# Learning about gravity: segmental assessment of upright control as infants develop independent sitting

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Saavedra SL, van Donkelaar P, Woollacott MH. Learning about gravity: segmental assessment of upright control as infants develop independent sitting. J Neurophysiol 108: 2215-2229, 2012. First published July 25, 2012; doi:10.1152/jn.01193.2011.-The question of how infants attain upright sitting is at the core of understanding the development of most functional abilities. Our simple, practical method of securing the hips and different trunk segments while evaluating the infant's ability to vertically align and stabilize the trunk in space contributes a useful method and new insights into the development of upright control. Previous studies have considered the trunk to develop as a single segment. The goal of the present study was to examine how postural control changes across multiple trunk segments during typical development (TD) of sitting balance. For this purpose, electromyography (EMG) and kinematic data were collected at four levels of trunk support (axillae, midribs, waist, hips), in a longitudinal study of eight TD infants (3-9 mo of age). We found that developmental changes in stability were specific to the region of the trunk being investigated, changes in antagonistic muscle activity differed for the anterior-posterior versus the medial-lateral axis, and the relationship between muscle activation and movement changed from erratic attempts to gain upright position to anticipatory graded responses as infants developed upright control through a four-stage behavioral process. This information can be used by researchers to further refine hypotheses regarding this developmental process and by clinicians who wish to develop and test more specific treatment programs for children with postural dysfunction.

posture; trunk; motor control; electromyography; internal model

WHILE POSTURAL CONTROL of the trunk creates the basis for most functional movement, little is known about how trunk stability develops. In adults and typically developing (TD) children, the sensorimotor control of the trunk is so well orchestrated that it has been an accepted practice to model it biomechanically as a single segment (Nashner et al. 1988; Winter et al. 1993; Winter 1995). Thus postural control studies have only recently addressed the musculoskeletal complexity necessary for upright control of the trunk (Goodworth and Peterka 2009; St-Onge et al. 2011). During development of sitting and more specifically in pathological conditions in which stability is immature or compromised, lack of a more detailed analysis of trunk control may prevent accurate analysis and/or treatment of the condition.

In adults, trunk stability is primarily controlled by muscle recruitment, active muscle stiffness, and reflex responses (McGill and Cholewicki 2001; Panjabi et al. 1989), resulting in highly coordinated muscle activation patterns involving many muscles. The recruitment patterns must continually change depending on postural alignment and task (Hodges and Gandevia 2000; Stokes and Gardner-Morse 2003). Adult models of trunk control include an intrinsic component that consists of properties of intervertebral joints (stiffness and damping) and muscles (active and passive stiffness and damping). This intrinsic component is considered to react instantaneously to create the torque necessary to remain upright in the gravitational field. In contrast, commands from the central nervous system (CNS) that alter the torque to deal with perturbations occur with sensory-motor delays (Goodworth and Peterka 2009, 2012; Xu et al. 2010).

Learning to sit independently is a nontrivial problem because of the enormous biomechanical and neural complexity required for control of the trunk. The task for the young infant is to stabilize the head in space over an inherently unstable, multisegmented column using an array of overlapping muscles. Acquisition of upright control requires learning about gravity. Gravitational force acts on the infant's head and trunk proportional to the infant's angular displacement from upright vertical. Gravitational force increases as the infant's angular displacement increases. Thus the force of gravity drives the system further away from equilibrium (Reeves et al. 2011). To achieve upright control, infants must learn to adjust the active stiffness of their muscles to create adequate torque to counteract the destabilizing effect of gravity. The intrinsic stiffness necessary to counteract gravity is usually modeled as instantaneous in adults (Goodworth and Peterka 2009, 2012; Xu et al. 2010); however, it may not be instantaneous during the learning process.

The first signs of upright control occur by 3 mo of age with the onset of upright head control; trunk control emerges over the next 4-6 mo (Shumway-Cook and Woollacott 2007). Previous studies of typical infants have focused on three primary areas when assessing acquisition of upright trunk control: 1) development of muscle synergies for reactive balance responses to external perturbations (Bertenthal et al. 1997; Hadders-Algra et al. 1996; Harbourne 1993; Hedberg et al. 2005; Hirschfeld and Forssberg 1994; Sveistrup and Woollacott 1996; Woollacott et al. 1987), 2) development of muscle synergies for anticipatory balance during learning to reach (Thelen and Spencer 1998; van der Fits et al. 1999a, 1999b; Witherington et al. 2002), and 3) development of ground reaction forces to stabilize the center of mass over the base of support (Cignetti et al. 2011; Harbourne and Stergiou 2003). All of these studies have considered the trunk as a single segment. They have dealt with the lack of trunk control in their subjects by using semireclined and supported seating (Bertenthal et al. 1997; van der Fits et al. 1999a, 199b; Woollacott et al. 1987), propping on arms (Cignetti et al. 2011; Harbourne

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and Stergiou 2003), or allowing the infant's spine to collapse and/or holding the infant up from the chest and releasing the support (Harbourne 1993; Harbourne and Stergiou 2003) just prior to surface perturbation (Hedberg et al. 2004, 2005). None of these methods has allowed evaluation of, or offered control for, variable contributions of different trunk segments to postural control, and none has addressed the question of how infants acquire a vertical sitting position.

The goal of the present study was to examine how postural control is acquired across multiple trunk segments during typical development of sitting balance. We did not use a perturbation paradigm; rather, we chose to focus on how infants learn to deal with gravity. For this purpose, electromyography (EMG) and kinematic data were collected longitudinally in a group of eight TD infants. Bilateral EMG data were used to examine changes in movement strategies and motor activation during development of upright postural equilibrium. To isolate and allow measurement of postural control relative to different trunk segments, an external support device combined with pelvic straps supported the infants in vertical alignment at four different levels of the trunk (axillae, midribs, waist, and hips). The device blocked movement at and below the level of support while allowing full range of movement to the segments above the support. Measurement of the orientation and stability of the spinous process of the 7th cervical vertebra was used to reflect the postural control available in the free segments of the trunk.

If trunk control develops as a single unit, improvements in postural control would be similar at all four levels of support. If trunk control develops in a gradient with control emerging first in the upper spine and progressing in a cephalo-caudal pattern, similar improvements in postural control would occur at each level of support but these would be offset in time, with the upper levels showing improved control earlier than the lower levels. Finally, if trunk control develops differently depending on the anatomical region, changes in postural control across developmental time would be unique for each level of support. With regard to muscle activity, we hypothesized that the muscles nearest the level of support would be pivotal and would make the strongest contribution to trunk alignment and stability at that level. If trunk control develops as a single unit, then muscle activity would be expected to change across developmental time but would be similar across levels of support for a single data collection. Coactivation of antagonist muscles could heighten passive stiffness of the trunk to partially compensate for lack of postural control (Cholewicki et al. 1999a; Gardner-Morse and Stokes 1998; McGill et al. 2003). We therefore expected to see higher levels of antagonist coactivation in younger infants and at lower levels of support.

#### MATERIALS AND METHODS

## Participants

Eight TD infants (3–9 mo of age) were recruited by word of mouth to participate in this longitudinal study. Eligibility criteria included the following: 1) born at term; 2) no prenatal, perinatal, or postnatal complications; and 3) no known neurological or musculoskeletal abnormalities. Infant characteristics were as follows: all infants were Caucasian; four infants were female and four were male; chronological age at intake to the study was  $106 \pm 18$  days; time from intake to onset of independent sit was  $106 \pm 11$  days; and chronological age at onset of independent sit was  $211 \pm 23$  days. The study was conducted in accordance with Declaration of Helsinki guidelines and had ethical approval from the Human Subjects Committee at University of Oregon. Written consent was obtained from the infants' legal guardians prior to the data collection.

Data from four healthy young adults were collected with the same experimental protocol. These data serve as the "gold standard" for expected postural orientation and stability with the different levels of support.

# Experimental Tasks

Infants were evaluated two times per month during a 6-mo period (3–9 mo of age). During each assessment, continuous, simultaneous EMG, kinematic, and video data were collected during 3 min of supported sitting at each of the four different levels of external support, presented in a counterbalanced order. In addition, three clinical measures of motor skill were completed to ensure that infants were developing typically: Alberta Infant Motor Scale (AIMS; Piper and Darrah 1994), Segmental Assessment of Trunk Control (SATCo; Butler et al. 2010), and a timed sit test.

*Trunk stabilizing device.* Infants were seated on a bench, facing a computer monitor. Pelvic strapping (Butler et al. 2010) was used to ensure that the pelvis remained vertically aligned and directly below the rigid posterior support that circled the trunk. Thus the support system provided a secure upright position below the level of interest and ensured that the pivot point would occur above the level of support. The posterior support was raised or lowered to allow evaluation of four different trunk segments [cervical-upper thoracic (axillae support), midthoracic (midrib support), thoracic-lumbar (waist support), and pelvis (hip support, strapping system only)] (Fig. 1, *left*). Infants were entertained (e.g., an infant video or visual distraction offered by parent or researcher) and encouraged to sit quietly with an erect spine and hands free of support.

Kinematics. Magnetic tracking (Minibird system, Ascension Technology, Burlington, VT) was used to record the position of the infant in relation to the support. One magnetic sensor was attached to the center of the forehead just above the eyes with a headband, to document head movement. A second sensor was taped to the spinous process of the 7th cervical vertebra to document trunk alignment and stability. Two additional sensors were inserted into neoprene arm bands placed on the distal humerus just above the elbow. These sensors provided a measurement of extraneous arm movements. Prior to data collection anterior-posterior and left-right edges of the base of support were digitized to document the location of the support in relation to the head and trunk. The traegus of each ear was digitized to allow transformation of the head sensor data into estimated center of mass of the head. The sampling frequency (84 Hz), placement of the magnetic field transmitter (lateral to the infant), and magnetic sensor placement in the armband (closer to transmitter than any EMG sensor) were used to eliminate magnetic noise from EMG. The magnetic tracking system had a recording volume of 1 m<sup>3</sup> with a spatial accuracy of 1.8 mm.

*Electromyography.* Surface EMG was collected with a 16-channel EMG system (MA300, Motion Lab Systems, Baton Rouge, LA) using disposable gel-adhesive Ag-AgCl electrodes (Softrace 1, Conmed, Utica, NY) with poles placed 2–3 cm apart. EMG signals were preamplified (gain  $\times$  20), band-pass filtered (10–375 Hz), and then further amplified, sampled at a rate of 1,000 Hz per channel, and time-synched with the position data. The electrodes were placed on bilateral trunk muscles as follows: sternocleidomastoid (SCM), rectus abdominus (RA), internal oblique (IO), and cervical ( $\sim C_{4-5}$ , CE), thoracic ( $\sim C_{7-8}$ , TE), and lumbar ( $\sim L_{3-4}$ , LE) erector spinae. Electrode placements were based on previous postural control studies for infants and adults (Beith and Harrison 2004; Hedberg et al. 2005). A custom electrode harness that contained preamplifiers and electrode

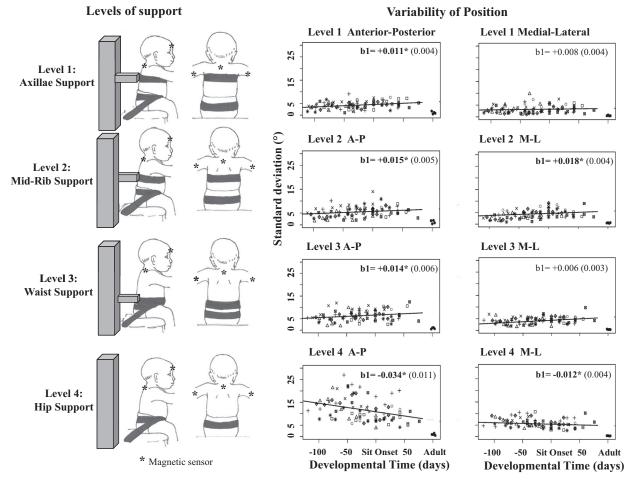


Fig. 1. *Left*: schematic of support device and sensor location. *Right*: changes in variability of angular position for the sensor on the 7th cervical spinous process are shown for movement along the medial-lateral (ML) and anterior-posterior (AP) axes at each level of support. Linear regression coefficient (b1) for change across developmental time and SE for the regression (shown in parentheses) are included in each plot. Significant changes across time are indicated by \* (P < 0.05) and bold font. Data for each infant are indicated by a different symbol.

wires covered by a T-shirt allowed quick application and prevented infants from noticing or attempting to grasp electrodes or wires.

Developmental timeline. The timed sit test was used to determine onset of stable sitting. The infant was placed in floor sitting and encouraged to raise both hands. A stopwatch was used to measure the amount of time the infant was able to remain upright with both hands free. To monitor the exact timeline for the emergence of sitting ability, stopwatches were loaned to parents. Parents conducted several trials of timed floor sitting 2-3 days each week, recorded results on a "probe card," and either mailed the card or brought it to the laboratory on their next visit. Comparison of technique and times between lab and home records allowed verification of consistent procedure. The first data set when the infant was able to sit independently with hands free for 60 s was labeled as the onset of stable sitting and served as the reference point for the developmental timeline. Each infant's data were adjusted to this reference point (onset of sit = 0). This continuous variable, rather than chronological age, was used to examine the developmental patterns in the data.

## Data Reduction and Analysis

Kinematic and EMG data were digitized for off-line analysis with custom MATLAB programs. All dependent variables were calculated from 3 min of continuous data from each level of support (axillae, midribs, waist, and hips). Thus there were 4 data sets for each session and 10-12 data sessions for each infant across time. At the earliest ages the infants were getting used to the experimental procedure. They

were younger and more easily fatigued by the protocol. It was therefore not always possible to collect data at all four levels during these early data sessions. With support at the hips, most of the youngest infants fell forward and became upset. In these cases infants were assisted back into a vertical alignment, encouraged to calm down, and then released again. For these cases the dependent variables were calculated for each segment of unassisted data. The final variable for that level of support is the average value for all unassisted segments.

Kinematic data were filtered with a zero-lag fourth-order low-pass Butterworth filter (cutoff frequency 6 Hz) prior to calculation of dependent variables. Postural orientation and stability of the trunk were measured by evaluating the angular displacement of the c7 sensor in relation to a vertical line located at the center of the base of support. Displacement-related measures (mean, standard deviation, and range of c7 angle) and rate-related measures (mean velocity, variability of velocity) were calculated along the anterior-posterior (AP) and medial-lateral (ML) axes. Standard deviation, mean velocity, and variability of velocity were calculated for the three-dimensional resultant of each arm sensor and the forehead sensor. These measurements were used to examine the concurrent changes in extraneous head and arm movements.

The technical difficulty of recording low-level EMG signal without heartbeat artifact was resolved by creating a custom MATLAB program, based on the adaptive sampling algorithm of Aminian (Aminian et al. 1988), to locate, average, and subtract the heart QRS waves from each channel of raw EMG. After heartbeat extraction, EMG data were high-pass filtered (4th-order, dual-pass, zero-phase shift Butterworth filter, 35-Hz cutoff), demeaned, half-wave rectified, and low-pass filtered (4th-order dual-pass Butterworth filter, 40-Hz cutoff) to create a linear envelope of muscle activation across time (Lockhart and Ting 2007). These data were used to document temporal features of muscle activation.

Muscle coordination was evaluated with pairwise cross correlation analyses  $(\pm 1 \text{ s})$ . The cross correlation function returned two sets of values: the lag, which is a measure of the relative timing between the two signals, and the *r* value, which is the linear correlation between the two signals at that lag. For our study purposes we selected a single lag value that refers to the specific time displacement associated with the highest absolute *r* value of the cross correlation function. The absolute *r* value indicates the strength of the correlation; the sign of the *r* value indicates whether the signals are in phase (+ correlation) or out of phase (- correlation). If the peak of the reference signal precedes the target signal, the lag is negative. If the peak of the reference signal occurs after the target signal, the lag is positive.

For analysis of antagonistic muscle coordination, muscle pairings included flexor/extensor pairs, with extensor muscles serving as the reference signal, and right/left bilateral pairs, with right-side muscles serving as the reference signal. Coactivation of antagonists would result in positive cross correlation r values, while reciprocal activation of these muscles would result in negative cross correlation r values.

For analysis of the contribution of each muscle to the resulting movement, muscle signals were paired with angular displacement of c7 along the AP axis or the ML axis. During quiet sitting with slow voluntary flexion and extension movements, healthy adults increase trunk extensor activation as they lean forward and increase trunk flexor activation as they lean backward, with a crossover area of low-level coactivation near midline (Cholewicki et al. 1997; Peach et al. 1998). In our experimental design, kinematic data became more positive with forward movement. Thus we expected correlations with movement along the AP axis to be positive for trunk extensors and negative for trunk flexors when infants achieved adultlike postural control.

During slow lateral bending movements, healthy adults activate trunk muscles contralateral to the direction of bending and activate IO bilaterally (Peach et al. 1998). In our experimental design, kinematic data became more positive with movement to the left side. Thus we expected correlations with movement along the ML axis to be positive for right-side muscles and negative for left-side muscles when infants achieved adultlike postural control.

Movement was used as the reference value in our cross correlations, so negative lags indicated that movement preceded muscle action and positive lags indicated that movement followed muscle action.

# Statistical Analysis

A standard linear model assumes that all measurements are independent. Because of repeated measurements per subject, the independence assumption does not hold. We used a linear mixed model to incorporate the dependence due to the repeated measures. Mixed models were fit with the lme4 package (Bates et al. 2011) for R (R Development Core Team 2011). Random effects for subject and fixed effects for support level were included in each model. Both linear and quadratic terms were used to assess the pattern of change across developmental time. The quadratic term was left in the final model only if the associated coefficient was significant.

## RESULTS

We were interested in the changes that occur in trunk postural control as typical infants learn to sit. For this purpose, we examined the developmental progression in movement and muscle activation patterns in infants from 3 to 9 mo of age. To better understand the coordination across different trunk segments, infants were provided with different levels of trunk support and the resulting changes in postural control were assessed.

# Kinematic Changes During Development of Trunk Control

Table 1 provides regression coefficients showing changes across developmental time for each kinematic variable at each level of support. The pattern of significant changes in c7 angle was unique across ML and AP axes at each level of support.

With support at the axillae, we observed increased variability of c7 angle and increased variability of velocity along the AP axis over time. Range of c7 angular movement increased along both the ML and AP axes over time.

With support at the midribs, range and variability of c7 angle increased significantly across time along both AP and ML axes. Other changes for c7 angle at this level of support were for movement along the AP axis: decreased mean position and increased variability of velocity.

When support was given at the waist, infants demonstrated increased variability of c7 angle along the AP axis as they gained trunk control. At this level of support most changes in movement occurred along the ML axis, with decreased mean c7 angle, increased range, and U-shaped changes in variability of velocity.

Developmental changes with support at the hips showed a quadratic change in mean c7 angle along the AP axis and decreased mean c7 angle along the ML axis. Along both axes, we observed decreased variability of position, mean velocity, and variability of velocity as infants gained upright control.

We also evaluated changes in extraneous movements of each arm and the head across developmental time. Infants demonstrated significant increases in variability of velocity and variability of position for right and left arm and forehead resultants across developmental time when support was at the axillae or the midribs (P < 0.05). Variability of position and variability of velocity changed in U-shaped patterns for both arms and increased linearly for the head resultant when support was at the waist. There were no significant changes in arm resultant parameters and decreased variability of velocity and variability of position for the head resultant across time when support was provided at the hip.

Overall, the trunk kinematic results support the third hypothesis that achievement of trunk postural control develops differently according to the region of the spine. Most significant decreases over time in AP and ML angle, velocity, and variability in these variables occurred at the level of hip support. With waist support, significant results were a mixture of increased, decreased, or U-shaped developmental patterns and significant changes occurred most frequently along the ML axis. There was greater similarity of results when support was provided to the rib cage (midribs, axillae). Developmental increases in c7 range, variability of angle, and variability of velocity occurred along the AP axis at both of these levels of support. Movements of the head and arms paralleled the changes observed in trunk stability.

### Antagonist Muscle Coordination

There were no significant changes across time for neck flexor/extensor [left CE/left SCM (LCE/LSCM), right CE/right SCM (RCE/RSCM)] cross correlation r value or lag at any level of support. Across time, bilateral correlation decreased for LSCM/RSCM (-0.0012/day, P < 0.001) and increased in a U-shaped pattern for LCE/RCE (linear P = 0.013, quadratic P = 0.019) when support was at the hip.

With development we found decreased correlation between TE and RA when support was at the midribs [LTE/LRA linear, -0.0008/day, P = 0.004; RTE/RRA U-shaped (linear, P =0.79, quadratic, P = 0.016] and when support was at the waist (LTE/LRA linear, -0.0008/day, P = 0.002). There were no significant changes in bilateral correlation or lag for TE or RA.

LE/IO pairs showed decreased correlation across development with support at the waist (RLE/RIO, -0.0011/day, P =0.004) and a U-shaped change with support at the hips (RLE/ RIO, linear P = 0.82, quadratic P = 0.004). In addition, the lag for LLE/LIO changed from LIO leading to LLE leading (-3.18 ms/day, P = 0.004). Bilateral correlation increased for RIO/LIO (+0.001/day, P = 0.001) when support was at the axillae, changed in a U-shaped pattern for RLE/LLE (linear P = 0.03, quadratic P = 0.018) with support at the midribs, and decreased for RLE/LLE (-0.0014/day, P < 0.001) with support at the hips.

Overall, with development, decreased coactivation of flexor/ extensor pairs occurred for muscles that were close to the level of support. Decreased coactivation in flexor/extensor pairs and in bilateral lumbar extensors over time is consistent with expectations for voluntary upright control seen in adults and suggests decreased coactivation in infants as they gain upright control. Developmental increases in bilateral cervical extensor coactivation with hip support, IOs with axillae support, and lumbar extensors with midrib support were not hypothesized. Thus other factors must be contributing to these changes.

# Contribution of Muscles to Movement

Regression coefficients for changes in muscle to movement correlation across time are provided for each level of support in Table 2.

With support at the axillae, the only change in muscle-tomovement cross correlation r value across time was a Ushaped change in RLE along the ML axis. We found a significant decrease in lag for LLE ( $-4.5 \pm 1.7$  ms/day), RRA  $(-4.2 \pm 1.6 \text{ ms/day})$ , and RIO  $(-5.3 \pm 1.6 \text{ ms/day})$  with respect to ML movement, indicating a transition from muscle activation preceding movement to muscle activation following movement. This represents a transition away from what we expected for adultlike movement coordination.

With support at the midribs, the r value became more negative over time for left-side cervical and thoracic extensors (LCE, LTE) when paired with ML movement. The r value for the right cervical extensor (RCE) became more positive over time when paired with AP movement. These changes are in alignment with expectations for transition toward adultlike activation patterns for voluntary control. There were no significant changes in muscle-to-movement lags at this level of support.

When support was at the waist, most significant changes in rvalue and lag were indicative of a transition toward adultlike trunk

vertebra. Developmental time is benchmarked by the number of days before and after stable sit was achieved. \*P < 0.05J Neurophysiol • doi:10.1152/jn.01193.2011 • www.jn.org Downloaded from www.physiology.org/journal/jn (088.175.239.202) on March 25, 2019.

Changes in c7 angular displacement from midline over developmental time at each support level Table 1.

		Anterior-Po	Anterior-Posterior Axis			Medial-L:	Medial-Lateral Axis	
	Axillae	Midrib	Waist	Hips	Axillae	Midrib	Waist	Hips
u	84	87	83	79	84	87	83	62
Mean position, $^{\circ}$	-0.054 (0.026)	-0.055*(0.018)	+0.029 (0.016)	+0.021 (0.018) + <b>0.001</b> * (0.0003)	+0.007 (0.013)	+0.014(0.009)	<b>-0.030</b> * (0.010)	-0.031* (0.009)
Variability of position, $^{\circ}$	+0.011*(0.004)	+0.015*(0.005)	+0.014*(0.006)	-0.034* (0.011)	+0.008(0.004)	+0.018*(0.004)	+0.006(0.003)	-0.012*(0.004)
Range, °	+0.075*(0.021)	+0.088* (0.024)	+0.061(0.027)	+0.007 (0.044)	+0.073*(0.026)	+0.092* (0.022)	+0.044*(0.018)	-0.018(0.026)
Mean velocity, °/s	+0.005(0.003)	+0.004(0.003)	-0.001(0.004)	-0.031* (0.01)	-0.0006(0.002)	+0.003(0.002)	-0.0001(0.003)	-0.029* (0.005)
Variability of velocity, °/s	+0.015*(0.005)	+0.013* (0.005)	+0.003 (0.006)	<b>-0.033</b> * (0.013)	+0.002(0.004)	+0.007 (0.004)	+0.008 (0.006) +0.0003* (0.0001)	<b>-0.030</b> * (0.005)

		Anterior-Posterior Axis	terior Axis			Medial-L	Medial-Lateral Axis	
	Axillae	Midrib	Waist	Hips	Axillae	Midrib	Waist	Hips
u	75	81	75	68	75	81	75	68
Extensor muscles Right cervical extensor	+0.0003 (0.0004)	+0.0011* (0.0004)	+0.0008 (0.0004)	+0.0006 (0.0004)	-0.0004 (0.0004)	-0.0001 (0.0004)	<b>-0.0011</b> * (0.0004)	<b>-0.0026</b> * (0.0007)
spinae Left cervical extensor	+0.0001 (0.0004)	+0.0010* (0.0004)	+0.0005(0.0004)	+0.0005 (0.0004)	-0.001* (0.0005)	-0.0015* (0.0004)	-0.011* (0.0004)	<b>-0.0003</b> * (0.00001) -0.0023* (0.0006)
spinae Right thoracic extensor	-0.0003 (0.0004)	-0.0003 (0.0005)	+0.0005(0.0004)	+0.0014* (0.0006)	-0.0005 (0.0004)	-0.0002 (0.0004)	-0.0010* (0.0003)	<b>-0.00002</b> * (0.00001) -0.0004 (0.0004)
spinae Left thoracic extensor	-0.0002 (0.0004)	-0.0002 (0.0004)	+0.0014* (0.0004)	0.00001 (0.00001) +0.0005 (0.0005)	-0.0006 (0.0004)	-0.0010* (0.0004)	-0.0014* (0.0004)	-0.0019* (0.0005)
spinae Rioht lumhar extensor	-0.0007 (0.0004)	-0.0007 (0.0004)	+0.0019* (0.0006)	+0.0010* (0.0005)	+0.0014* (0.0007)	-0.0008(0.0005)	-0.0005 (0.0004)	-0.00002* (0.000002) -0.0004 (0.0003)
spinae I.eff lumbar extensor	-0.0001 (0.0004)	+0.0003(0.0004)	+0.0024* (0.0005)	0.00002 (0.0001) + 0.001 (0.0005)	+0.0003*(0.0001) -0.0001(0.005)	-0.001 (0.005)	-0.0022* (0.004)	-0.0010* (0.004)
spinae								
Flexor muscles								
Right	-0.0001 (0.0004)	-0.0002 (0.0004)	+0.0001 (0.0004)	+0.0012*(0.0005)	-0.0004 (0.005)	-0.0001 (0.0005)	$-0.001\ (0.0005)$	-0.0011*(0.0005)
sternocleidomastoid								
Left sternocleidomastoid	-0.0004(0.0004)	-0.0006(0.0004)	+0.0003(0.0004)	+0.0015*(0.0004)	-0.0007 ( $0.0004$ )	-0.0006(0.0004)	-0.001* (0.0004)	-0.0003 (0.0005)
Right rectus abdominus	-0.0002 (0.0004)	+0.0001 (0.0003)	-0.0006 (0.0004)	+0.0016* (0.0008) +0.00001 (0.00001)	-0.0002(0.0003)	-0.0001 (0.0003)	-0.0003 (0.0004)	-0.0001 (0.0005)
Left rectus abdominus	-0.0005 (0.0004)	-0.0005 (0.0005) -0.00002* (0.00001)	-0.0007 (0.0005)	+0.0009(0.0005)	-0.0002 (0.0003)	+0.0001 (0.0003)	<b>-0.001</b> * (0.0004)	+0.0001 (0.0004)
Right internal oblique Left internal oblique	$\begin{array}{c} -0.0004 \; (0.0004) \\ -0.0006 \; (0.0004) \end{array}$	-0.00004 (0.0004) -0.00001 (0.0004)	$\begin{array}{r} -0.0003 \ (0.0004) \\ -0.0001 \ (0.0004) \end{array}$	+0.0015* (0.0006) +0.0015* (0.0005)	-0.0004 (0.0004) -0.0005 (0.0004)	$\begin{array}{c} -0.0001 \ (0.0003) \\ -0.0001 \ (0.0003) \end{array}$	-0.0005 (0.0004) -0.001* (0.0004)	-0.0004 (0.0005) -0.0006 (0.0004)

Table 2. Change in correlation of muscle to c7 angular displacement over developmental time at each support level

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# LEARNING ABOUT GRAVITY: DEVELOPMENT OF UPRIGHT TRUNK CONTROL

control. Cross correlation *r* values for trunk extensors (LTE, RLE, LLE) paired with AP movement changed from negative to positive. The lag for these correlations also increased significantly over time [LTE (+4.1  $\pm$  1.7 ms/day), LLE (+5.1  $\pm$  1.7 ms/day), RLE (+4.5  $\pm$  1.7 ms/day)], indicating a transition from muscle activation following movement to muscle activation preceding movement. Along the ML axis, *r* values of all left-side muscles (LCE, LTE, LLE, LSCM, LRA, LIO) as well as RCE and RTE became more negative over time.

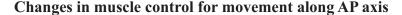
With support at the hip, muscles near the level of support (RLE, RIO, LIO) as well as the left neck flexor (LSCM) became more positively correlated with AP movement. There were quadratic decreases in correlation for RCE, LCE, and LTE and a linear decrease in correlation for LLE across time when paired with ML movement. The decreases in left-side muscles with ML movement and increased positive correlation for RLE with movement along the AP axis suggest transition toward adultlike control.

Figure 2 shows time series data for two infants with support at the waist before and after achieving sitting

L3: Waist Support

balance. These examples demonstrate the change in coordination of flexors and extensors with AP movement. Prior to development of trunk control both infants exhibited minimal activation of the extensors during forward movement (Fig. 2, C and D). These passive episodes were interspersed with active attempts to achieve an upright position. Note that activation of trunk flexors and extensors is most often paired with movement of the head toward midline and that muscle amplitude was often highest when the infants were close to midline. These attempts to achieve upright position resulted in negative r values between trunk extensors and AP movement (Fig. 2A). Examples of muscle activation profiles after the infants learned to sit (Fig. 2, E and F) show trunk extensor activity that precedes and mirrors changes in forward position. Note that muscle amplitude increased as the infants moved away from midline and decreased with movement toward midline. Thus cross correlation r values between trunk extensors and AP movement became positive (Fig. 2A). Positive correlation between extensors and AP movement is expected for adultlike voluntary control. These time series examples of muscle

**B** RLE.RIO Correlation L3



A RLE.AP.movement Correlation L3

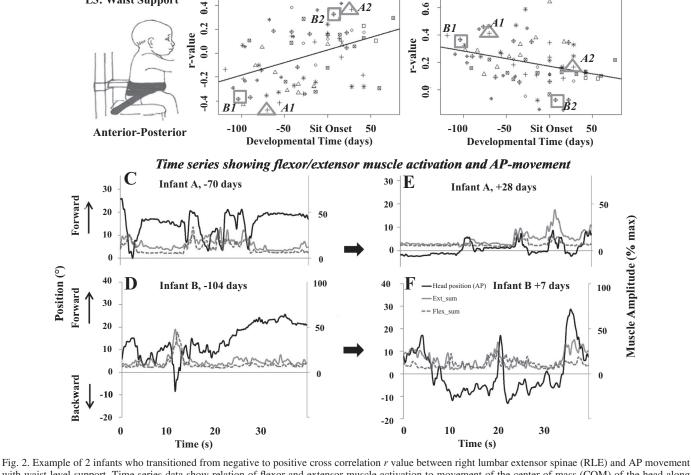


Fig. 2. Example of 2 infants who transitioned from negative to positive cross correlation r value between right lumbar extensor spinae (RLE) and AP movement with waist level support. Time series data show relation of flexor and extensor muscle activation to movement of the center of mass (COM) of the head along the AP axis before (*C* and *D*) and after (*E* and *F*) sitting onset. For these plots, the muscle activation is the sum of all flexor muscles (Flex\_sum) normalized to max seen across all 4 levels of support for that data session. The EMG has been low-pass filtered with a dualpass, 4th-order Butterworth, with 3-Hz cutoff to improve visualization. Head COM is plotted for the time series because it is more representative of the distribution of upper body mass along the AP axis than c7. Group data show how these 2 infants' data are aligned with the rest of the infants (*A* and *B*). Each infant's data are indicated by a unique symbol in *A* and *B*. RIO, right internal oblique.

activation also demonstrate the reduction in flexor/extensor coactivation (Fig. 2B).

Time series exploration demonstrates an interesting sequence of changes in muscle coordination for movement along the ML axis when support was at the waist (Fig. 3, C-H). Initially this infant showed bursts of bilateral flexor and extensor activity that were inconsistently paired with head movement toward or away from midline (Fig. 3, C and D). This was followed by a period with decreased variability of velocity and positive correlation between LTE and ML movement (Fig. 3, A and B, data point C2). At this developmental time, muscle activation for bilateral flexors and extensors closely paralleled ML movement. Note that this pattern is similar to the early pattern of AP muscle activation (Fig. 2, C and D) in that muscle amplitude increased with movement toward midline and decreased with movement away from midline (Fig. 3, E and F). After achievement of independent sitting, bilateral activation of flexors and extensors mirrored head movement with the adultlike pattern of increased activation during movement

away from midline and decreased activation when the infant approached midline (Fig. 3, G and H). These time series examples demonstrate the change to negative correlation between left-side muscles and ML movement (Fig. 3*B*, *data point C3*).

Taken together, these results suggest that infants began learning upright control by using erratic muscle activity that brought them closer to midline but often overshot or undershot the goal. With improved control, muscle activation preceded movement and muscle amplitude increased during movement away from midline and decreased during movement toward midline, similar to the patterns previously documented during voluntary leaning in adults. These patterns of change in muscle responses were observed during movement along both the AP and ML axes.

# Behavioral Analysis

In addition to kinematic data we used video analysis to assist in characterization of the development of upright control. The most diverse sway patterns were observed when support was provided at the hip. At this level infants progressed through



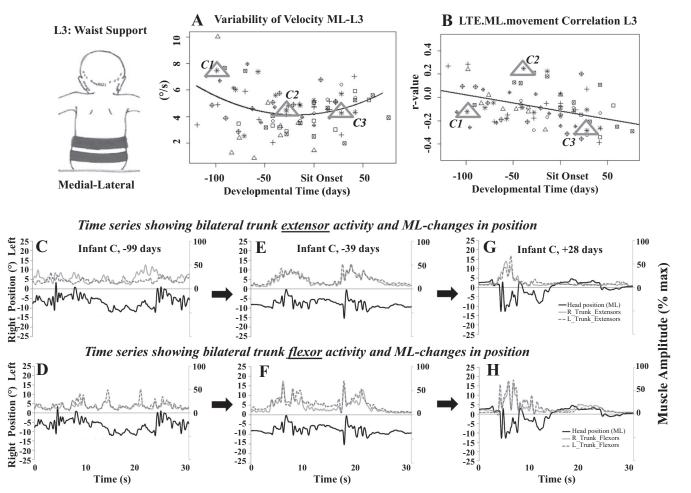


Fig. 3. Example of 1 infant demonstrating the changes in muscle coordination that accompany the quadratic pattern of change in kinematic values along the ML axis with support at the waist. C-H: time series data show relation of right- and left-side flexor and extensor muscle activation to movement of c7 along the ML axis during early development (C and D), at the midpoint in variability (E and F), and after sitting onset (G and H). For these plots, muscle activation is the sum of right and left flexor muscles (R\_Trunk\_Flexors,  $L_T$ runk\_Flexors; D, F, and H) and the sum of right and left extensor muscles ( $R_T$ runk\_Flexors,  $L_T$ runk\_Flexors; D, F, and H) and the sum of right and left extensor muscles ( $R_T$ runk\_Extensors,  $L_T$ runk\_Flexors, and G) normalized to max seen across all 4 levels of support for that data session. The EMG has been low-pass filtered with a dual-pass, 4th-order Butterworth, with 3-Hz cutoff to improve visualization. Group data show how these time points in this infant's data aligned with the rest of the infants (A and B).

four stages of upright control. The first stage consisted of slow collapse. In the second stage infants initiated vertical alignment but were unable to sustain it. During the third stage infants sustained a partially upright position but wobbled in all directions. The final stage was consistent upright posture that allowed functional interaction with the environment (see Supplemental materials for video examples of each stage).

Figure 4 shows the progression of one infant at each of the four behavioral stages. In addition to a photograph showing the behavior (Fig. 4, A-D), data plots reflect postural performance over the course of the full 3 min. Histograms (Fig. 4, E-H) show the frequency of position along the AP axis in relation to midline over the course of the full 3-min data collection. During the "collapse" and "rise and fall" stages, increased time was spent on the edges of range of motion. This changed dramatically during the "wobble" stage, when the infant spent the most time in the middle of his range. The histogram for the wobble stage took on a Gaussian shape, as the infant quickly changed direction at the edges and came back toward a central

location. The change toward stable control was reflected as a narrowing of the range and more vertical alignment of the central location. Time series plots of flexor and extensor activation with relation to AP movement for this infant are provided for each of these behavioral stages (Fig. 4, I-L). During the "collapse" stage, the infant activated flexors and extensors simultaneously but was not effectively able to improve alignment. During the "rise and fall" stage, the infant was able to come up to midline but was unable to sustain midline position. Alternating bursts of flexors and extensors were seen as the infant attempted to come upright and then fell forward or backward (Fig. 4J). During the "wobble" stage the infant primarily controlled head position by grading the extensor response (Fig. 4K). Note that this pattern is more adultlike; trunk extensor amplitude increased as the head moved away from midline and decreased as the head moved toward midline. During the final "functional" stage, the infant was aligned closer to midline and trunk extensor amplitude paralleled movement in an adultlike pattern (Fig. 4L).

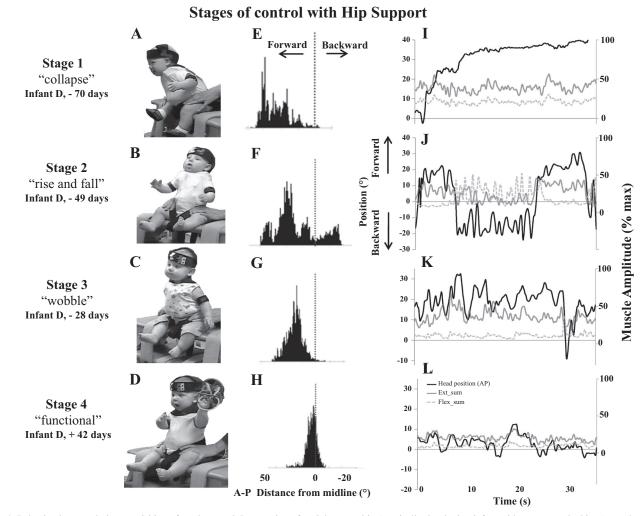


Fig. 4. Behavioral stages during acquisition of trunk control. Progression of upright control in 1 typically developing infant with support at the hip. A–D: photographs show an example of the behavior. E–H: dwell time histograms show the frequency of angular displacement of the COM of the head (°) with respect to midline (dotted line) along the AP axis. I–L: time series plots show the relation of flexor and extensor muscle activation to angular displacement of the COM of the head. (°) with respect to mass each activation is the sum of all flexor muscles (Flex\_sum) and the sum of all extensor muscles (Ext\_sum) normalized to max seen across all 4 levels of support for that data session. The EMG has been low-pass filtered with a dual-pass, 4th-order Butterworth, with 3-Hz cutoff to improve visualization. Head COM is plotted for the histograms and time series because it is more representative of the distribution of upper body mass along the AP axis than c7.

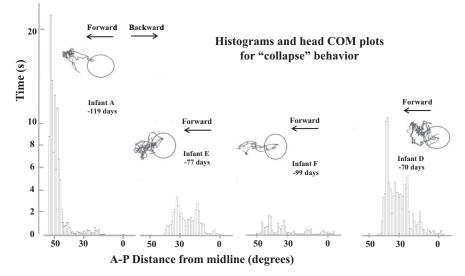


Fig. 5. Examples of 4 infants showing "collapse" behavior. Histograms show frequency of head position along AP axis with respect to midline. *Insets* show path of head COM (solid line) with respect to base of support (gray ellipse). Subject numbers match those in Table 3 and Figs. 2–4.

Evaluation of other infants showed progression through similar behavioral stages with support at the hip. There was variability among and within infants; for example, more than one type of behavior could be observed during a 3-min trial, especially for the first three behavioral stages. Nevertheless, we found reasonably pure behavioral patterns for "collapse" for four infants (Fig. 5), for "rise and fall" in six infants (Fig. 6), for "wobble" in seven infants (Fig. 7), and for "functional" in all eight infants (Fig. 8). From the seven infants who had reasonably pure wobble patterns, four infants wobbled across the full range of motion with large excursions forward and backward (Fig. 7, *infants A, B, C, H*), while three infants wobbled within a forward lean position (Fig. 7, *infants D, E, G*).

We attempted to classify the stage of control for each infant across time with information from the video analysis and distribution of position along the AP axis. Table 3 shows the criteria used for stage identification, and Table 4 shows results for stage classification. If data met two out of three criteria for one stage the session was classified in that stage. If data met criteria for three stages, the session was not classified.

## DISCUSSION

To our knowledge, this is the first study to consider segmental contributions to the development of upright trunk control. We hypothesized that changes in kinematics and EMG over time would be similar at all levels of support if trunk control developed as a single unit, that changes would occur earlier at higher levels of support and in more rostral muscle groups if there was a cephalo-caudal progression of trunk control, and that kinematic and EMG changes across developmental time would be unique for each level of support if trunk control developed differently depending on the anatomical region.

We found that developmental changes in head stability were specific to the region of the trunk being investigated, that changes in antagonistic muscle activity differed for AP axis

# Histograms and COM plots showing "rise and fall" behavior

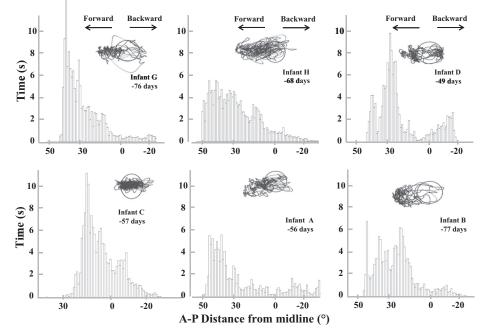


Fig. 6. Examples of 6 infants showing "rise and fall" behavior. Histograms show frequency of head position along AP axis with respect to midline. *Insets* show path of head COM (solid line) with respect to base of support (gray ellipse). Subject numbers match those in Table 3 and Figs. 2–4.

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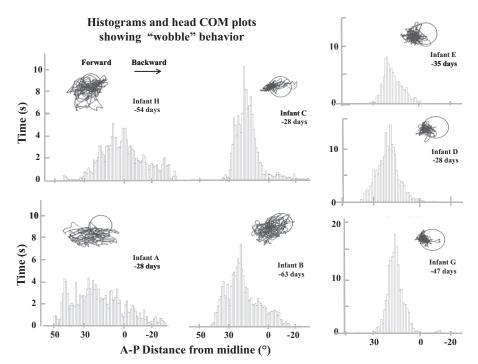


Fig. 7. Examples of 7 infants showing "wobble" behavior. Histograms show frequency of head position along AP axis with respect to midline. *Insets* show path of head COM (solid line) with respect to base of support (gray ellipse). Subject numbers match those in Table 3 and Figs. 2–4.

and ML axis, and that the relationship between muscle activation and movement changed from erratic responses to anticipatory graded responses along both AP and ML axes, as infants developed upright control through a four-stage behavioral process.

Previous research examining postural sway via center of pressure changes in standing adults has suggested that anatomical differences account for the independence between sway parameters along the AP and ML axes (Winter et al. 1996). It is likewise sensible that our results showing regional differences in the development of stability along the AP and ML axes can be accounted for by the biomechanical properties of the segment just above the level of support.

With support at the axillae or midribs, the thoracic vertebrae serve as the pivotal component for movement of the trunk. The spinous processes of the thoracic vertebrae limit the range of motion along the AP axis by blocking extension, and the attachments of the ribs limit the amount of lateral bending available along the ML axis. The greatest challenge to postural control at these segments is for the TE to prevent forward collapse into flexion. These biomechanical constraints are consistent with our results showing greater similarity in kine-

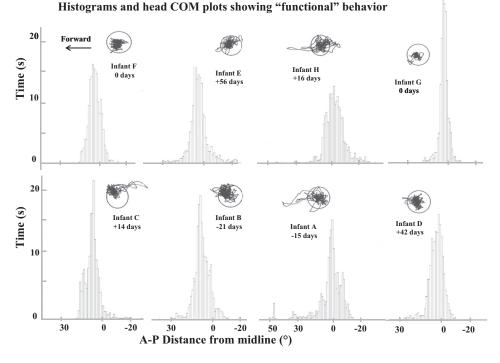


Fig. 8. Examples of 8 infants showing "functional" behavior. Histograms show frequency of head position along AP axis with respect to midline. *Insets* show path of head COM (solid line) with respect to base of support (gray ellipse). Subject numbers match those in Table 3 and Figs. 2–4.

Tał	ole 3	. Criteria	for	classification	of	<sup>r</sup> developmental	stage
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Criteria for Stage Classification	Stage 1 "Collapse"	Stage 2 "Rise and Fall"	Stage 3 "Wobble"	Stage 4 "Functional"
Kurtosis of data distribution along AP axis Gaussian = 3.0 Distribution of head COM over BOS along AP axis Manual assistance (video analysis)	<35% Requires manual assistance to bring head COM over midline	35–59% >3 episodes of active correction that brings head COM to midline	Kurtosis 2.5–3.9 60–89% No assistance needed to remain upright	Kurtosis >4.0 90% or more No assistance needed to remain upright

Four behavioral stages in acquisition of upright spinal control with support at the hip are shown. If manual assistance was needed to regain vertical, the session is *stage 1*. If data met 2 out of 3 criteria for 1 stage the session was classified in that stage. If data met criteria for 3 stages the session was not classified. AP, anterior-posterior; COM, center of mass; BOS, base of support.

matic changes between these two levels, and most of the changes over time occurred along the AP axis.

With support at the waist, the pivot point was at the upper lumbar vertebrae. These vertebrae are blocklike, with few bony interfaces. They allow a large range of motion along both the AP and ML axes. At this level of support synchronous coordination between trunk flexors and extensors is necessary to prevent collapse into extension, flexion, or lateral flexion. We found more changes in c7 stability along the ML axis than the AP axis when support was at the waist. At this level of support a padded band was placed firmly across the abdomen. Thus the external support system created increased abdominal pressure. This has been shown to increase stiffness and resist or stabilize the body against trunk flexion (Cholewicki et al. 1999a, 199b); therefore the external support might account for reduced changes along the AP axis.

With support at the hips, the pelvis was blocked from backward movements but the trunk was free to move in all directions without obstruction. Only with support at the hips did we see improved alignment paired with reduction in all parameters of postural sway across the developmental time frame we examined.

We had anticipated that, with development, improved postural control would result in reduced amplitude, speed, and variability of c7 angle at all levels of support. Instead we found that variability increased with support at the axillae and midribs, was increased, decreased, or U-shaped with support at the waist, and decreased with support at the hips. Variability has been suggested as a hallmark of the developmental process across multiple domains and has been shown to increase, decrease, or change in U-shaped patterns across age and experience (Siegler

Table 4. Stage classification for individual infants

Subject	Stage 1	Stage 2	Stage 3	Stage 4
Α	-119, -98	-56	-42	-15, +16
В	-104	-90		-21,0
С	-99, -80, -71		-14	0, +14, +28
D	-70	-42	-14, 0	+42, +60
Ε	-77		-42, -35	0, +42, +56
F	-91		-42	-14, +14, +28
G	-98, -84, -76	-61		0
Η		-82	-54	+12

Trials with hip support for each data session are shown. Numbers in each column represent days before or after sit onset. Letters identify each infant and match those on plots in Figs. 2–8. Sessions not listed reflected combinations of different behavioral stages.

2007). U-shaped developmental curves are of particular interest because efforts to explain such patterns often produce insights into the underlying processes (Siegler 2004). Dynamic systems theory postulates that development proceeds through a series of stable and unstable states, with increased variability signaling an unstable state that is necessary for a system to change (Thelen 1994). According to neuronal group selection theory, variability is initially high as infants select responses from a wide range of possible motor options, is reduced as infants select and use the most efficient strategies, and increases again as infants gain control and increase their movement repertoire with a second stage of developmental exploration (Hadders-Algra 2011). Harbourne and Stergiou (2003) found U-shaped changes in dimensionality of center of pressure measurements during the process of learning to sit. They attributed the reduction to constraint of degrees of freedom and subsequent release of the degrees of freedom as sitting independence emerged.

Our observations seem most consistent with the theory that infants must form an internal representation of erect posture (Hirshfield and Forssberg 1994; Massion 1998) and then learn to scale their motor responses to accommodate for gravitational torque. Infants' initial attempts to gain verticality were erratic, awkward, often unsuccessful movements that undershot or overshot the goal of upright posture, contributing to high variability. This was followed by apparent perception of and reaction to the edges of stability, contributing to reduced variability and producing a Gaussian distribution on histograms. Our data suggest that the critical constraint in achieving upright control was the infant's ability to anticipate and grade muscle responses to counteract gravitational torque.

Adult studies have demonstrated consistently recognizable activation patterns for trunk muscles during seated and standing trunk movements. The parameters of interest in this study are the patterns that contribute to upright postural control: reduced agonist/antagonist cocontraction as stability is achieved (Cholewicki et al. 1999a; Gardner-Morse and Stokes 1998; McGill et al. 2003), reduced activation in the mechanical neutral zone as postural sway approaches midline (Cholewicki et al. 1997; Eversull et al. 2001), and development of symmetrical bilateral activation of IOs during most postural activities (intra-abdominal pressure mechanism important for stability of the lumbar spine) (Butler 1998; Cholewicki et al. 1999a; Hodges et al. 2004; Hodges and Gandevia 2000).

Our results are consistent with many of these expectations. Correlation of flexor/extensor muscle pairs and bilateral extensor muscle pairs decreased over time at lower levels of support, suggesting reduction in coactivation as infants gained trunk stability. In contrast, coactivation increased for bilateral IOs. Extensor muscle activity changed from negative to positive correlation with movement along the AP axis, and left-side muscles changed from positive to negative correlation with movement along the ML axis. These changes suggest a transition toward adultlike voluntary control of sitting.

Although we did not hypothesize a specific process of learning to deal with gravity, it was not surprising to find behavioral evidence of stagelike changes in postural control. Previous research offers support for each of these stages during the development of sitting balance.

The earliest behavioral stage was characterized by a slow "collapse." The infants did not make many recognizable attempts to right themselves and gradually came to rest at the end of their available range. This stage is consistent with reports from previous researchers who found a period of limited postural responses to perturbation in 3- to 4-mo-old infants (Hedberg et al. 2005; Woollacott et al. 1987), lack of organized patterns of muscle activity to counteract gravity prior to 4 mo of age (Schloon et al. 1976), and increased range and velocity of trunk collapse when trunk support was removed from infants while sitting erect (2–3 mo compared with 5 mo) (Harbourne 1993).

During the next behavioral stage, "rise and fall," infants appeared to recognize vertical orientation and made visible attempts to rise to an upright position. Infants were occasionally successful in coming to vertical alignment but were unable to sustain that position and "fell" away from midline in the opposite direction. Previous research has reported an early period of higher complexity and dimensionality of postural sway at 4-5.5 mo (Harbourne and Stergiou 2003, 2009), large variation of directionally specific responses to surface perturbations during sitting in 5- to 6-mo-olds (Hadders-Algra et al. 1996; Hedberg et al. 2005), greater variability and jerkiness of response to sudden release of trunk support during sitting in 4-to 5-mo-olds (Harbourne 1993), and higher variability of postural responses to visual perturbations in 5-mo-olds (Bertenthal et al. 1997). These findings are consistent with our observation of a more chaotic "rise and fall" type behavior prior to development of upright trunk control.

The third stage was one of more constrained upright control, in that infants appeared to have developed an internal model that provided a reference and led them to consistently make postural corrections, creating a "wobbling" type movement around this set point. Similar periods of constrained postural sway have been reported in previous studies as a reduction of complexity and dimensionality at 5–6.5 mo (Harbourne and Stergiou 2003, 2009), increased consistency of direction-specific muscle responses to sitting perturbations at 6–7 mo (Hadders-Algra et al. 1996; Harbourne 1993; Hirschfield and Forssberg 1994; Woollacott et al. 1987), and decreased positional variability during visual perturbations in 7-mo-old infants compared with 5 and 9 mo olds (Bertenthal et al. 1997).

The final stage of upright control occurred when infants were able to sit independently. During this stage infants became more interactive with toys and the environment. While they spent the majority of their time aligned vertically over the base of support, they used more range of motion and had greater variability of movements than during the "wobble" stage. Previous studies of postural development have demonstrated increased degrees of freedom and increasing variability of responses in 6- to 8-mo-old infants as independent sitting emerges (Harbourne and Stergiou 2003, 2009), increased response to visual perturbation in 9-mo-olds following a reduction at 7 mo (Bertenthal et al. 1997), and an increased repertoire of available motor actions (Hadders-Algra 2011).

The four stages that we observed were on a continuum, blending from one to the next rather than changing in discrete steps. Nevertheless, we believe they may be helpful milestones in understanding where a child is along the continuum of postural development. We showed examples of these stages with hip support and observed them at other levels of support.

# Methodological Considerations

The question of how infants attain upright sitting is at the core of understanding the development of most functional abilities. Our simple, practical method of securing the lower segments of the spine and evaluating the infant's ability to achieve stable, vertical alignment with the free segments contributes a useful method and new insights into the understanding and development of upright control.

Readers may consider our application of specific support levels to be artificial and not related to real-world experiences of the infants. We would argue that most vertical positioning equipment for young infants includes some level of trunk support. For example, infant carriers begin with support for the head that is removable as infants gain control; the "Bumbo" infant chairs have become very popular in the US, and they offer support at the axillae for young infants. The level of support is gradually reduced to midrib support as the infant grows taller. All of the walkers, jumpers, and "exercisers" advertised for young infants include some type of trunk support. Thus most infants in this study had exposure to devices with varying levels and rigidity of trunk support.

Infants never sit quietly, yet we chose to use the full 3-min data set for calculation of our variables. We believe the type of movements made by infants when in supported seating were relevant to the amount of control available to them. Thus we did not exclude any data for arm waves, head turns, or other movements. We did, however, monitor extraneous movement by placing sensors on each arm in addition to the sensors on the headband and c7. We showed that changes in arm and head movement paralleled changes in trunk movement.

## Future Studies

We provide evidence for development of anticipatory voluntary control and describe stages of postural sway behavior that can serve as milestones for evaluating progression of upright control. This information can be used by researchers to further refine hypotheses regarding development of trunk control and by clinicians who wish to develop and test more specific treatment programs for children with postural dysfunction.

Infants frequently demonstrated more than one behavioral stage during the 3-min data collection. We attempted to classify the behavioral stage across the entire data set and indicated those data sets that demonstrated predominantly one stage. This left gaps in the developmental progression when data sets showed a mixture of stages. Future studies should attempt to

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develop localized quantitative criteria (EMG and kinematic) that could be applied in a sliding window across the time series for identification of different stages. The percentage of time spent in each stage during a single data session would help to clarify how infants progress from one stage of control to another. These criteria would also be helpful for comparison of sitting behavior in children with neuromotor deficits to sitting behavior of typical infants.

Our data refute the concept of trunk development occurring as a single unit and expand previous work by demonstrating the contributions of and unique challenges created by different anatomical regions of the trunk. These data do not, however, rule out a cephalo-caudal pattern of development of upright control. Future studies must evaluate younger infants with support at the axillae or midribs and older infants with hip support before conclusions can be drawn regarding cephalocaudal progression of trunk postural control.

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#### DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

## AUTHOR CONTRIBUTIONS

Author contributions: S.L.S., P.v.D., and M.H.W. conception and design of research; S.L.S. performed experiments; S.L.S. analyzed data; S.L.S., P.v.D., and M.H.W. interpreted results of experiments; S.L.S. prepared figures; S.L.S. drafted manuscript; S.L.S., P.v.D., and M.H.W. edited and revised manuscript; S.L.S., P.v.D., and M.H.W. approved final version of manuscript.

#### REFERENCES

- Aminian K, Ruffieus C, Robert PH. Filtering by adaptive sampling (FAS). Med Biol Eng Comput 26: 658–662, 1988.
- Bates D, Maechler M, Bolker B. lme4: Linear mixed-effects models using S4 classes. *R package version 0.999375-39*. http://CRAN.R-project.org/package=lme4, 2011.
- Beith ID, Harrison PJ. Stretch reflexes in human abdominal muscles. *Exp* Brain Res 159: 206–213, 2004.
- Bertenthal BI, Rose JL, Bai DL. Perception-action coupling in the development of visual control of posture. J Exp Psychol Hum Percept Perform 23: 1631–1643, 1997.
- **Butler PB.** A preliminary report on the effectiveness of trunk targeting in achieving independent sitting balance in children with cerebral palsy. *Clin Rehabil* 12: 281–293, 1998.
- Butler PB, Saavedra S, Sofranac M, Jarvis S, Woollacott M. Development and reliability of the Segmental Assessment of Trunk Control (SATCo). *Pediatr Phys Ther* 22: 246–257, 2010.
- **Cholewicki J, McGill S.** Mechanical stability of the in vivo lumbar spine: implications for injury and chronic low back pain. *Clin Biomech (Bristol, Avon)* 11: 1–15, 1996.
- Cholewicki J, Panjabi MM, Khachatryan A. Stabilizing function of trunk flexor-extensor muscles around a neutral spine posture. *Spine* 22: 2207– 2212, 1997.
- Cholewicki J, Juluru K, McGill SM. Intra-abdominal pressure mechanism for stabilizing the lumbar spine. J Biomech 32: 13–17, 1999a.

- Cholewicki J, Juluru K, Radebold A, Panjabi M, McGill SM. Lumbar spine stability can be augmented with an abdominal belt and/or increased intraabdominal pressure. *Eur Spine J* 8: 388–395, 1999b.
- Cignetti F, Kyvelidou A, Harbourne RT, Stergiou N. Anterior-posterior and medial-lateral control of sway in infants during sitting acquisition does not become adult-like. *Gait Posture* 33: 88–92, 2011.
- **Eversull BS, Solomonow M, Bing He Zhou EE, Baratta RV, Zhu BP.** Neuromuscular neutral zones sensitivity to lumbar displacement rate. *Clin Biomech* 16: 102–113, 2001.
- Gardner-Morse MG, Stokes IA. The effects of abdominal muscle coactivation on lumbar spine stability. *Spine* 23: 86–91, 1998.
- **Goodworth AD, Peterka RJ.** Contribution of sensorimotor integration to spinal stabilization in humans. *J Neurophysiol* 102: 496–512, 2009.
- Goodworth AD, Peterka RJ. Sensorimotor integration for multisegmental frontal plane balance control in humans. J Neurophysiol 107: 12–28, 2012.
- Hadders-Algra M. Variation and variability: key words in human motor development. *Phys Ther* 90: 1823–1837, 2011.
- Hadders-Algra M, Brogren E, Forssberg H. Ontongeny of postural adjustments during sitting in infancy: variation, selection and modulation. J Physiol 493: 273–288, 1996.
- Harbourne RT, Stergiou N. Nonlinear analysis of the development of sitting postural control. *Dev Psychobiol* 42: 368–377, 2003.
- **Harbourne RT, Stergiou N.** Movement variability and the use of nonlinear tools; principles to guide therapist practice response. *Phys Ther* 89: 284–285, 2009.
- Harbourne RT. A kinematic and electromyographical analysis of the development of sitting posture in infants. *Dev Psychobiol* 26: 51–64, 1993.
- Hedberg A, Carlberg EB, Forssberg H, Hadders-Algra M. Development of postural adjustments in sitting position during the first half year of life. *Dev Med Child Neurol* 47: 312–320, 2005.
- Hedberg A, Forssberg H, Hadders-Algra M. Postural adjustments due to external perturbations during sitting in 1-month-old infants: evidence for the innate origin of direction specificity. *Exp Brain Res* 157: 10–17, 2004.
- Hirschfeld H, Forssberg H. Epigenetic development of postural responses for sitting during infancy. *Exp Brain Res* 97: 528–540, 1994.
- Hodges PW, Gandevia SC. Changes in intra-abdominal pressure during postural and respiratory activation of the human diaphragm. *J Appl Physiol* 89: 967–976, 2000.
- Hodges PW, Cresswell AG, Thorstensson A. Intra-abdominal pressure response to multidirectional support-surface translation. *Gait Posture* 20: 163–170, 2004.
- Lockhart DB, Ting LH. Optimal sensorimotor transformations for balance. Nat Neurosci 10: 1329–1336, 2007.
- Massion J. Postural control systems in developmental perspective. *Neurosci Biobehav Rev* 22: 465–472, 1998.
- McGill SM, Cholewicki J. Biomechanical basis for stability: an explanation to enhance clinical utility. J Orthop Sports Phys Ther 31: 96–100, 2001.
- McGill SM, Grenier S, Kavcic N, Cholewicki J. Coordination of muscle activity to assure stability of the lumbar spine. J Electromyogr Kinesiol 13: 353–359, 2003.
- Nashner LM, Shupert CL, Horak FB. Head-trunk movement coordination in the standing posture. *Prog Brain Res* 76: 243–251, 1988.
- Panjabi M, Yamamoto I, Oxland T, Crisco J. Spinal stability and intersegmental muscle forces—a biomechanical model. *Spine* 14: 194–200, 1989.
- Peach JP, Sutarno CG, McGill SM. Three-dimensional kinematics and trunk muscle myoelectric activity in the young lumbar spine: a database. Arch Phys Med Rehabil 79: 663–669, 1998.
- Piper MC, Darrah J. Motor Assessment of the Developing Infant (AIMS), Philadelphia, PA: Saunders, 1994.
- **R Development Core Team.** *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing, http://www. R-project.org/, 2011.
- Reeves NP, Narendra KS, Cholewicki J. Spine stability: lessons from balancing a stick. *Clin Biomech* 26: 325–330, 2011.
- St-Onge N, Cote JN, Preuss RA, Patenaude I, Fung J. Direction-dependent neck and trunk postural reactions during sitting. J Electromyogr Kinesiol 21: 904–912, 2011.
- Schloon H, Obrien JM, Scholten CA, Prechtl HF. Muscle activity and postural behaviour in newborn infants. A polymyographic study. *Neuropadiatrie* 7: 384–415, 1976.
- Shumway-Cook A, Woollacott MH. Development of postural control. In: Motor Control: Translating Research into Clinical Practice (3rd ed.). Philadelphia, PA: Lippincott, Williams & Wilkins, 2007.

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Siegler RS. U-shaped interest in U-shaped development and what it means. J Cogn Dev 5: 1–10, 2004.

Siegler RS. Cognitive variability. Dev Sci 10: 104–109, 2007.

- Siegler RS, Fazio LK, Pyke A. There is nothing so practical as a good theory. In: Cognition in Education, vol. 55, Psychology of Learning and Motivation, San Diego, CA: Academic, 2011.
- Stokes IA, Gardner-Morse M. Spinal stiffness increases with axial load: another stabilizing consequence of muscle action. J Electromyogr Kinesiol 13: 397–402, 2003.
- Sveistrup H, Woollacott MH. Longitudinal development of the automatic postural response in infants. J Mot Behav 28: 58–70, 1996.
- Thelen E, Spencer JP. Postural control during reaching in young infants: a dynamic systems approach. *Neurosci Biobehav Rev* 22: 507–514, 1998.
- Thelen E. Three-month-old infants can learn task specific patterns of interlimb coordination. *Psychol Sci* 5: 280–85, 1994.
- van der Fits IB, Otten E, Klip AW, Van Eykern LA, Hadders-Algra M. The development of postural adjustments during reaching in 6- to 18-monthold infants. Evidence for two transitions. *Exp Brain Res* 126: 517–528, 1999a.

- van der Fits IBM, Klip AW, van Eykern LA, Hadders-Algra M. Postural adjustments during spontaneous and goal-directed arm movements in the first half year of life. *Behav Brain Res* 106: 75–90, 1999b.
- Winter DA. A.B.C. (Anatomy, Biomechanics and Control) of Balance During Standing and Walking. Waterloo, ON, Canada: Waterloo Biomechanics, 1995.
- Winter DA, Prince F, Frank JS, Powell C, Zabjek F. Unified theory regarding A/P and M/L balance in quiet stance. J Neurophysiol 75: 2334– 2343, 1996.
- Winter DA, Mackinnon CD, Ruder GK, Wieman C. An integrated EMG/ biomechanical model of upper-body balance and posture during human gait. *Prog Brain Res* 97: 359–367, 1993.
- Witherington DC, vonHofsten C, Rosander K, Robinette A, Woollacott MH, Bertenthal BI. The development of anticipatory adjustments in infancy. *Infancy* 3: 495–517, 2002.
- Woollacott M, Debu B, Mowatt M. Neuromuscular control of posture in the infant and child—is vision dominant? J Mot Behav 19: 167–186, 1987.
- Xu Y, Choi J, Reeves NP, Cholewicki J. Optimal control of the spine system. *J Biomech Eng* 132: 051004, 2010.

