | 10, 65.2 | $3.69^{c}$ |
| Area | 10, 65.9 | $6.70^{c}$ | 1, 7.82 | $31.61^{c}$ | 10, 65.3 | $5.09^{c}$ |
| Velocity | 10, 65.2 | $4.15^{c}$ | 1, 5.54 | $20.41^{b}$ | 10, 60.6 | $2.60^{a}$ |

$^{a}$ $p < 0.05$; $^{b}$ $p < 0.005$; $^{c}$ $p < 0.001$

## *Discussion*

The present study revealed that learning to walk affects infant sitting posture by means of increasing the magnitude of distance-related sway properties. Our results are consistent with our prediction that infants need to re-calibrate the sensorimotor relationship as walking emerges. Indeed, not only did we find instability in sitting, but we observed that it occurred for only a short period of time (no longer than one month). Further, the influence of somatosensory information on postural control varied with the infants' sitting posture during this transition. That is, touching a contact surface attenuated infants' sitting postural sway only when they became unstable during the transition to independent walking. Our results are consistent with the concept that the development of infant postural control results from improvements in an internal model for the sensorimotor control of infant posture (Chen, Metcalfe, & Clark, 2003; Metcalfe et al., 2005a). The present study suggests that the re-calibration of the internal model during the transition to independent walking not only affects infants' postural control in the current task (stance and walk) but also affects the control of a previously stable postural behavior (sitting). Moreover, this putative sensorimotor re-calibration occurs before the infant is able to successfully walk even a few steps, suggesting a process that is initiated well before the new behavior emerges.

The sensorimotor relationship between perception and action can be represented as an internal model that is acquired and modified in the central nervous system and mimics the dynamics between motor responses and the sensory inputs (Kawato, 1999; Wolpert et al., 1995). For postural control, this internal model of motor and sensory dynamics is used for state estimation and producing appropriate postural responses in the given task (Kuo, 2005). As the postural demands change under different tasks and contextual conditions, an adaptable internal model is required to assure accurate postural estimates. When the infant learn a new postural task, the sensory-motor dynamics change dramatically and, therefore, this internal model may need to be updated. As the human transitions from sitting to standing tasks, the motor system is likely challenged to a greater extent for a variety of reasons, among which is that sensory information from multiple modalities may play different roles dependant on the postural context. For example, the proprioceptive feedback from the feet and ankles may not be critical in sitting, but adopts a more prominent role for balancing and moving in a bipedal fashion. For the transition from sitting to independent walking, therefore, the internal model for postural control would potentially need to re-weight the sensory information from proprioceptive sensors involved in lower limb control. Moreover, a likely consequence of such re-weighting is that modifications would be required in terms of expected reafference of motor commands in remote sensory modalities (e.g. ocular, vestibular), in order to form better estimates of whole-body dynamics to ultimately sub-serve adaptive switching across multiple tasks with varying postural demands. This sensorimotor re-calibration process implies a developmental continuum in which the underlying bases for estimation (internal model) are common across a variety of postural behaviors. Yet, postural development maintains an appearance of being discontinuous and as a result, already established postural behaviors could be influenced or modified by the emergence of a new posture.

Our results show that the sensorimotor re-organization for postural control during the transition to walk affects the established sitting behavior only temporarily. Infants regained control of sitting posture soon after the destabilization induced by this transition. This temporary change and its discrete and relatively short-term influence may indicate a process of re-organization that is built upon the existing ‘knowledge’ or calibration established within the sitting postural control system. This suggestion is in contrast to a series of studies on infants’ responses to risky locomotor tasks which have been interpreted as providing little-to-no transfer of prior sensorimotor learning when the infant learns a new postural behavior (Adolph, 1997; 2000). Our results suggest a different conclusion. Here we have shown a disruption in sitting posture during the transition to walking while our previous results demonstrated consistent developmental changes of infants’ upright stance during the first year of independent walking (Chen et al., 2003; Metcalfe et al., 2005a). We argue that different postural behaviors may share the same internal model for postural control. Re-calibration of the internal model is necessary so that infants can integrate the new sensorimotor relationship and the established behaviors in the overall postural repertoire. With the re-calibration, the estimation of the well-established sitting posture suffers temporarily and thus leads to increased postural sway variability. The new behavior is therefore built upon some of the basic control elements utilized in managing the previously learned behavior, with updating the existed internal model accounting for transient disruptions appearing as discontinuities.

Our findings of increased sitting postural sway before or at the onset of walking suggest that new motor behavioral patterns are borne out of periods of high behavioral instability – a notion that is compatible with dynamical systems perspectives (Thelen & Smith, 1994). According to this perspective, the increase in variability would be indicative of an exploration of the control parameter space that leads to expansion and subsequent refinement the internal model for the overall postural repertoire. Our results also provide an alternative explanation for Corbetta and her colleagues' observation on the development of infants' reaching pattern during the transition to walk (Corbetta & Bojczyk, 2002). The internal model re-calibration for postural control may also affect how the infants control their arms in the upright posture and therefore disrupt the previously established reaching pattern. Posture is a fundamental component for most motor skills (Bertenthal & Clifton, 1998). We suggest that future studies on motor development during this transition period should consider the possible developmental changes in postural control.

In contrast to upright stance (Chen et al., 2003; Metcalfe et al., 2005a; Newell et al., 1997), haptic cues appear less critical for the control of infants' sitting posture. Touching a contact surface has been shown to attenuate postural sway in upright stance even in young adults (Jeka & Lackner, 1994). However, it did not lead to an observable attenuation of infants' sitting postural sway except for when the infants' sitting posture became unstable during the transition period. This may be due to the fact that sway was much higher during this period, making the effect of touch easier to measure. Another explanation, however, is the necessity of sensory redundancy. Postural control is influenced by vision, vestibular and somatosensory information (Horak & Macpherson, 1996). The multiple sources of sensory information may be redundant when postural control is not challenged (e.g., sitting). However, this sensory redundancy may lead to more precise estimates of body dynamics and stabilize postural sway more effectively when needed. Previous research found that seated infants increased their postural responses to an oscillating visual stimulus with increasing sitting experience (Bertenthal et al., 1997). This sensorimotor coupling reached a plateau by nine months of age and did not differ at 13 months of age. However, it is unknown whether this sensorimotor adaptation of postural control might show transitional changes when the infants learned to walk. Further research carefully examining the sensorimotor adaptation of postural control during this transition period would help with further understanding the development of the internal model for postural control.

Compared to upright stance (Chen et al., 2003), infants' postural sway variability, amplitude and area were smaller in sitting position. However, the velocity of infant postural sway was not slower in sitting compared to standing. Velocity information is suggested to be  more critical than position in the control of adult upright posture (Jeka et al., 2004). Our previous study has suggested that the development of infants' postural control in stance involves rate-related (e.g., velocity and frequency) changes (2005b; Metcalfe et al., 2005a). Although our present study did not show postural velocity changes, it was not designed to examine infants' postural development from the emergence of sitting onset. Future research is needed to examine whether the rate-related changes occur early in the development of sitting postural control.

In conclusion, our present study showed that learning to walk affects infants' postural control for the already mastered sitting behavior during the transition period. We suggest that the internal model for postural control needs to be re-calibrated for the transition from sitting to walking. This sensorimotor re-calibration temporarily disrupts the development of the previously established sitting posture. Redundant sensory information (i.e., touch) is necessary during this transition period to help control the destabilized posture.

# Chapter 5

# Development of Adaptive Visuo-Motor control in Infant Sitting Posture

## *Introduction*

Postural control is one of the most important motor skills that human infants acquire in early motor development. It takes infants about 6 months to sit independently and about one year to stand and walk on two feet. Around two years of age, infants are able to walk without falling in most situations. In order to control the multi-segmented body over its support base in various environmental conditions and tasks, a reliable and adaptive relationship between action and perception is necessary. However, this relationship may not be innately well established at birth but rather must be acquired over the first months and possibly years of life. While it has been shown that adults are able to adapt their postural responses to changing sensory information (Oie et al., 2002; Peterka, 2002), little is known about how this adaptive postural behavior develops during infancy when dramatic postural behavior changes occur. This study investigates the dynamics of the adaptive sensorimotor relationship in infant postural development. Specifically, we examined infants' ability to adapt their postural responses to different properties, i.e., the frequency and amplitude, of visual information.

Sensory information for postural control comes from multiple sources, including the visual, somatosensory, and vestibular systems (Horak & Macpherson, 1996). This multiple sensory information provides redundancy that helps assure successful postural control. For example, if a source of sensory information is unreliable or misleading, the postural system may need to ignore or attenuate this source and rely more on another sensory system. This ability to 're-weight' sensory information between the sensory inputs is a critical component of the adaptive sensorimotor control required to maintain upright posture in an ever-changing world (Horak & Macpherson, 1996; Oie et al., 2002; Peterka, 2002). Developmentally, this sensorimotor relationship involves continuous calibration and refinement. Contemporary theoretical perspectives on motor development view the integration of perception and action as necessary for the regulation of coordinated movements (Bertenthal & Clifton, 1998; von Hofsten, 2004).

It has been established that adults rapidly adapt to a new environment through the sensory re-weighting process in which postural responses are modified depending on the properties of the sensory information (Jeka et al., 2000; Oie et al., 2002). Young healthy adults demonstrate adaptive visual-postural coupling to changes in the frequency and amplitude of the visual stimulus (Dijkstra et al., 1994; Jeka et al., 2000; Oie et al., 2002; Peterka, 2002). Adults' visual-postural coupling shows greatest in-phase entrainment when the visual stimuli are oscillating at frequencies near their natural frequency of sway (~ 0.2 Hz) but this entrainment becomes weaker and out of phase as the stimulus frequency decreases or increases (Dijkstra et al., 1994). However, this frequency-dependent feature of postural behavior alone may not directly indicate an adaptation process. More direct evidence of postural adaptation comes from the postural responses across different stimulus amplitudes at the same frequency. Research has shown that adults' postural responses are proportional to the amplitude of the visual stimulus within a certain range (Peterka, 2002; Peterka & Benolken, 1995). However, when the amplitude exceeds a certain value, postural sway is no longer responsive to the driving stimulus and indeed decreases with increasing stimulus amplitude (Peterka, 2002; Peterka & Benolken, 1995). This change in the postural response to a change in the visual stimuli is taken as evidence of intra-modal re-weighting (Oie et al., 2002).

Research evidence indicates that newborn infants show directionally appropriate postural responses with their heads to visual flow information and these responses are scaled to the velocity of the stimulus (Jouen, 1990; Jouen et al., 2000). This would suggest that the visual-postural relationship may be a fundamental component of the sensorimotor control system that exists at birth. However, it remains unclear how this relationship may change as the infant develops better postural control in various motor tasks and situations. Only a few studies have analyzed infants' postural responses in sitting (Barela et al., 2000; Bertenthal et al., 2000; Bertenthal et al., 1997) or standing (Foster, Sveistrup, & Woollacott, 1996) to changes in the frequencies of dynamic visual stimuli. However, the results were conflicting as to whether visual-postural entrainment depends on the frequency properties of visual stimuli and whether there are age- or experience-related changes in the visual-postural relationship. While some studies have shown that infants' postural entrainment increased as the frequency of the room motion increased (Barela et al., 2000; Bertenthal et al., 1997), others reported a linear decline in sway coherence as a function of visual frequency (Bertenthal et al., 2000). Further, the developmental changes in infants' visual-postural coupling were reported in one study (Bertenthal et al., 1997) but not the other (Barela et al., 2000). These conflicts may be due to differences in the postural entrainment measures as well as the visual stimulus amplitudes and velocities employed. Different postural behaviors may share the same sensorimotor relationship and that the emergence of a new postural milestone may results in sensorimotor re-calibration (Chen, Metcalfe, Jeka, & Clark, 2007). Further, the previous studies have only examined infants' sitting posture from sitting to newly walking and therefore may not have fully characterized the development of infants' sensorimotor control in sitting.

Therefore, the purpose of this study was to systematically examine the dynamic visual-postural relationship and its relation to the properties of visual stimuli in infant postural development. The frequency- and amplitude- dependent properties of the postural responses to dynamic visual stimuli were examined during the period when infants develop their posture from sitting to standing and walking.

## *Method*

### *Participants*

Twenty healthy infants (13 males and 7 females; 12 Caucasian, 6 Asian, and 2 others) were recruited from the University of Maryland, College Park, Maryland area, and its surrounding communities. All infants were born full-term with no birth complications or any history of developmental delay, neuromuscular disease, or sensory system problems. These infants were divided into 4 developmental groups (each n=5): 1) sit onset (SO) (Mean chronological age (CA): 6.7 ± 1.1 months; and mean number of days after sit onset: 6.0 ± 5.1), 2) stand alone (ST) (Mean CA for standing without support but unable to take independent steps: 10.6 ± 1.2 months; and mean number of days before walk onset: 28.8 ± 11.9), 3) walk onset (WO) (Mean CA for walk onset: 11.7 ± 1.4 months; and mean number of days after walk onset: 8.8 ± 8.1), and 4) 1-year walking (W12) (Mean CA for one-year post walking: 23.5 ± 1.2 months; and mean walking age after walk onset: 11.7 ± 1.0 months). Sit onset was defined as the time when the infant could sit on the floor without any support for 10 seconds. Walk onset was defined as the time when the infant could walk independently for three continuous steps without falling. Each infant's parents gave written informed consent prior to inclusion in the study and received a small remuneration ($15) after completing the experiment. All experimental procedures were approved by the Institutional Review Board at the University of Maryland, College Park.

### *Apparatus and Measures*

Fig 5.1 illustrates the experimental set-up in which the infant sat on a customized chair in a 3-wall room. The chair was approximately 100 cm from the front wall. To prevent the infant seeing the floor during the experiment, the chair was set on a 45 cm high pedestal. For the infant's safety, the chair had a small back support and a safety belt across the hip.

*Visual apparatus:* The visual display was created in a Fakespace Systems CAVE Automatic Virtual Environment™. It is a room-sized advanced visualization tool that combines high-resolution, stereoscopic projection and 3-D computer graphics to create a visual virtual environment. The CAVE is a rear-projected 2.5 × 3.0 $m^2$ three-wall projection display system with 1280 × 1024 pixels spatial resolution and 60 Hz framing rate. The animated visual display consisted of a virtual wall specified by white 2-D triangles projected on a black background, excluding the foveal region. Each triangle was approximately 0.2° × 0.3° × 0.2° on a side and was randomly positioned on the front wall and two side walls. The visual displays were preprogrammed in C++ and OpenGL. A PC workstation along with Optotrak system and Labview data acquisition software (National Instruments, Inc.) were used to generate the visual displays as well as collect data from multiple apparatuses. To attract and maintain the infant's attention to the front wall, a video (image size: 15 cm diameter circle) was projected onto the middle of the stimulus array (in the foveal region) with the auditory outputs played through speakers behind the front wall.

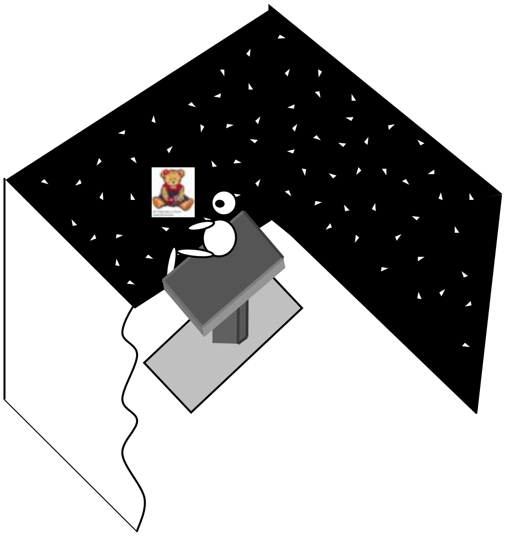


Figure 5.1. Illustration for experimental set up in which the infant sat independently on a chair in a 3-wall room.

*Postural measures:* Infants' postural sway was measured using an active infrared position tracking system (Optotrak, Northern Digital, Inc.). Three small infrared LEDs were affixed comfortably to the infant's occipital prominence (H), upper trunk (UT, T1 level), and middle trunk (MT, T10 level). A bank of three cameras was positioned parallel to the front screen and 2 m behind the infant during testing to record 3-dimensional movements of the infant's head ($H_{AP}$, $H_{ML}$, $H_V$), upper trunk ($UT_{AP}$, $UT_{ML}$, $UT_V$), and middle trunk ($MT_{AP}$, $MT_{ML}$, $MT_V$) in real time.

*Video recording:* A standard sVHS recorder (Panasonic AG-7350) was placed behind the infant to videotape the testing session for later coding of the infant's engagement to the visual display. The videotape recording was synchronized with the analog data using an event synchronization unit (PEAK Performance Technologies; Englewood, CO) and time-stamped with a SMPTE code generator (Horita RM-50 II; Mission Veijo, CA).

All equipment, including the Optotrak, visual apparatus, and video recording were synchronized for data collection.

*Experimental Design*

A sum-of-sines technique in which all selected input frequencies were presented simultaneously was used in this study (Kiemel et al., 2006). This method allowed us to examine infants' visual-postural coupling over a large range of frequencies as well as amplitude variations without increasing the testing burden on the infants. The visual stimulus consisted of a summation of 5 sinusoids (sum-of-sines) at frequencies 0.12, 0.28, 0.52, 0.76, and 1.24 Hz with baseline amplitudes of 0.417, 0.179, 0.096, 0.065, 0.040 cm respectively. These frequencies were chosen as prime multiples of a base frequency (0.004 Hz) to avoid low-order harmonics. Amplitudes were varied as 0.05/frequency to maintain a constant peak velocity across frequencies.

During the experiment, three 60-second trials were collected in each of five conditions that vary in the amplitude of visual motion.

Amplitude 0 (A0): The visual display was stationary on all three walls.

Amplitude 1 (A1): The sum-of-sines visual stimulus oscillated with the baseline amplitudes as described above.

Amplitude 2 (A2): The amplitudes of the sum-of-sines were twice as large as the baseline amplitude in Amplitude 2 condition.

Amplitude 3 (A3): The amplitudes of the sum-of-sines were twice as large as those in Amplitude 2 (four times of the baseline amplitude in Amplitude 1).

Amplitude 4 (A4): The amplitudes of the sum-of-sines were three times as large as those in Amplitude 3 (twelve times of the baseline amplitude in Amplitude 1).

Data were collected in 3 randomized blocks (with one trial for each amplitude condition in each block). We utilized the sum-of-sines technique to reduce the number of trials needed to characterize infants' visual-postural coupling relationship and its relation to sensory properties. This procedure presents the selected input frequencies simultaneously allowing the computation of the transfer function at all input frequencies based on the same trials. Comparing the responses to various frequencies within the same trial enables us to capture the nature of the coupling relationship to different properties of the visual stimulus. Using different amplitudes of sum-of-sines allows us to further examine whether infants are able to adapt and re-weight their visual-postural relationship among various frequencies.

### *Procedures*

Before a testing session, the infant was given a brief period of acclimation to the laboratory (e.g., playing toys, interacting with the experimenters). Following this period, infrared LEDs were affixed to the infant's back of head, upper and lower trunk and her/his shoes were removed. The infant then was placed in the customized chair with a seat-belt fastened across the hip. A children video was played at the infant's foveal region on the front wall to attract the infant's visual attention. One experimenter and the parent stayed near the infant but not at his/her sight to prevent falls and to provide help when needed. When the experimenter indicated that the infant was quiet and attending to the front wall, a second experimenter initiated data acquisition. A third experimenter real-time coded the infant's engagement to ensure data collection for each amplitude condition.

### *Data Reduction and Analysis*

*Behavioral coding:* Following data collection, two trained coders independently reviewed all trials for usable time series segments. The coding criterion for time series inclusion was infant's quiet posture and continuous eye engagement onto the front wall for at least 10 seconds (a time epoch that we have found sufficient for analyses in our previous studies). Small movements of the head, trunk, or arms were accepted. Only those time series segments independently coded as acceptable by two coders were used for sequent data analysis.

*Sitting duration:* After behavioral coding, the duration of each sitting data segment varied from 10 (shortest accepted duration) to 60 (whole trial) seconds. Mean segment time (MST) was calculated as the averaged duration across all segments of each infant and each amplitude condition. Although the experimental design was to collect 3 trials for each amplitude condition, infants might be tested for more trials to ensure sufficient data for subsequent analysis. Percentage Time (% Time) was calculated as total segment duration divided by total testing time for each infant and each amplitude condition. Percentage Time represents the infant's engagement in the sitting task in each amplitude condition.

As the visual stimulus was driven in the anterior-posterior (AP) direction, the infant's postural sway was analyzed only in this direction. Raw signals of the AP displacements of head ($H_{AP}$), upper trunk ($UT_{AP}$), and middle trunk ($MT_{AP}$) were mean-detrended. All data extraction and signal processing were performed using customized Matlab programs (Version 7.0, Mathworks Inc., Natick, MA).

*Unperturbed sitting postural sway:* To characterize infants' quiet, unperturbed sitting posture, infants' postural sway ($H_{AP}$, $UT_{AP}$, $MT_{AP}$) in the stationary vision condition (A0) were examined. Postural sway signals were low-pass filtered using a recursive 2nd-order Butterworth filter ($f_{cut}$-off = 5 Hz) and then position (Pos_var) and velocity variability (Vel_var), mean velocity (Vel_m), and median frequency (F_m) were computed. Variability was calculated as the standard deviation of the position and velocity displacements of postural sway. Vel_m was computed as the total sway path length divided by the segment duration. For F_m, power spectrum density of postural sway time series was computed using multi-taper method with 8 tapers to characterize the frequency distribution of infants' sitting posture. Total power was calculated as the integrated area of the power spectrum from 0 to 5 Hz. To describe the distribution of postural sway across frequencies, median frequency was determined as the frequency that accumulated 50% power of the frequency spectrum. After the postural measures were computed for each time segment, mean for each measure was calculated for each infant and each amplitude condition, weighted by the segment duration.

*Postural sway at the driving frequencies:* For the moving vision conditions (A1~4), a linear systems spectral analysis was performed on all time segments by calculating the individual Fourier transforms of the time series from the postural sway and the visual stimulus. The transfer function (frequency-response function) at each driving frequency was computed by dividing the transform of the postural response by the transform of the stimulus. Since our visual signal is deterministic, this procedure for computing the transfer function is consistent with its definition in terms of power spectra. Gain and phase measures were derived from the transfer function. Gain is the ratio of the amplitude of the response to the amplitude of the stimulus at each driving frequency and represents the strength of the postural response relative to the stimulus. It was calculated as the absolute value of the transfer function at the stimulus frequency. Gain values close to one indicate that body or head sway is the same as the amplitude of the driving signal. Phase is a measure of the temporal relationship, a normalized representation of the time delay between postural sway and the stimulus motion. It was calculated as the complex value of the transfer function at the stimulus frequency. A positive phase value indicates that the body movement leads the visual stimulus, whereas a negative phase indicates that body sway lags behind the stimulus. Transfer functions were averaged across the time series segments, weighted by the segment duration, for each infant and each amplitude condition.

*Postural responses at the non-driving frequencies:* To examine infants' postural responses at the non-driving frequencies, position (Pos_var) and velocity variability (Vel_var) were calculated for the residual postural sway, with the component of all 5 driving frequencies removed. Mean Pos_var and Vel_var were calculated for each infant and each amplitude condition, weighted by the segment duration.

### *Statistical Analysis*

For sway variability, velocity, and frequency measures in the stationary vision condition (A0), a mixed model repeated measures ANOVA was performed for each variable to examine whether infants' unperturbed sitting posture differed among the 4 developmental groups. For sitting time measures and Pos_var and Vel_var of the residual postural sway, individual mixed model repeated measures ANOVA was conducted for all visual amplitude conditions to assess the effect of group (4), amplitude (5), and their interactions.

To examine infants' postural responses to the moving visual stimulus, transfer functions were compared in the complex plane using a linear model of repeated measures MANOVA. The real and imaginary parts were taken from the weighted-mean transfer functions of each infant and each amplitude condition and each driving frequency. The dependent variables were the real and imaginary parts and the independent variables including frequency, amplitude, group, and their interactions. This MANOVA analysis assessed the transfer function distributions among the independent variables and therefore took into account both gain and phase. Transfer functions with different gain responses but large phase variability may not be seen as different in this analysis because of the overlapping transfer function distributions in the complex plane. To better examine the infants' spatial and temporal postural responses to the visual stimulus, gain and phase were also separately examined. Gain and phase were calculated for weighted mean transfer functions of each infant, amplitude, and frequency. Separate mixed model of repeated measures ANOVAs were performed for gain and phase to assess the effect of group (4), amplitude (4), frequency (5), and their interactions.

For all statistical tests, amplitude and frequency were treated as within-subject factors and group as a between-subject factor. All statistical analyses were performed with the Statistical Analysis Software (SAS) program (Release 9.1, SAS Institute Inc., Cary NC, USA). A *p* value equal to or less than 0.05 was defined as statistically significant. Post-hoc comparisons were performed when applicable using a Tukey adjustment for *p* value to control for type I error.

## *Results*

### *Sitting Duration*

During the experiment, most infants did not have difficulties engaging in the sitting task. However, infants showed disruptive behaviors, including looking around, turning to the parent, or becoming fussy, in the largest amplitude condition (A4). All infants were able to perform the experimental task in each amplitude condition except for one SO infant who was unable to engage in the task in the A4 condition. While SO infants needed to take frequent rest breaks, W12 infants usually finished the entire testing session with few or no rest breaks (total time of testing about 30 minutes). Mean Segment Time (MST) results showed a significant Group effect ($p<0.05$). As shown in Fig 5.2A, W12 infants were able to engage in the sitting task longer than all other three groups (all adjusted $p<0.05$). No Amplitude or Group*Amplitude interaction effect was significant for MST. Examining %Time for infants' engagement in all trials, the results revealed both significant Group and Amplitude effects (both $p<0.005$) with no Group*Amplitude interaction effect ($p>0.05$). Post-hoc comparison revealed that W12 infants were able to engage in the experimental task more than in all other three groups (all adjusted $p<0.05$). When comparing among the amplitude conditions, infants engaged in A4 less than in A2 condition (adjusted $p<0.05$) (Fig 5.2B).

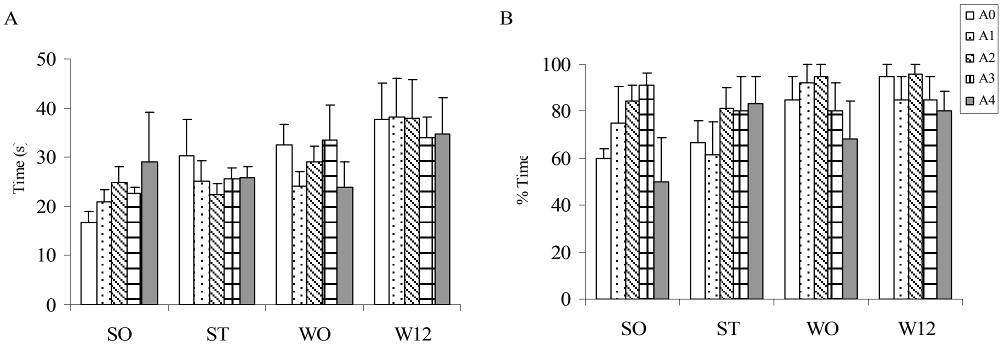


Figure 5.2. MST (A) and %Time (B) (mean ± s.e.) for each group and amplitude condition.

Results of infants' postural responses from $H_{AP}$, $UT_{AP}$, and $MT_{AP}$ showed similar patterns among the groups, amplitude conditions, and frequencies with $H_{AP}$ more responsive than the two trunk segments. Therefore, only $H_{AP}$ results are presented below.

*Unperturbed Sitting Posture*

Examining infants' quiet sitting postural sway in the stationary vision condition (A0), all variability, velocity, and frequency measures showed a significant Group effect (all $p<0.05$) (Fig 5.3). Post-hoc comparison revealed larger Pos_var in SO infants than in ST and W12 infants (adjusted all $p<0.05$). SO infants showed higher Vel_m and Vel_var than all other infants (all adjusted $p<0.05$) and lower F_m than WO and W12 infants (both adjusted $p<0.05$).

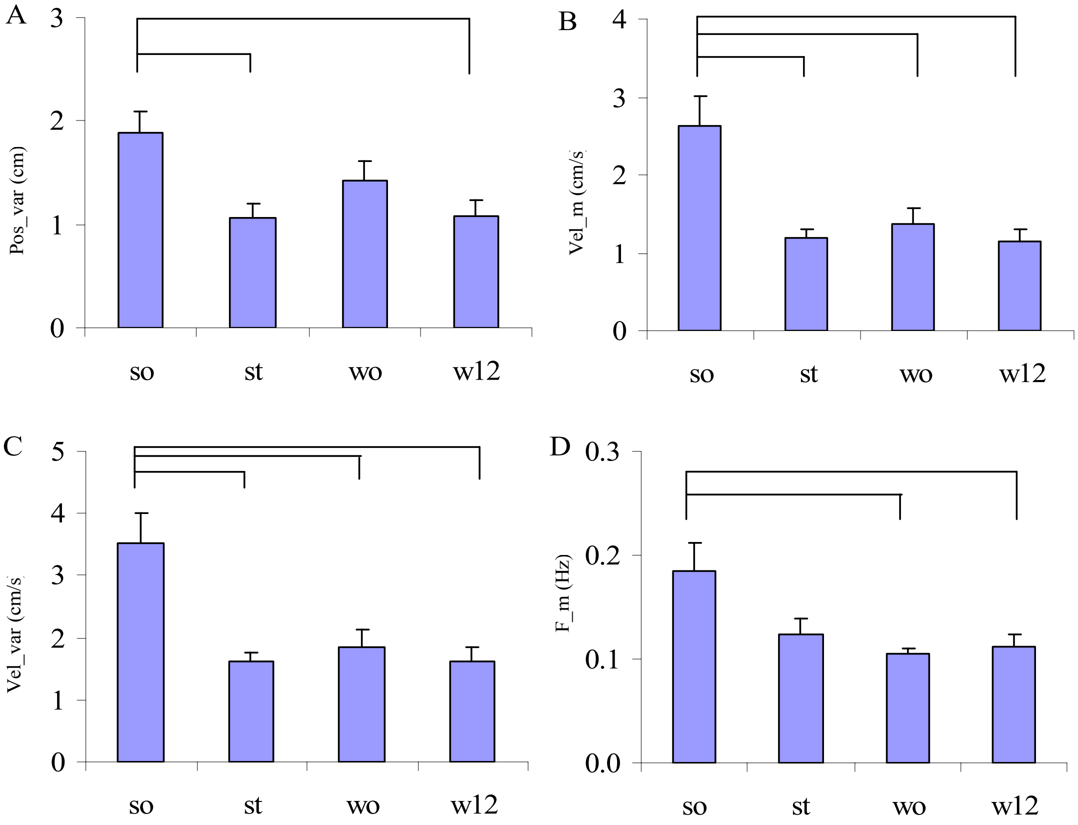


Figure 5.3 Position variability (A), Mean velocity (B), Velocity variability (C), and Median frequency (D) (mean ± s.e.) of the $H_{AP}$ sway across groups. Brackets indicate significant pair-wise comparisons.

### *Postural Responses at the Driving Frequencies*

Examining the transfer functions of infants' postural responses at driving frequencies in the complex plane, repeated measures MANOVA revealed a significant Frequency effect (Wilks' Lambda=0.79, $p$<0.05) and a marginal Group*Amplitude effect (Wilks' Lambda=0.89, $p$=0.064). Neither Amplitude, Group, nor any other interaction effect was significant (Wilks' Lambda $p$>0.05). Based on the distribution of transfer functions, estimated mean and 95% confidence interval (CI) were computed for Gain (Fig 5.4) and Phase (Fig 5.5). As the transfer functions for infants' postural responses to the visual stimulus were not clustered on the complex plane, most of the estimated Gain responses were not significantly different from 0 (Fig 5.4).

To further examine the spatial and temporal characteristics of infants' postural responses to the visual stimulus, Gain and Phase were calculated and separately analyzed. For infants' gain responses, repeated measures ANOVA showed significant main effects for Frequency, Amplitude, and Group, as well as Group*Amplitude interaction (all $p<0.001$). Post-hoc analyses showed that infants' gain responses at 0.52 and 0.76 Hz were higher than those at 0.12 and 1.24 Hz (all adjusted $p<0.05$). As shown in Fig 5.6, all infants showed lower gain with increasing amplitude (all adjusted $p<0.05$). Significant Group effect existed only in A1 condition in which SO infants showed higher gain than all other infants (all adjusted $p<0.05$). For infants' phase responses, repeated measures ANOVA revealed significant Frequency main effect as well as Frequency*Group, Frequency*Amplitude, and Frequency*Amplitude*Group interaction effects (all $p<0.05$). Post-hoc analyses revealed that W12 infants showed phase differences between 0.52 and 1.24 Hz occurred in all amplitude conditions but newly sitting infants only showed the difference in the large amplitude (A4) condition.

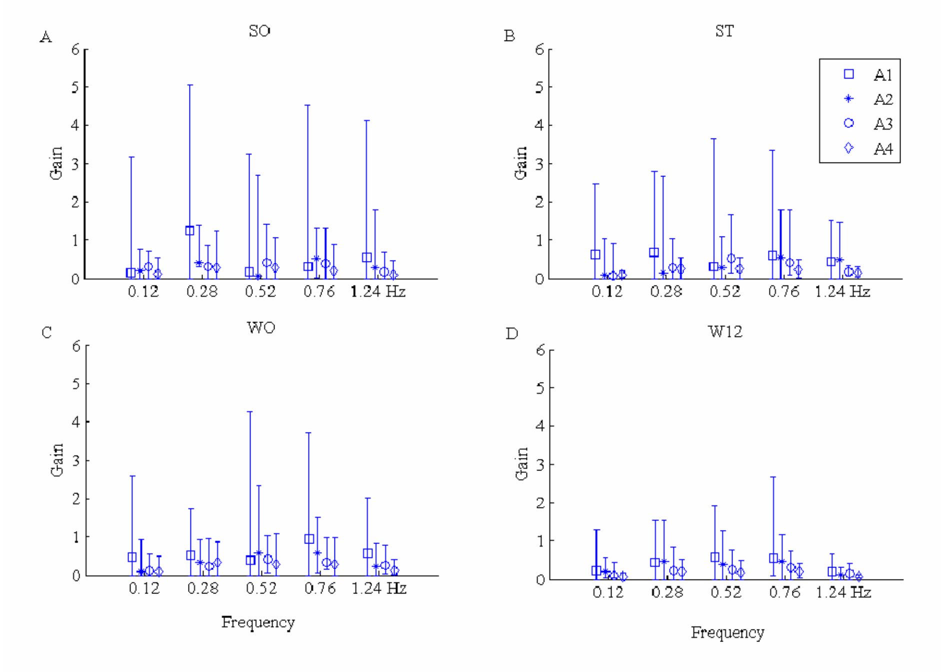


Figure 5.4 Estimated Gain (mean ± 95%CI) of the $H_{AP}$ responses to the visual stimulus across Frequency and Amplitude in group SO (A), ST (B), WO (C), and W12 (D).

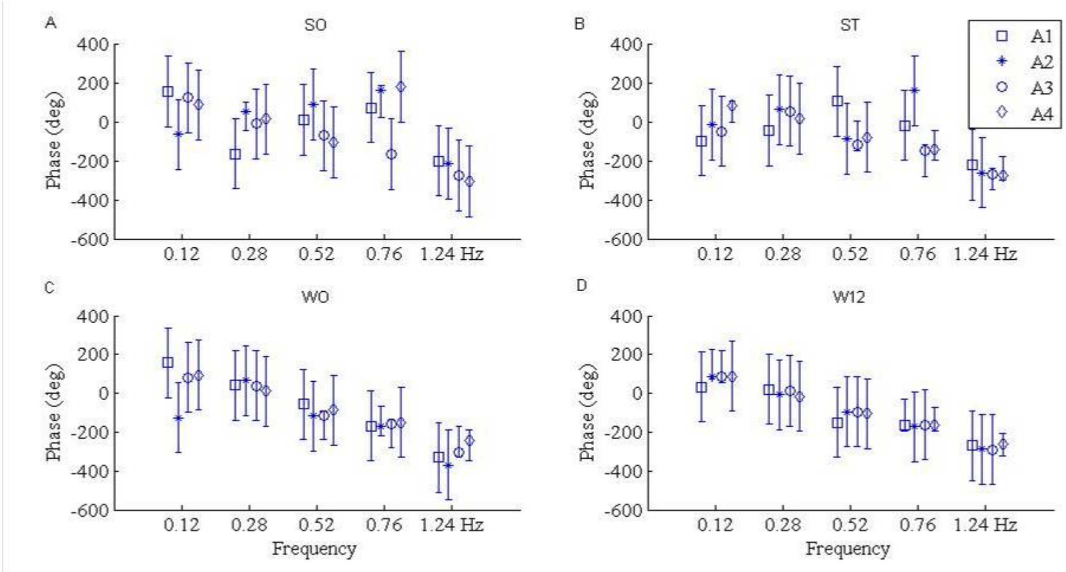


Figure 5.5 Estimated Phase (mean ± 95%CI) of the $H_{AP}$ responses to the visual stimulus across Frequency and Amplitude in group SO (A), ST (B), WO (C), and W12 (D).

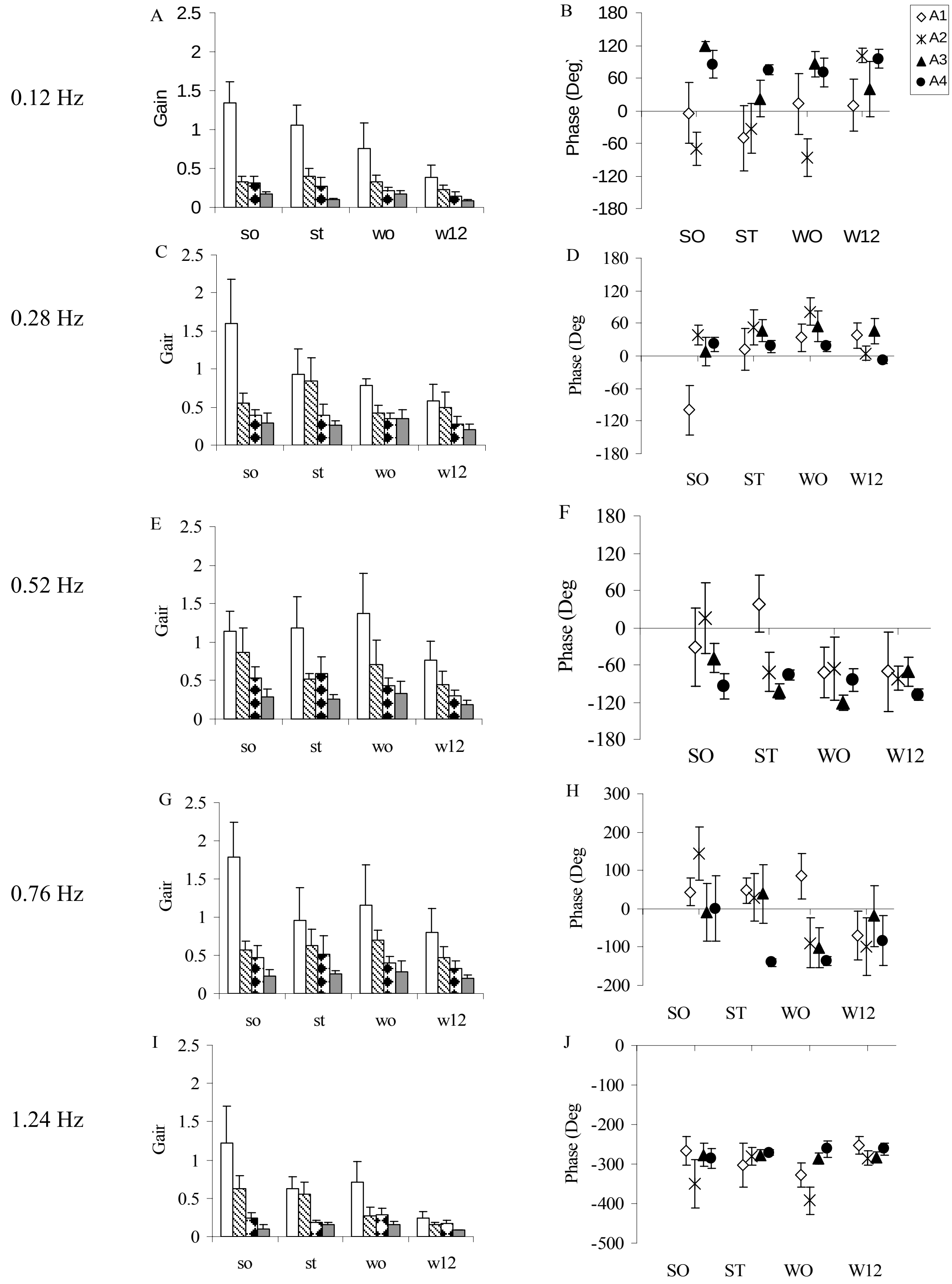


Figure 5.6 Gain (A,C,E,G,I) and corresponding phase (B,D,F,H,J) (mean ± s.e.) of the $H_{AP}$ responses to the visual stimulus across amplitude conditions and groups at each frequency.

*Postural Responses at the Non-Driving Frequencies*

After removing the components of the driving frequencies, infants' residual postural sway showed similar results with their sway in the stationary vision condition. Repeated measures ANOVA revealed a significant Group main effect for both Pos_var and Vel_var (both $p<0.0001$). The Group effect for Pos_var was due to SO infants higher than ST and W12 infants, and WO infants higher than W12 infants (all adjusted $p<0.005$). Vel_var was higher in SO infant than all other infants and lower in W12 infants than all other infants (all adjusted $p<0.005$). No significant Amplitude or Group*Amplitude effect was found for Pos_var and Vel_var of infants' residual postural sway.

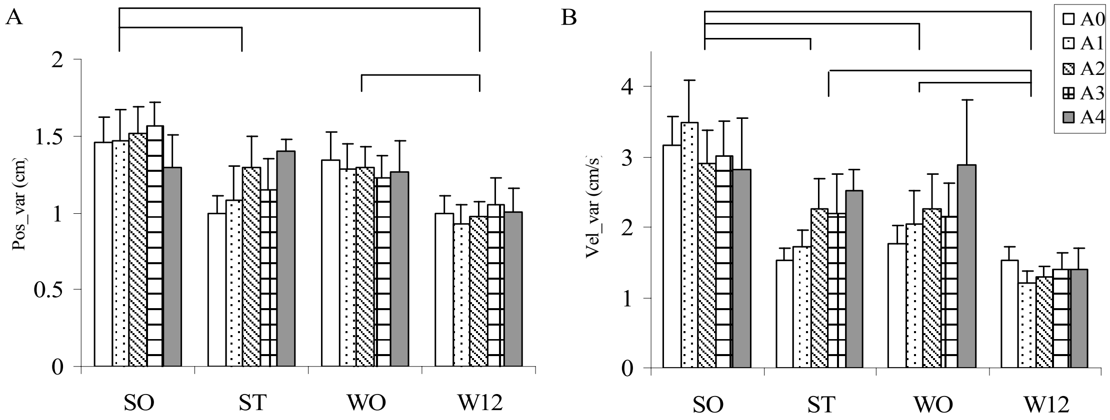


Figure 5.7 Position (A) and velocity (B) variability (mean ± s.e.) of the $H_{AP}$ residual sway, with the components of driving frequencies removed, across groups and amplitude conditions. Brackets indicate significant pair-wise comparisons.

## *Discussion*

The purpose of this experiment was to systematically examine the adaptive visual-postural dynamics in sitting, specifically the frequency- and amplitude- dependent features, as infants develop this capability in sitting, standing, and walking. Our results revealed that infants as young as sitting onset responded to an oscillating visual stimulus and, more importantly, re-weighted the visual information as the stimulus amplitude changed. The postural responses of experienced walkers (W12) exhibited adult-like frequency and amplitude dependency to the visual inputs. Newly sitting infants also demonstrated similar frequency and amplitude dependency in their visual-postural relationship, except in the low amplitude condition in which they showed more responsive but variable postural behaviors. Residual variability was consistently lower in experienced walkers, indicating more stable overall posture. These results suggest that infants as young as sitting onset are able to adapt their sitting posture to the frequency and amplitude properties of perceived visual information revealing a complementary relationship between improved control of self-motion and sensitivity to environmental motion.

### *Infants Re-weight to Changes in Visual Amplitude*

In order to facilitate infants' responses to the visual stimulus, infants in the current study sat independently on a chair with minimal back support and a seat belt. Our design might lead to the results that newly sitting infants engaged in the experimental task shorter than standing and walking infants. Interestingly, %Time results showed that all infants, especially new sitters, were less successful in maintaining quiet postural behavior when the visual stimulus oscillated in large amplitude. Behavioral observation during the experiment suggests that infants were disturbed by the large visual stimulus and showed disruptive behaviors. Indeed, one newly sitting infant was not able to maintain quiet postural behavior in the largest amplitude condition. Visual flow provides information about self-motion. This inability to engage in the quiet sitting task in the large amplitude condition may suggest that infants are less able to successfully re-weight the visual information and thus are disturbed by the conflict between sensation and their self-motion when the amplitude of visual stimulus was large. These results may help to explain previous findings that infants become less and less perturbed by optic flow and are more able to maintain equilibrium as postural experience increases (Butterworth & Cicchetti, 1978; Butterworth & Hicks, 1977; Forssberg & Nashner, 1982; Stoffregen et al., 1987).

Surprisingly, infants as young as sitting onset showed evidence of sensory re-weighting when they were able to engage in the task. When the stimulus amplitude increased, infants down-weighted the visual information and thus showed a decreased gain response; evidence for intra-modal re-weighting. These results for infants, like adults (Kiemel et al., 2006; Oie et al., 2002) and children (Bair, Kiemel, Jeka, & Clark, 2007), suggest that human postural behavior is adaptive as early as the onset of infant's achievement of the first upright independent postural behavior, sitting. If this relationship exists at the ondet of independent upright posture, what is developing as the infant develops postural control for sitting, standing, and walking? As shown in Fig 5.6, newly sitting infants were more responsive to the visual information than standing and walking infants when the stimulus amplitude was small. This high responsiveness may lead to postural instability even when small changes occur in the sensory environment. Combining these results with our behavioral observation, we suggest that postural development may involve a refinement of the visual-postural relationship that allows the infant to respond appropriately to visual information and to successfully re-weight the information when condition changes. This sensorimotor refinement is an important and continuous process that allows the infant to estimate and control their body motion as she/he develops different postural behaviors from sitting, standing, to walking (Chen et al., 2007).

### *Infants Respond to Changes in Visual Frequency*

Our study is the first to show a non-linear pattern for infants' postural responses to different frequencies of the visual information. Infants as young as sitting onset demonstrated higher gain responses at 0.52 and 0.76 Hz but lower at 0.12 and 1.24 Hz. Unlike adults who show the strongest postural entrainment around 0.2 Hz (Dijkstra et al., 1994; Jeka et al., 2000), the highest gain responses for infants were observed at higher frequencies in infants. These results are consistent with Barela and his colleagues (Barela et al., 2000) who showed higher gain response at 0.5 Hz in 6-9 month-olds. This discrepancy in which visual frequency elicits the highest gain between adults and infants may be due to different tasks (standing vs sitting) and/or differences in the natural postural sway frequency in adults and infants owing, in large part, to the differences in height. In the current study, although newly sitting infants showed higher sway frequency than older infants in the stationary vision condition, no clear evidence was found for changes in the frequency response pattern among the four groups of infants. Interestingly, infants showed in-phase behavior between the visual stimulus and their postural responses around 0.28 Hz. Although sum-of-sine technique was used in the current study to allow a thorough examination of infants' visual-postural relationship, infants were unable to engage in the experimental task as long as adults. Our estimation of infants' gain and phase response across frequencies may be limited by the insufficient segment duration as well as the total amount of data we were able to collect in the current study. However, our results characterize the non-linear frequency response pattern of infants' sitting posture and offer an explanation for previous findings of infants' linear frequency response which may be due the limited frequency range.

Consistent with previous studies in infants (Barela et al., 2000; Bertenthal et al., 2000) and adults (Dijkstra et al., 1994; Jeka et al., 2000; Kiemel et al., 2006), a frequency-dependent phase response was observed in this study. From low (0.12 Hz) to high (1.24 Hz) frequencies, infants showed their sitting postural sway changing from leading to lagging behind the visual motion. Interestingly, this frequency-dependent phase response is influenced by the stimulus amplitude in newly sitting infants. While one-year-walkers demonstrated the frequency-dependent temporal relationship between their sitting posture and the visual stimulus regardless of the stimulus amplitude, newly sitting infants did not show this feature when the stimulus amplitude was small. These results are similar to our previous study in which infants, through the first 9 months of walking, show increased temporal consistency between their standing postural sway and an oscillating somatosensory drive (Metcalfe et al., 2005b). Consistent with previous studies that examined muscle activities in sitting (Hadders-Algra, 2005; Hedberg et al., 2005), our results showed that newly sitting infants' postural sway are more variable than experienced walkers in the stationary vision condition as well as in the dynamic conditions. Their high level of self-motion may prevent precise detection and responses to the parameter (frequency) of the visual information. Combining the results of newly sitters' high responsiveness with variable temporal relationship in the small amplitude condition, we suggest that perception-action coupling of postural behavior may exist early in life but the developmental process involves fine tuning the spatial and temporal properties of this coupling relationship.

### *Changes of Sitting Posture when Walking Emerges*

As expected, infants' quiet sitting posture becomes more stable, as indicated by decreases in sway variability and velocity, after few months of sitting when infants learned to stand. Around the onset of walking, infants become less stable and increased their postural sway in sitting. This postural instability in WO infants can also be observed from the residual postural sway in the dynamic visual conditions. These results duplicate our previous study in which infants showed a transient disruption in sitting posture as infants learn to walk (Chen et al., 2007). This transient postural disruption suggests a sensorimotor re-calibration as a new postural behavior emerges. Interestingly, the transient disruption was not present in the median frequency of infants' sitting postural sway. All standing and walking infants showed lower sway frequency in sitting than newly sitting infants. The decrease of sway frequency during the developmental course has also been shown in our previous study which examined infants' quiet standing posture during the first 9 months of independent walking (Chen, Metcalfe, Chang, Jeka, & Clark, 2007). Decreases in the postural sway frequency suggest that, during early development, infant postural control relies more on the estimation process and less on the fast corrective corrections. Motor development is a continuous process with discontinuous characteristics. With increased sitting experience, infants learn to better use sensory information to form postural estimates. However, sensorimotor re-calibration during the emergence of walking temporally leads to postural instability.

### *Conclusion*

In conclusion, this study demonstrated that infants as young as sitting onset are able to control their sitting posture responding to an oscillating visual stimulus and to re-weight the visual information as the stimulus amplitude changes. While the experienced walkers showed adult-like frequency- and amplitude-dependent features of their visual-postural relationship, newly sitting infants were more responsive but variable at very low amplitudes of visual motion where their higher level of self-motion may prevent precise detection. We suggest that visual-postural coupling and sensory re-weighting are fundamental processes that are present early in the developmental course of postural control. Infant postural development may involve a refinement of the sensorimotor dynamics that entails a complementary relationship between improved control of self-motion and sensitivity to environmental motion.

# Chapter 6

# Summary and Future Direction

Postural control is a fundamental component in the development of many motor skills, such as reaching and walking (Bertenthal & Clifton, 1998). Contemporary theories conceptualize human postural control as the result of dynamic interactions between the neuromuscular and sensory systems under the constraints of the surrounding environment and task demands (Horak & Macpherson, 1996). While the sensorimotor control of postural behavior has been extensively studied in adults, in comparison, little is known about how this adaptive motor behavior develops during infancy; a time when postural behavior changes dramatically. An important component of postural control is the integration of perception and action. The development of this process is the focus of this dissertation.

In this dissertation, we sought to study the development of sensorimotor control of infant posture by systemically examining infants' quiet postural sway and how it responds to various sensory inputs. This dissertation addressed three specific aims: 1) to characterize the development of infants' independent, unperturbed upright posture in sitting and standing; 2) to establish the influence of static somatosensory information from light touch contact on infants' upright posture in sitting and standing; 3) to examine the visual-postural relationship of infant sitting posture and how it adapts to changing sensory information.

### *The Development of Infants' Unperturbed Standing Posture*

Human posture, even quiet upright stance, is never motionless. Small deviations from the system's equilibrium point result in gravity-induced torque that pulls the body further away from its centered position. Postural sway represents a system that continuously adapts to the internal and external perturbations (Oie et al., 2002). While many studies have characterized the postural sway during quiet stance in adults (Collins & De Luca, 1994; Kiemel et al., 2002; Prieto et al., 1996) and children (Kirshenbaum et al., 2001; Riach & Hayes, 1987; Woollacott et al., 1987), little is known about how infants' unperturbed upright postural sway changes as they learn to sit, stand, and walk.

In this dissertation, we longitudinally examined infants' quiet stance in the 9 months following the onset of independent walking (Chapter 3). Our results indicated that early development of upright postural control involves changes in the rate-related characteristics rather than a progressive attenuation of postural sway. Along with increasing walking experience, infants' postural sway changes toward lower frequency, slower and less variable velocity oscillations without changing the spatial characteristics of sway. Consistent with adult research (Jeka & Lackner, 1994), additional touch contact stabilized infants' postural sway as indexed by decreases in sway position variance, amplitude, and area as well as changing frequency and velocity features of the sway.

It has been suggested that postural control involves a combination of estimation and control processes (Kiemel et al., 2002; van der Kooij et al., 2001). Sensory information from multiple sources is integrated to estimate and predict body position and velocity. Motor commands, based upon the current estimates of body dynamics, are then sent to the musculature to maintain the upright posture. Our results from the first experiment suggest that early development of upright postural control may involve a refinement of sensorimotor dynamics that enhances estimation of self-motion for controlling upright stance.

### *Postural Disruption during the Transition to a New Postural Behavior*

During the first two years of life, infants gradually develop the control of their body in various postural tasks, such as sitting, standing, and then walking. As the postural demands differ under different tasks and contextual conditions, the sensorimotor dynamics of postural control changes. The sensorimotor relationship can be represented as an internal model that is acquired and modified in the central nervous system and mimics the dynamics between motor responses and the sensory inputs (Kawato, 1999; Wolpert et al., 1995). This internal model requires a re-calibration during the developmental transition to assure accurate postural estimation and response generation in the already established as well as the newly acquired postural behaviors. This sensorimotor re-calibration during the transition to a new postural behavior may have an impact on the already established postures. In this dissertation, we longitudinally examined infants' postural sway in quiet sitting as they learn to stand and walk (Chapter 4). More specifically, we examined how the emergence of walking affects infants' previously established sitting posture.

Our results from the second experiment indicate that learning to walk affects infant sitting posture. Infants showed a temporary increase in their sitting postural sway before or at walk onset. Further, touching a contact surface attenuated infants' sitting postural sway only during this transition. We suggest that this transient disruption in sitting posture results from a process involving re-calibration of the sensorimotor relationship for postural control so as to accommodate the newly emerging bipedal behavior of independent walking. Additional sensory information is used only when the posture becomes unstable during the transition. These results are consistent with the concept that postural development involves a continuous re-calibration and refinement of the sensorimotor relationship to better form postural estimates and generate motor responses. This sensorimotor re-calibration and refinement not only affects infants' postural control in the current task (stance and walk) but also affects the control of a previously stable postural behavior (sitting), suggesting a continuous developmental process across various postural tasks. Sensorimotor re-calibration allows the infant to integrate the new sensorimotor relationship and the established behaviors in the overall postural repertoire.

### *The Development of Adaptive Sensorimotor Control of Infants' Sitting Posture*

In order to control the multi-segmented body over its support base in various environmental conditions and tasks, a reliable and adaptive relationship between action and perception is necessary. While it has been established that adults rapidly adapt to a new environment through the sensory re-weighting process in which postural responses are modified depending on the properties of the sensory information (Jeka et al., 2000; Oie et al., 2002), little is known about how this adaptive postural behavior develops during infancy when dramatic postural behavior changes occur. In the third experiment, we investigated the development of adaptive sensorimotor control of infants' sitting posture (Chapter 5). Specifically, we examined infants' ability to change their postural responses to different properties, i.e., the frequency and amplitude, of visual stimuli.

Our study suggests that infants as young as sitting onset are able to control their sitting posture while responding to dynamic visual stimuli and, more importantly, to re-weight the visual information as the stimulus amplitude changes. Newly sitting infants, comparing to experienced walkers, were more responsive but variable when the amplitude of the visual stimulus was small. We suggest that perception-action coupling and sensory re-weighting are fundamental processes that exist early in infancy. Infant postural development may entail a complementary relationship between improved control of self-motion and sensitivity to environmental motion.

Taken together the results from three experiments, this dissertation provides evidence supporting the concepts that postural development involves a continuous refinement and re-calibration of sensorimotor relationship. Perception-action coupling and sensory re-weighting are fundamental processes that are present as early as when the infant learn to sit independently. Through the developmental course, the sensorimotor dynamics of postural control is refined as the infant improve the capability of self-motion control and sensitivity to the sensory information. The sensorimotor refinement and re-calibration processes allow the infant to form reliable and accurate postural estimates and motor responses in the changing environment and in various motor tasks.

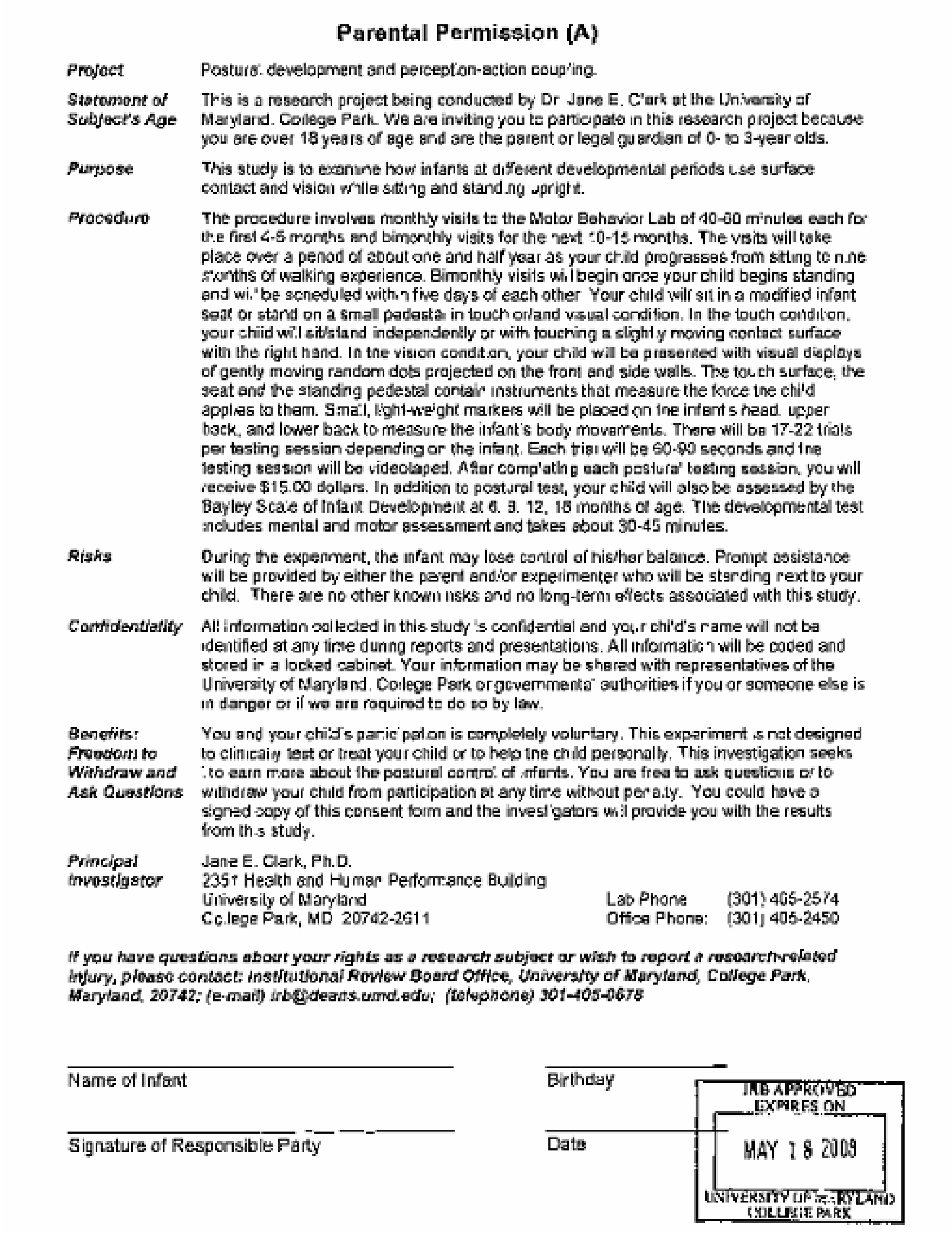
### *Future Research Direction*

Sensory information for postural control comes from multiple sources, including the visual, somatosensory, and vestibular systems (Horak & Macpherson, 1996). This multiple sensory information provides redundancy that helps assure successful postural control. However, sensory conflict may occur as changes in one sensory modality may not always correspond to changes in others. The central nervous system needs to integrate multisensory information adaptively to establish coherent and accurate postural estimates. This multisensory integration ability has been proposed to be critical for adults' postural control (Jeka et al., 2000; Peterka, 2002). In this dissertation, we examined how infants' postural behaviors adapt to changing sensory information within the same system (intra-modal re-weighting). However, newly sitting infants were unable to maintain quiet sitting posture when the visual stimulus oscillated in large amplitude. These findings suggest that their postural control system might not be able to successfully re-weight to other sources of sensory information presented at the same time, namely inter-modal re-weighting. To fully understand the development of sensory integration of postural control, future research is necessary to examine how this inter-modal sensory re-weighting process develops as the infant develops to sit, stand, and walk.

It is estimated that 17% of the children in the United States have a developmental or behavioral disability that may impact their motor development (Boyce, Decoufle, & Yeargin-Allsopp, 1994). Although postural control proficiency expands dramatically over the first years of life in typically developing infants, there are often significant delays in gaining comparable postural control for those born prematurely, or with cerebral palsy, or Down syndrome. As suggested in this dissertation, sensorimotor refinement and re-calibration are important processes for the development of postural control. Our studies serve as a backdrop to investigate whether sensorimotor refinement is the underlying mechanism for their postural disabilities. Understanding the underlying mechanism for infants' postural control disabilities would further facilitate effective and efficient early intervention programs.

# Appendices

Appendix 1: Parent permission form I.



## Parental Permission (A)

| | |
|---|---|
| ***Project*** | Postural development and perception-action coupling. |
| ***Statement of Subject's Age*** | This is a research project being conducted by Dr Jane E. Clark at the University of Maryland. College Park. We are inviting you to participate in this research project because you are over 18 years of age and are the parent or legal guardian of 0- to 3-year olds. |
| ***Purpose*** | This study is to examine how infants at different developmental periods use surface contact and vision while sitting and standing upright. |
| ***Procedure*** | The procedure involves monthly visits to the Motor Behavior Lab of 40-60 minutes each for the first 4-6 months and bimonthly visits for the next 10-15 months. The visits will take place over a period of about one and half year as your child progresses from sitting to nine months of walking experience. Bimonthly visits will begin once your child begins standing and will be scheduled within five days of each other Your child will sit in a modified infant seat or stand on a small pedestal in touch or/and visual condition. In the touch condition, your child will sit/stand independently or with touching a slightly moving contact surface with the right hand. In the vision condition, your child will be presented with visual displays of gently moving random dots projected on the front and side walls. The touch surface, the seat and the standing pedestal contain instruments that measure the force the child applies to them. Small, light-weight markers will be placed on the infant's head, upper back, and lower back to measure the infant's body movements. There will be 17-22 trials per testing session depending on the infant. Each trial will be 60-90 seconds and the testing session will be videotaped. After completing each postural testing session, you will receive $15.00 dollars. In addition to postural test, your child will also be assessed by the Bayley Scale of Infant Development at 6. 9. 12, 18 months of age. The developmental test includes mental and motor assessment and takes about 30-45 minutes. |
| ***Risks*** | During the experiment, the infant may lose control of his/her balance. Prompt assistance will be provided by either the parent and/or experimenter who will be standing next to your child. There are no other known risks and no long-term effects associated with this study. |
| ***Confidentiality*** | All information collected in this study is confidential and your child's name will not be identified at any time during reports and presentations. All information will be coded and stored in a locked cabinet. Your information may be shared with representatives of the University of Maryland, College Park or governmental authorities if you or someone else is in danger or if we are required to do so by law. |
| ***Benefits: Freedom to Withdraw and Ask Questions*** | You and your child's participation is completely voluntary. This experiment is not designed to clinically test or treat your child or to help the child personally. This investigation seeks to learn more about the postural control of infants. You are free to ask questions or to withdraw your child from participation at any time without penalty. You could have a signed copy of this consent form and the investigators will provide you with the results from this study. |
| ***Principal Investigator*** | Jane E. Clark, Ph.D.<br>2351 Health and Human Performance Building<br>University of Maryland<br>College Park, MD 20742-2611<br>Lab Phone (301) 405-2574<br>Office Phone: (301) 405-2450 |

***If you have questions about your rights as a research subject or wish to report a research-related injury, please contact: Institutional Review Board Office, University of Maryland, College Park, Maryland, 20742; (e-mail) irb@deans.umd.edu; (telephone) 301-405-0678***

Name of Infant ____________________

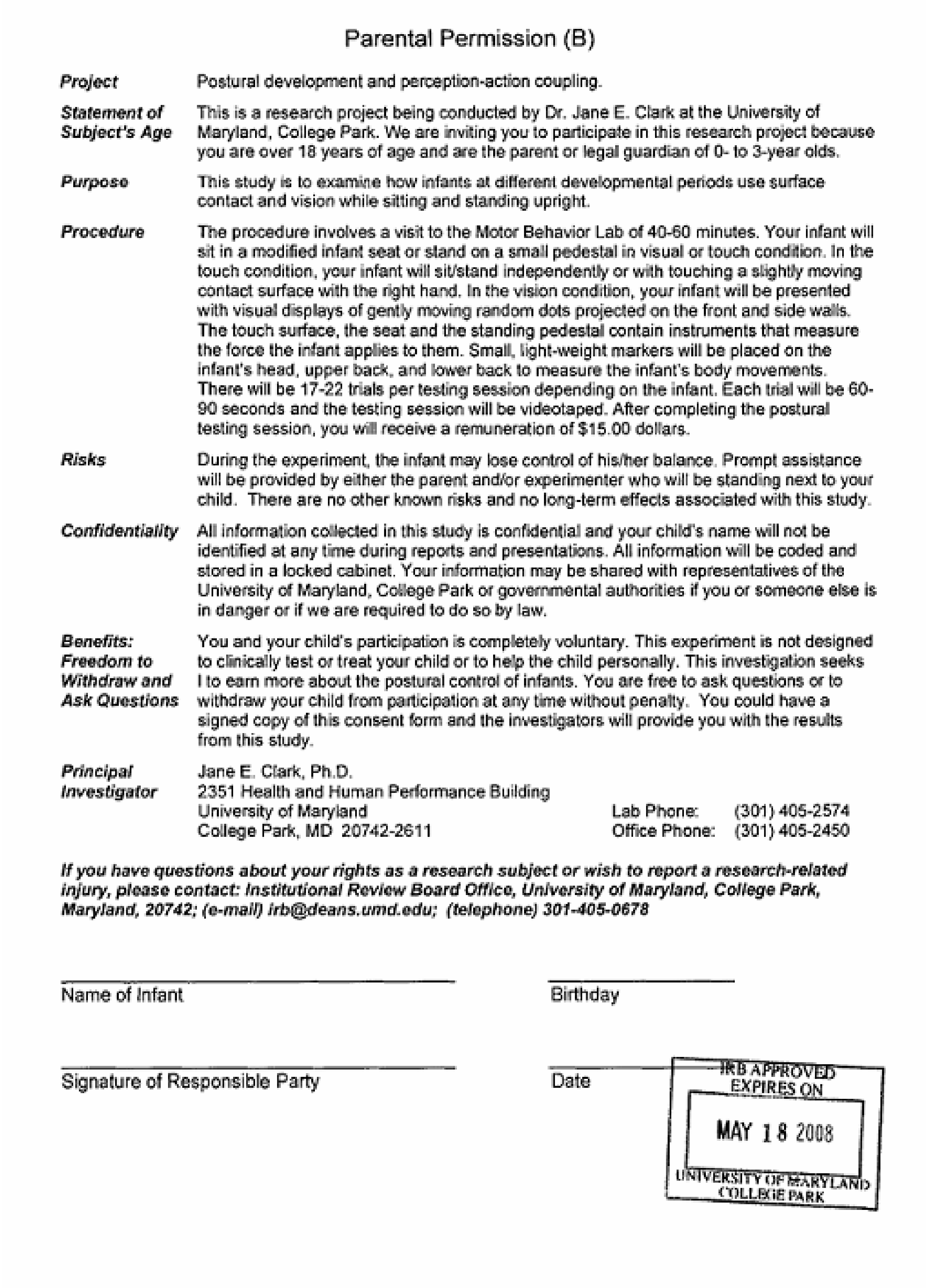
Birthday ____________________

Signature of Responsible Party ____________________

Date ____________________

IRB APPROVED
EXPIRES ON
MAY 18 2009
UNIVERSITY OF MARYLAND
COLLEGE PARK

Appendix 2: Parent permission form II.



## Parental Permission (B)

| | |
|---|---|
| ***Project*** | Postural development and perception-action coupling. |
| ***Statement of Subject's Age*** | This is a research project being conducted by Dr. Jane E. Clark at the University of Maryland, College Park. We are inviting you to participate in this research project because you are over 18 years of age and are the parent or legal guardian of 0- to 3-year olds. |
| ***Purpose*** | This study is to examine how infants at different developmental periods use surface contact and vision while sitting and standing upright. |
| ***Procedure*** | The procedure involves a visit to the Motor Behavior Lab of 40-60 minutes. Your infant will sit in a modified infant seat or stand on a small pedestal in visual or touch condition. In the touch condition, your infant will sit/stand independently or with touching a slightly moving contact surface with the right hand. In the vision condition, your infant will be presented with visual displays of gently moving random dots projected on the front and side walls. The touch surface, the seat and the standing pedestal contain instruments that measure the force the infant applies to them. Small, light-weight markers will be placed on the infant's head, upper back, and lower back to measure the infant's body movements. There will be 17-22 trials per testing session depending on the infant. Each trial will be 60-90 seconds and the testing session will be videotaped. After completing the postural testing session, you will receive a remuneration of $15.00 dollars. |
| ***Risks*** | During the experiment, the infant may lose control of his/her balance. Prompt assistance will be provided by either the parent and/or experimenter who will be standing next to your child. There are no other known risks and no long-term effects associated with this study. |
| ***Confidentiality*** | All information collected in this study is confidential and your child's name will not be identified at any time during reports and presentations. All information will be coded and stored in a locked cabinet. Your information may be shared with representatives of the University of Maryland, College Park or governmental authorities if you or someone else is in danger or if we are required to do so by law. |
| ***Benefits: Freedom to Withdraw and Ask Questions*** | You and your child's participation is completely voluntary. This experiment is not designed to clinically test or treat your child or to help the child personally. This investigation seeks I to earn more about the postural control of infants. You are free to ask questions or to withdraw your child from participation at any time without penalty. You could have a signed copy of this consent form and the investigators will provide you with the results from this study. |
| ***Principal Investigator*** | Jane E. Clark, Ph.D.<br>2351 Health and Human Performance Building<br>University of Maryland<br>College Park, MD 20742-2611<br>Lab Phone: (301) 405-2574<br>Office Phone: (301) 405-2450 |

***If you have questions about your rights as a research subject or wish to report a research-related injury, please contact: Institutional Review Board Office, University of Maryland, College Park, Maryland, 20742; (e-mail) irb@deans.umd.edu; (telephone) 301-405-0678***

Name of Infant ____________________

Birthday ____________________

Signature of Responsible Party ____________________

Date ____________________

IRB APPROVED
EXPIRES ON
MAY 18 2008
UNIVERSITY OF MARYLAND
COLLEGE PARK

# Appendix 3: Infants' sitting duration across amplitude conditions and groups.

| Infant | Group | Amplitude | Mean Time (s) | Tot Time Collected (s) | Tot Time Good (s) | % Time |
|---:|---:|---:|---:|---:|---:|---:|
| 1 | so | 0 | 14.93 | 180 | 29.87 | 16.59 |
| 1 | so | 1 | 21.05 | 180 | 105.25 | 58.47 |
| 1 | so | 2 | 22.96 | 300 | 114.78 | 38.26 |
| 1 | so | 3 | 20.46 | 240 | 143.18 | 59.66 |
| 1 | so | 4 | 15.06 | 240 | 60.23 | 25.10 |
| 2 | so | 0 | 14.55 | 240 | 43.65 | 18.19 |
| 2 | so | 1 | 27.16 | 180 | 135.82 | 75.45 |
| 2 | so | 2 | 22.38 | 180 | 89.50 | 49.72 |
| 2 | so | 3 | 20.04 | 240 | 100.22 | 41.76 |
| 2 | so | 4 | 20.65 | 120 | 41.30 | 34.42 |
| 3 | so | 0 | 24.73 | 180 | 74.18 | 41.21 |
| 3 | so | 1 | 15.85 | 240 | 31.70 | 13.21 |
| 3 | so | 2 | 20.46 | 240 | 102.28 | 42.62 |
| 3 | so | 3 | 21.89 | 180 | 65.68 | 36.49 |
| 3 | so | 4 | 21.42 | 180 | 85.67 | 47.59 |
| 4 | so | 0 | 17.93 | 180 | 35.87 | 19.93 |
| 4 | so | 1 | 25.49 | 240 | 76.47 | 31.86 |
| 4 | so | 2 | 21.14 | 180 | 105.68 | 58.71 |
| 4 | so | 3 | 25.14 | 300 | 125.72 | 41.91 |
| 4 | so | 4 | 58.95 | 180 | 58.95 | 32.75 |
| 5 | so | 0 | 12.05 | 120 | 12.05 | 10.04 |
| 5 | so | 1 | 15.21 | 120 | 45.63 | 38.03 |
| 5 | so | 2 | 37.77 | 180 | 75.53 | 41.96 |
| 5 | so | 3 | 26.24 | 180 | 78.73 | 43.74 |
| 5 | so | 4 | 0.00 | 180 | 0.00 | 0.00 |
| 6 | st | 0 | 19.95 | 120 | 19.95 | 16.63 |
| 6 | st | 1 | 11.23 | 360 | 22.47 | 6.24 |
| 6 | st | 2 | 20.07 | 240 | 60.22 | 25.09 |
| 6 | st | 3 | 29.02 | 240 | 29.02 | 12.09 |
| 6 | st | 4 | 20.45 | 420 | 81.80 | 19.48 |
| 7 | st | 0 | 22.62 | 180 | 90.47 | 50.26 |
| 7 | st | 1 | 26.61 | 180 | 133.05 | 73.92 |
| 7 | st | 2 | 21.39 | 180 | 128.33 | 71.30 |
| 7 | st | 3 | 24.21 | 300 | 145.23 | 48.41 |
| 7 | st | 4 | 24.26 | 180 | 97.03 | 53.91 |
| 8 | st | 0 | 27.54 | 240 | 137.68 | 57.37 |
| 8 | st | 1 | 24.33 | 240 | 121.65 | 50.69 |
| 8 | st | 2 | 20.48 | 240 | 143.35 | 59.73 |
| 8 | st | 3 | 19.87 | 240 | 99.35 | 41.40 |
| 8 | st | 4 | 33.72 | 180 | 101.15 | 56.19 |
| 9 | st | 0 | 20.82 | 180 | 62.45 | 34.69 |
| 9 | st | 1 | 26.32 | 240 | 78.95 | 32.90 |
| 9 | st | 2 | 19.48 | 240 | 116.90 | 48.71 |
| 9 | st | 3 | 22.22 | 240 | 111.08 | 46.28 |
| 9 | st | 4 | 28.58 | 240 | 114.33 | 47.64 |
| 10 | st | 0 | 59.98 | 120 | 59.98 | 49.99 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 10 | st | 1 | 37.22 | 180 | 74.43 | 41.35 |
| 10 | st | 2 | 31.09 | 300 | 155.45 | 51.82 |
| 10 | st | 3 | 32.20 | 180 | 161.02 | 89.45 |
| 10 | st | 4 | 21.69 | 180 | 130.17 | 72.31 |
| 11 | wo | 0 | 30.05 | 240 | 60.10 | 25.04 |
| 11 | wo | 1 | 17.87 | 300 | 53.62 | 17.87 |
| 11 | wo | 2 | 23.75 | 240 | 71.25 | 29.69 |
| 11 | wo | 3 | 38.12 | 240 | 76.23 | 31.76 |
| 11 | wo | 4 | 12.32 | 360 | 12.30 | 3.42 |
| 12 | wo | 0 | 23.38 | 240 | 70.15 | 29.23 |
| 12 | wo | 1 | 26.80 | 240 | 133.98 | 55.83 |
| 12 | wo | 2 | 37.75 | 180 | 113.25 | 62.92 |
| 12 | wo | 3 | 22.49 | 240 | 179.93 | 74.97 |
| 12 | wo | 4 | 39.67 | 180 | 119.02 | 66.12 |
| 13 | wo | 0 | 25.85 | 180 | 77.55 | 43.08 |
| 13 | wo | 1 | 18.42 | 180 | 92.12 | 51.18 |
| 13 | wo | 2 | 25.24 | 180 | 126.18 | 70.10 |
| 13 | wo | 3 | 25.41 | 180 | 101.63 | 56.46 |
| 13 | wo | 4 | 27.17 | 240 | 108.67 | 45.28 |
| 14 | wo | 0 | 36.90 | 180 | 147.60 | 82.00 |
| 14 | wo | 1 | 34.40 | 240 | 137.60 | 57.33 |
| 14 | wo | 2 | 23.19 | 180 | 92.77 | 51.54 |
| 14 | wo | 3 | 21.30 | 180 | 106.48 | 59.16 |
| 14 | wo | 4 | 27.80 | 240 | 111.20 | 46.33 |
| 15 | wo | 0 | 46.32 | 120 | 92.63 | 77.19 |
| 15 | wo | 1 | 22.63 | 180 | 67.88 | 37.71 |
| 15 | wo | 2 | 35.57 | 120 | 71.13 | 59.28 |
| 15 | wo | 3 | 59.98 | 120 | 59.98 | 49.99 |
| 15 | wo | 4 | 12.80 | 120 | 25.60 | 21.33 |
| 16 | w12 | 0 | 27.66 | 180 | 110.63 | 61.46 |
| 16 | w12 | 1 | 22.32 | 180 | 111.62 | 62.01 |
| 16 | w12 | 2 | 27.44 | 180 | 109.77 | 60.98 |
| 16 | w12 | 3 | 43.95 | 120 | 43.95 | 36.63 |
| 16 | w12 | 4 | 21.02 | 180 | 63.05 | 35.03 |
| 17 | w12 | 0 | 56.69 | 240 | 226.77 | 94.49 |
| 17 | w12 | 1 | 55.99 | 240 | 223.97 | 93.32 |
| 17 | w12 | 2 | 53.90 | 240 | 215.60 | 89.83 |
| 17 | w12 | 3 | 40.79 | 300 | 285.52 | 95.17 |
| 17 | w12 | 4 | 57.49 | 240 | 229.97 | 95.82 |
| 18 | w12 | 0 | 54.52 | 240 | 163.55 | 68.15 |
| 18 | w12 | 1 | 58.99 | 180 | 176.98 | 98.32 |
| 18 | w12 | 2 | 59.98 | 180 | 179.95 | 99.97 |
| 18 | w12 | 3 | 35.68 | 240 | 142.70 | 59.46 |
| 18 | w12 | 4 | 47.35 | 240 | 236.75 | 98.65 |
| 19 | w12 | 0 | 22.50 | 180 | 90.00 | 50.00 |
| 19 | w12 | 1 | 30.33 | 240 | 90.98 | 37.91 |
| 19 | w12 | 2 | 21.90 | 300 | 153.28 | 51.09 |
| 19 | w12 | 3 | 20.69 | 180 | 124.13 | 68.96 |
| 19 | w12 | 4 | 25.22 | 240 | 100.87 | 42.03 |
| 20 | w12 | 0 | 27.11 | 180 | 135.55 | 75.31 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| 20 | w12 | 1 | 23.10 | 240 | 115.48 | 48.12 |
| 20 | w12 | 2 | 26.08 | 180 | 130.42 | 72.45 |
| 20 | w12 | 3 | 28.95 | 180 | 115.80 | 64.33 |
| 20 | w12 | 4 | 23.17 | 300 | 69.52 | 23.17 |

Appendix 4: Infants' Head$_{AP}$ sway in unperturbed, quiet sitting posture (weighted mean).

| Infant | Group | Median Freq (Hz) | Pos Var (cm) | Vel Var (cm/s) | Mean Vel (cm/s) |
|---:|---:|---:|---:|---:|---:|
| 1 | so | 0.27 | 1.82 | 4.74 | 3.56 |
| 2 | so | 0.17 | 2.23 | 3.20 | 2.43 |
| 3 | so | 0.14 | 2.03 | 3.92 | 3.03 |
| 4 | so | 0.12 | 1.12 | 1.77 | 1.35 |
| 5 | so | 0.23 | 2.22 | 3.92 | 2.81 |
| 6 | st | 0.12 | 1.03 | 1.61 | 1.25 |
| 7 | st | 0.13 | 1.25 | 1.97 | 1.40 |
| 8 | st | 0.16 | 1.18 | 1.84 | 1.32 |
| 9 | st | 0.14 | 0.60 | 1.02 | 0.78 |
| 10 | st | 0.07 | 1.28 | 1.61 | 1.18 |
| 11 | wo | 0.12 | 1.53 | 2.07 | 1.46 |
| 12 | wo | 0.11 | 1.52 | 1.62 | 1.24 |
| 13 | wo | 0.11 | 2.02 | 2.84 | 2.10 |
| 14 | wo | 0.10 | 0.97 | 1.20 | 0.93 |
| 15 | wo | 0.09 | 1.07 | 1.48 | 1.10 |
| 16 | w12 | 0.14 | 1.25 | 2.05 | 1.46 |
| 17 | w12 | 0.07 | 0.90 | 1.17 | 0.74 |
| 18 | w12 | 0.10 | 0.85 | 1.22 | 0.98 |
| 19 | w12 | 0.11 | 1.62 | 2.28 | 1.61 |
| 20 | w12 | 0.14 | 0.79 | 1.39 | 0.88 |

Appendix 5: Gain (weighted mean) of infants' $H_{AP}$ responses to the visual stimulus across amplitude conditions and groups at each frequency.

| Infant | Group | Amp | Gain | | | | | Phase (Deg) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 0.12 Hz | 0.28 Hz | 0.52 Hz | 0.76 Hz | 1.24 Hz | 0.12 Hz | 0.28 Hz | 0.52 Hz | 0.76 Hz | 1.24 Hz |
| 1 | 1 | 1 | 0.82 | 3.53 | 1.80 | 1.29 | 0.48 | -113.50 | -159.61 | -7.27 | -3.78 | 55.94 |
| 1 | 1 | 2 | 0.26 | 1.08 | 1.89 | 0.20 | 0.68 | -68.64 | 95.49 | -21.60 | 71.26 | 164.31 |
| 1 | 1 | 3 | 0.30 | 0.60 | 0.93 | 1.05 | 0.37 | 143.74 | -13.01 | -89.86 | 168.56 | 108.26 |
| 1 | 1 | 4 | 0.19 | 0.39 | 0.44 | 0.18 | 0.14 | 157.71 | 15.05 | -121.66 | -135.53 | 17.42 |
| 2 | 1 | 1 | 0.66 | 0.85 | 0.50 | 0.51 | 0.89 | 107.19 | -163.17 | -170.41 | 34.67 | 152.09 |
| 2 | 1 | 2 | 0.38 | 0.36 | 0.74 | 0.37 | 0.23 | 23.78 | 46.14 | -179.08 | 149.64 | -33.97 |
| 2 | 1 | 3 | 0.22 | 0.42 | 0.26 | 0.34 | 0.17 | 96.65 | -59.37 | 29.86 | 179.66 | 70.12 |
| 2 | 1 | 4 | 0.15 | 0.13 | 0.19 | 0.17 | 0.01 | 39.67 | 60.22 | -119.06 | 117.46 | 72.71 |
| 3 | 1 | 1 | 1.39 | 0.83 | 1.32 | 2.07 | 3.01 | -146.10 | 65.92 | 170.84 | -50.15 | 169.67 |
| 3 | 1 | 2 | 0.56 | 0.37 | 0.14 | 0.63 | 1.20 | -79.80 | 45.68 | 22.16 | 154.41 | 122.09 |
| 3 | 1 | 3 | 0.62 | 0.44 | 0.78 | 0.43 | 0.28 | 126.64 | -13.48 | -99.58 | -90.01 | -17.27 |
| 3 | 1 | 4 | 0.23 | 0.60 | 0.46 | 0.47 | 0.22 | 74.13 | 3.05 | -99.11 | 175.98 | 62.87 |
| 4 | 1 | 1 | 1.65 | 2.37 | 0.61 | 3.24 | 1.32 | 131.63 | -167.57 | -164.22 | 160.66 | -33.45 |
| 4 | 1 | 2 | 0.25 | 0.52 | 0.29 | 0.93 | 0.50 | -165.64 | -16.00 | 110.85 | 165.04 | -173.42 |
| 4 | 1 | 3 | 0.24 | 0.32 | 0.22 | 0.10 | 0.01 | 119.18 | 23.43 | -62.19 | -135.82 | 151.38 |
| 4 | 1 | 4 | 0.10 | 0.07 | 0.09 | 0.11 | 0.05 | 69.88 | 9.08 | -35.21 | -156.84 | 141.95 |
| 5 | 1 | 1 | 2.16 | 0.40 | 1.50 | 1.83 | 0.41 | -1.15 | -74.84 | 15.54 | 74.57 | 123.50 |
| 5 | 1 | 2 | 0.21 | 0.42 | 1.24 | 0.69 | 0.52 | -61.99 | 17.93 | 145.47 | 176.72 | -27.21 |
| 5 | 1 | 3 | 0.23 | 0.18 | 0.49 | 0.45 | 0.40 | 113.42 | 99.57 | -22.57 | -162.06 | 104.38 |
| 6 | 2 | 1 | 1.52 | 2.12 | 2.62 | 2.43 | 1.23 | -143.48 | -68.33 | 121.19 | -37.78 | 158.75 |
| 6 | 2 | 2 | 0.43 | 1.89 | 0.68 | 1.26 | 1.04 | -136.00 | 175.74 | -156.16 | 148.79 | 115.93 |
| 6 | 2 | 3 | 0.18 | 0.53 | 1.01 | 0.36 | 0.55 | 12.04 | 99.43 | -171.02 | -137.22 | 149.99 |
| 6 | 2 | 4 | 0.08 | 0.32 | 0.38 | 0.25 | 0.09 | 66.63 | 23.21 | -97.27 | -136.66 | 100.93 |
| 7 | 2 | 1 | 1.66 | 1.11 | 1.29 | 1.35 | 0.55 | -66.40 | -40.49 | -76.39 | -2.83 | -155.73 |
| 7 | 2 | 2 | 0.45 | 0.92 | 0.54 | 1.00 | 0.79 | -44.17 | -0.66 | -24.49 | 138.18 | 93.00 |
| 7 | 2 | 3 | 0.15 | 0.09 | 0.53 | 0.27 | 0.18 | 9.56 | 83.40 | -69.10 | -169.53 | 84.40 |
| 7 | 2 | 4 | 0.06 | 0.16 | 0.19 | 0.15 | 0.11 | 56.62 | 52.02 | -43.78 | -121.16 | 98.55 |
| 8 | 2 | 1 | 1.23 | 0.64 | 1.12 | 0.66 | 0.50 | -38.74 | 4.87 | 60.40 | 154.69 | 77.33 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 8 | 2 | 2 | 0.19 | 0.91 | 0.43 | 0.15 | 0.18 | -121.19 | 21.38 | -119.67 | 142.59 | -2.60 |
| 8 | 2 | 3 | 0.22 | 0.57 | 0.40 | 0.25 | 0.13 | 94.19 | 7.22 | -112.30 | 173.10 | 63.80 |
| 8 | 2 | 4 | 0.17 | 0.43 | 0.12 | 0.24 | 0.18 | 87.00 | -4.62 | -79.01 | -173.23 | 97.62 |
| 9 | 2 | 1 | 0.43 | 0.35 | 0.67 | 0.20 | 0.38 | -174.12 | 151.45 | -60.48 | 57.56 | 128.68 |
| 9 | 2 | 2 | 0.20 | 0.11 | 0.66 | 0.45 | 0.26 | 98.14 | 56.94 | -78.91 | -148.90 | 118.19 |
| 9 | 2 | 3 | 0.07 | 0.15 | 0.31 | 0.18 | 0.26 | 0.32 | 26.68 | -89.99 | 169.14 | 96.71 |
| 9 | 2 | 4 | 0.11 | 0.12 | 0.17 | 0.19 | 0.13 | 102.78 | -13.83 | -83.42 | -122.74 | 77.28 |
| 10 | 2 | 1 | 0.41 | 0.44 | 0.23 | 0.16 | 0.44 | 169.05 | 11.29 | 144.93 | 67.38 | 73.46 |
| 10 | 2 | 2 | 0.72 | 0.38 | 0.26 | 0.26 | 0.47 | 38.69 | 6.51 | 18.60 | -133.59 | 77.26 |
| 10 | 2 | 3 | 0.21 | 0.31 | 0.35 | 0.37 | 0.13 | 94.87 | 12.32 | -98.09 | 147.41 | 54.28 |
| 10 | 2 | 4 | 0.09 | 0.30 | 0.42 | 0.42 | 0.27 | 63.24 | 29.36 | -78.45 | -147.09 | 68.38 |
| 11 | 3 | 1 | 2.01 | 1.07 | 2.20 | 2.49 | 1.42 | 143.52 | 81.93 | 76.81 | -141.69 | 10.60 |
| 11 | 3 | 2 | 0.12 | 0.27 | 0.17 | 0.85 | 0.47 | -86.45 | 47.43 | 127.31 | 154.25 | -3.00 |
| 11 | 3 | 3 | 0.15 | 0.31 | 0.40 | 0.26 | 0.15 | 98.40 | 53.20 | -98.22 | 107.95 | 103.75 |
| 11 | 3 | 4 | 0.19 | 0.52 | 0.33 | 0.04 | 0.32 | -23.07 | -15.71 | -135.02 | -111.33 | 163.49 |
| 12 | 3 | 1 | 0.27 | 0.91 | 0.53 | 0.12 | 0.16 | -14.83 | 7.91 | -127.45 | 169.28 | 136.57 |
| 12 | 3 | 2 | 0.42 | 0.17 | 0.79 | 0.40 | 0.18 | -115.25 | 173.06 | -155.36 | -145.90 | 51.10 |
| 12 | 3 | 3 | 0.31 | 0.17 | 0.34 | 0.31 | 0.13 | 164.52 | 23.74 | -112.48 | -153.41 | 97.94 |
| 12 | 3 | 4 | 0.13 | 0.09 | 0.16 | 0.22 | 0.15 | 80.16 | 21.05 | -19.17 | -145.35 | 57.81 |
| 13 | 3 | 1 | 0.60 | 0.64 | 3.02 | 2.36 | 1.34 | -122.76 | 66.32 | -61.24 | 176.07 | 60.12 |
| 13 | 3 | 2 | 0.50 | 0.61 | 1.92 | 1.06 | 0.57 | 42.75 | 60.23 | -95.23 | -177.77 | -23.51 |
| 13 | 3 | 3 | 0.26 | 0.62 | 0.85 | 0.63 | 0.58 | 25.27 | 23.90 | -99.74 | -145.49 | 36.14 |
| 13 | 3 | 4 | 0.20 | 0.53 | 0.92 | 0.82 | 0.17 | 92.78 | 17.98 | -79.13 | -161.28 | 119.25 |
| 14 | 3 | 1 | 0.17 | 0.69 | 0.52 | 0.35 | 0.36 | -85.70 | -52.55 | -83.90 | 64.98 | -0.67 |
| 14 | 3 | 2 | 0.11 | 0.51 | 0.47 | 0.52 | 0.07 | -108.92 | 29.61 | -148.76 | -176.93 | -37.21 |
| 14 | 3 | 3 | 0.05 | 0.29 | 0.37 | 0.27 | 0.12 | 88.18 | 6.60 | -135.75 | -175.65 | 77.61 |
| 14 | 3 | 4 | 0.05 | 0.10 | 0.10 | 0.18 | 0.08 | 67.98 | 41.70 | -90.24 | -155.62 | 103.51 |
| 15 | 3 | 1 | 0.72 | 0.62 | 0.59 | 0.48 | 0.26 | 141.03 | 63.59 | -165.93 | 155.80 | -42.14 |
| 15 | 3 | 2 | 0.46 | 0.59 | 0.21 | 0.71 | 0.05 | -163.95 | 97.63 | -59.10 | -99.55 | -152.50 |
| 15 | 3 | 3 | 0.30 | 0.36 | 0.21 | 0.55 | 0.43 | 54.12 | 165.90 | -161.46 | -143.13 | 52.20 |
| 15 | 3 | 4 | 0.08 | 0.18 | 0.26 | 0.16 | 0.11 | 133.52 | 17.92 | -78.25 | -116.90 | 75.54 |
| 16 | 4 | 1 | 0.24 | 0.84 | 1.18 | 0.75 | 0.41 | 11.85 | -30.20 | -111.63 | -55.01 | 86.08 |
| 16 | 4 | 2 | 0.43 | 0.39 | 0.71 | 0.29 | 0.15 | 81.07 | 25.37 | -80.74 | 162.33 | 23.58 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 16 | 4 | 3 | 0.11 | 0.07 | 0.31 | 0.24 | 0.15 | 90.70 | 68.42 | -82.16 | -160.37 | 73.26 |
| 16 | 4 | 4 | 0.12 | 0.33 | 0.14 | 0.24 | 0.10 | 122.08 | -15.80 | -139.78 | -160.68 | 108.49 |
| 17 | 4 | 1 | 0.09 | 0.12 | 0.37 | 0.32 | 0.06 | -159.87 | 89.37 | -176.50 | -132.54 | 174.35 |
| 17 | 4 | 2 | 0.08 | 0.20 | 0.13 | 0.39 | 0.07 | 143.87 | 42.97 | -117.70 | -174.68 | 92.34 |
| 17 | 4 | 3 | 0.11 | 0.10 | 0.17 | 0.15 | 0.02 | 95.52 | 49.56 | -67.70 | 176.18 | 86.35 |
| 17 | 4 | 4 | 0.07 | 0.04 | 0.07 | 0.13 | 0.07 | 54.41 | 12.00 | -86.40 | -151.84 | 82.64 |
| 18 | 4 | 1 | 0.42 | 0.13 | 0.40 | 0.38 | 0.06 | 131.19 | 18.05 | 168.47 | -172.50 | 127.31 |
| 18 | 4 | 2 | 0.25 | 0.55 | 0.28 | 0.42 | 0.14 | 80.15 | -21.95 | -79.03 | -166.94 | 55.19 |
| 18 | 4 | 3 | 0.06 | 0.50 | 0.52 | 0.48 | 0.24 | 113.14 | -18.49 | -103.39 | 171.58 | 57.34 |
| 18 | 4 | 4 | 0.13 | 0.28 | 0.33 | 0.34 | 0.10 | 62.75 | -24.73 | -109.47 | 174.70 | 49.14 |
| 19 | 4 | 1 | 1.01 | 1.22 | 1.52 | 2.07 | 0.26 | 9.74 | 21.25 | -178.22 | 171.28 | 38.97 |
| 19 | 4 | 2 | 0.23 | 1.24 | 0.95 | 1.00 | 0.16 | 80.16 | -16.69 | -119.32 | -171.10 | 133.55 |
| 19 | 4 | 3 | 0.35 | 0.56 | 0.40 | 0.61 | 0.30 | 59.99 | 14.66 | -120.41 | -144.55 | 54.67 |
| 19 | 4 | 4 | 0.02 | 0.30 | 0.33 | 0.19 | 0.07 | 143.88 | -14.26 | -89.23 | -131.61 | 130.48 |
| 20 | 4 | 1 | 0.14 | 0.62 | 0.35 | 0.45 | 0.45 | 57.23 | 89.39 | -53.93 | -160.47 | 107.07 |
| 20 | 4 | 2 | 0.12 | 0.06 | 0.20 | 0.26 | 0.24 | 120.35 | -6.08 | -10.03 | -142.94 | 70.15 |
| 20 | 4 | 3 | 0.11 | 0.12 | 0.13 | 0.19 | 0.13 | -160.21 | 115.97 | 18.29 | -139.01 | 118.35 |
| 20 | 4 | 4 | 0.08 | 0.09 | 0.04 | 0.10 | 0.07 | 91.47 | 1.78 | -114.32 | -151.60 | 119.35 |

## Appendix 6: Infants' residual postural sway ($Head_{AP}$) with the components of driving frequencies removed, across groups and amplitude conditions.

| Infant | Group | Amplitude | Res Pos var (cm) | Res Vel Var (cm/s) |
|---:|---:|---:|---:|---:|
| 1 | so | 0 | 1.32 | 4.15 |
| 1 | so | 1 | 2.01 | 4.82 |
| 1 | so | 2 | 1.96 | 4.40 |
| 1 | so | 3 | 1.97 | 4.55 |
| 1 | so | 4 | 1.56 | 4.54 |
| 2 | so | 0 | 1.74 | 2.99 |
| 2 | so | 1 | 1.09 | 2.19 |
| 2 | so | 2 | 1.21 | 2.04 |
| 2 | so | 3 | 1.50 | 3.00 |
| 2 | so | 4 | 1.47 | 2.02 |
| 3 | so | 0 | 1.93 | 3.78 |
| 3 | so | 1 | 1.83 | 4.82 |
| 3 | so | 2 | 1.78 | 3.36 |
| 3 | so | 3 | 1.81 | 3.28 |
| 3 | so | 4 | 1.49 | 3.48 |
| 4 | so | 0 | 0.96 | 1.68 |
| 4 | so | 1 | 1.40 | 2.10 |
| 4 | so | 2 | 1.02 | 1.73 |
| 4 | so | 3 | 1.07 | 1.41 |
| 4 | so | 4 | 0.67 | 1.28 |
| 5 | so | 0 | 1.34 | 3.17 |
| 5 | so | 1 | 1.02 | 3.55 |
| 5 | so | 2 | 1.61 | 2.95 |
| 5 | so | 3 | 1.46 | 2.81 |
| 6 | st | 0 | 0.97 | 1.55 |
| 6 | st | 1 | 0.72 | 1.38 |
| 6 | st | 2 | 1.81 | 3.90 |
| 6 | st | 3 | 1.82 | 4.32 |
| 6 | st | 4 | 1.56 | 3.38 |
| 7 | st | 0 | 1.17 | 1.91 |
| 7 | st | 1 | 1.86 | 2.66 |
| 7 | st | 2 | 1.55 | 2.06 |
| 7 | st | 3 | 0.88 | 1.56 |
| 7 | st | 4 | 1.11 | 1.69 |
| 8 | st | 0 | 1.03 | 1.68 |
| 8 | st | 1 | 1.02 | 1.64 |
| 8 | st | 2 | 1.07 | 1.79 |
| 8 | st | 3 | 0.97 | 1.52 |
| 8 | st | 4 | 1.55 | 2.44 |
| 9 | st | 0 | 0.58 | 0.95 |
| 9 | st | 1 | 0.65 | 1.39 |
| 9 | st | 2 | 0.60 | 1.30 |
| 9 | st | 3 | 0.72 | 1.22 |
| 9 | st | 4 | 1.40 | 2.10 |
| 10 | st | 0 | 1.24 | 1.59 |
| 10 | st | 1 | 1.18 | 1.51 |

|  |  |  |  |  |
|---|---|---|---|---|
| 10 | st | 2 | 1.43 | 2.22 |
| 10 | st | 3 | 1.37 | 2.35 |
| 10 | st | 4 | 1.38 | 2.97 |
| 11 | wo | 0 | 1.48 | 1.99 |
| 11 | wo | 1 | 1.75 | 3.50 |
| 11 | wo | 2 | 1.13 | 2.10 |
| 11 | wo | 3 | 1.19 | 1.75 |
| 11 | wo | 4 | 0.75 | 2.61 |
| 12 | wo | 0 | 1.40 | 1.61 |
| 12 | wo | 1 | 1.32 | 1.40 |
| 12 | wo | 2 | 1.41 | 1.68 |
| 12 | wo | 3 | 1.21 | 1.62 |
| 12 | wo | 4 | 1.60 | 1.97 |
| 13 | wo | 0 | 1.91 | 2.64 |
| 13 | wo | 1 | 1.31 | 2.90 |
| 13 | wo | 2 | 1.58 | 4.22 |
| 13 | wo | 3 | 1.70 | 3.75 |
| 13 | wo | 4 | 1.87 | 6.56 |
| 14 | wo | 0 | 0.95 | 1.17 |
| 14 | wo | 1 | 0.72 | 1.12 |
| 14 | wo | 2 | 0.87 | 1.67 |
| 14 | wo | 3 | 0.78 | 1.08 |
| 14 | wo | 4 | 1.07 | 1.48 |
| 15 | wo | 0 | 1.00 | 1.41 |
| 15 | wo | 1 | 1.32 | 1.29 |
| 15 | wo | 2 | 1.48 | 1.65 |
| 15 | wo | 3 | 1.27 | 2.58 |
| 15 | wo | 4 | 1.02 | 1.78 |
| 16 | w12 | 0 | 1.10 | 1.94 |
| 16 | w12 | 1 | 0.92 | 1.46 |
| 16 | w12 | 2 | 0.96 | 1.35 |
| 16 | w12 | 3 | 0.77 | 1.24 |
| 16 | w12 | 4 | 0.83 | 1.21 |
| 17 | w12 | 0 | 0.88 | 1.13 |
| 17 | w12 | 1 | 0.77 | 0.85 |
| 17 | w12 | 2 | 0.89 | 0.89 |
| 17 | w12 | 3 | 0.94 | 0.88 |
| 17 | w12 | 4 | 1.33 | 0.91 |
| 18 | w12 | 0 | 0.82 | 1.15 |
| 18 | w12 | 1 | 1.00 | 0.97 |
| 18 | w12 | 2 | 1.02 | 1.17 |
| 18 | w12 | 3 | 1.44 | 1.62 |
| 18 | w12 | 4 | 0.99 | 1.55 |
| 19 | w12 | 0 | 1.42 | 2.09 |
| 19 | w12 | 1 | 1.34 | 1.73 |
| 19 | w12 | 2 | 1.30 | 1.79 |
| 19 | w12 | 3 | 1.48 | 2.18 |
| 19 | w12 | 4 | 1.36 | 2.48 |
| 20 | w12 | 0 | 0.74 | 1.32 |
| 20 | w12 | 1 | 0.60 | 1.02 |

| | | | | |
|---|---|---|---|---|
| 20 | w12 | 2 | 0.69 | 1.23 |
| 20 | w12 | 3 | 0.65 | 1.07 |
| 20 | w12 | 4 | 0.51 | 0.81 |

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