

Developmental changes in motor cortex activity as infants develop functional motor skills

Ryota Nishiyori^{1,2*} | Silvia Bisconti² | Sean K. Meehan¹ | Beverly D. Ulrich^{1,2}

¹ School of Kinesiology, University of Michigan, Ann Arbor, Michigan

² Center for Human Growth and Development, University of Michigan, Ann Arbor, Michigan

*Correspondence

Ryota Nishiyori, Center for Human Growth and Development, School of Kinesiology, University of Michigan, 401 Washtenaw Ave. 4732CCRB, Ann Arbor, MI 48109-2214.
Email: ryonish@umich.edu

Abstract

Despite extensive research examining overt behavioral changes of motor skills in infants, the neural basis underlying the emergence of functional motor control has yet to be determined. We used functional near-infrared spectroscopy (fNIRS) to record hemodynamic activity of the primary motor cortex (M1) from 22 infants (11 six month-olds, 11 twelve month-olds) as they reached for an object, and stepped while supported over a treadmill. Based on the developmental systems framework, we hypothesized that as infants increased goal-directed experience, neural activity shifts from a diffused to focal pattern. Results showed that for reaching, younger infants showed diffuse areas of M1 activity that became focused by 12 months. For elicited stepping, younger infants produced much less M1 activity which shifted to diffuse activity by 12 months. Thus, the data suggest that as infants gain goal-directed experience, M1 activity emerges, initially showing a diffuse area of activity, becoming refined as the behavior stabilizes. Our data begin to document the cortical activity underlying early functional skill acquisition.

KEYWORDS

developmental systems, fNIRS, motor cortex, motor development

1 | INTRODUCTION

Our ability to explore our surroundings by moving through space or reaching and manipulating objects allows us to acquire new information about our environment and is essential for human development and learning. But how do we develop these adaptive and complex skills? How do these skills, like reaching and walking, emerge and become stable?

Motor development researchers have constructed a body of evidence that describes the diversity, variability, and dynamic nature of motor skill acquisition particularly during infancy. To explain the bases for these behavioral outcomes, scientists have focused on studying the processes of change that drive these behaviors. With this goal researchers have investigated the relations among kinematic, kinetic, and overt functional changes of both successful and unsuccessful limb movements (Chang, Kubo, & Ulrich, 2009; Corbetta & Thelen, 1996; Teulier, Sansom, Muraszko, & Ulrich, 2012; Thelen et al., 1993; Thelen & Spencer, 1998). Efforts to interpret these relations based on current neuroscience and developmental theories, have led to hypotheses about the development of the central nervous system (CNS) and its role in the emergence of neuromotor control.

Currently, however, we do not have direct evidence, or even descriptive evidence, relating brain activity with functional motor skills as they emerge. As a result, we have a knowledge gap in efforts to support or revise these hypothesized links between the brain and motor behaviors in infants. With the recent development of new infant-friendly neuroimaging techniques, we can begin to construct a body of empirical evidence identifying the neural links to neuromotor control.

A set of overlapping theories, commonly referred to as dynamic systems theory (Thelen & Smith, 1994), developmental systems approach (Gottlieb, Wahlsten, & Lickliter, 1998), dynamic field theory (Wiebe, Morton, Buss, & Spencer, 2014), and interactive specialization (Johnson, 2001, 2011) all embrace and argue that new skills (patterns of behavior) are emergent, not prescribed. This framework posits that functional behaviors are outcomes of the interactions among multiple subsystems such as the nervous system, intrinsic body dynamics, environment, and the task or goal. New patterns are both discovered through exploration and stabilized through repetition or practice (Lewis, 2011; Smith & Thelen, 2003; Thelen & Smith, 1994; Ulrich & Ulrich, 1993). Here, we will use the term developmental systems framework as the phrase and approach to effectively capture the

essence of all aforementioned approaches. Infants must achieve a sufficient level of development of many components, such as postural control, motivation to achieve the goal, capacity to coordinate muscle activations, for new motor skills to emerge. But only with repetitions of the goal-directed pattern, do stability and control follow. A growing body of empirical data regarding the changes in behavioral, kinetic, and kinematic patterns supports the developmental systems framework that explains the ontogeny of many new patterns of behavior such as reaching, stepping, and kicking (Corbetta & Thelen, 1996; Jensen, Thelen, Ulrich, Schneider, & Zernicke, 1995; Kanemaru, Watanabe, & Taga, 2012; Lockman & Thelen, 1993; Teulier, Lee, & Ulrich, 2015; Thelen, 1995; Thelen et al., 1993; Thelen, Corbetta, & Spencer, 1996; Watanabe, Homae, & Taga, 2010). Yet, there is very limited empirical evidence regarding neural basis that underlies the emergence of new patterns of behavior, specifically with functional motor skills.

Theories focused on how the brain becomes organized to control functional behavior compliment the developmental systems approach; particularly relevant are Edelman's theory of neuronal group selection (TNGS, Edelman, 1987; Sporns & Edelman, 1993) and dynamic neural field theory led by Gregor Schöner, Kopecz, and Erlhagen (1997). Both theories link behavior and the neural dynamics as co-evolving over time (Samuelson, Jenkins, & Spencer, 2015; Sporns & Edelman, 1993). Specifically, TNGS proposes that early in skill acquisition, there is a particularly high redundancy in the nervous system. This redundancy is manifested in the intrinsic overproduction of unspecified neurons and synaptic connections and facilitates discovery of ecologically meaningful goals (Bertenthal & Campos, 1987; Greenough, Black, & Wallace, 1987). Selection drives much of neural organization, that is, as infants identify a goal and attempt to achieve it, such as to reach for an object they see or move their bodies through space, they activate neural circuits in multiple relevant areas of their brains. For example, over time and much practice, as seen in adults, the primary motor cortex becomes functionally and topographically specialized, activating efficiently muscles used to perform voluntary movements (Halsband & Lange, 2006; Muellbacher et al., 2002; Nishiyori, Biscconti, & Ulrich, 2016). Early in skill acquisition, however, large and diverse areas of neurons would be active as movement options are explored. As the movement outcomes become more reliable, neural activity in parallel would become more focal and efficient, gradually evolving into the topographic organization seen in adults. Thus, we must begin to determine the neural activation patterns during early skill acquisition in infants.

Our goal here was to begin to describe the early activation of motor cortex neurons as infants acquire skills. We chose two well-studied functional motor skills in infants: reaching for a toy with the upper limbs and the production of stepping patterns with the legs while supported upright on a treadmill. Reaching, is an important functional skill that emerges during the first 6 months after birth. For reaching to emerge, theorists argue that infants must be able to visually locate the target, control the muscles of the arms, and control their posture and head (Clearfield & Thelen, 2001). Moreover, we know that young infants show variable patterns of movement as they attempt to obtain a toy; and as they gain more experience moving their arms and attempting to reach their goals, their movement

become smoother, reliable, accurate, and muscle activation patterns become more efficient (Thelen et al., 1993, 1996). That multiple subsystems converge and patterns of movement become stable as infants gain experience through repeated cycles of action and perception has been established by behavioral studies. That is, as infants make repeated attempts to reach for objects, they fine-tune their actions with the environment as stable patterns of movement form (Corbetta & Bojczyk, 2002; Corbetta & Snapp-Childs, 2009; Williams, Corbetta, & Guan, 2015). Later in the first year, infants experience similar cycles, but with their lower limbs as they begin to engage in upright leg activity.

Functional control over the legs, unlike the arms, does not emerge until the second half of the first year. While step-like patterns, such as newborn stepping, can be elicited from birth to approximately 6–8 weeks, voluntary stepping in the form of cruising (walking with support) and walking (independently) emerge between 9 and 12 months. Thelen and colleagues, used a series of studies to illustrate the dynamic confluence of many subsystems over time in this developmental trajectory of the production of infant stepping patterns. They documented, for example, that when newborn stepping “disappeared” in the upright posture, similar lower-limb kinematics persisted in other contexts: when supine, infants kicked and when legs were submerged in water, they stepped (Thelen, Fisher, & Ridley-Johnson, 1984, Thelen, Fisher, & Ridley-Johnson, 2002; Thelen & Fisher, 1982). Furthermore, across the first year post-birth, when supported over a treadmill, researchers could elicit from infants alternating stepping patterns, though infants also displayed multiple inter-limb coordination patterns (Thelen, 1986; Thelen & Ulrich, 1991; Ulrich, Jensen, & Thelen, 1991). Thus, the adaptive and changing nature of stepping behaviors, like other behaviors, demonstrate that the subsystems available to produce body segment trajectories including factors external to the infant are softly assembled and can affect the presence or absence of any particular overt behaviors across time. Based on the behavioral data amassed thus far and theories about the development of the CNS, the next logical step in explaining early skill acquisition would then be to examine more directly infants' brain activation patterns as they begin to improve their control of their limbs during essential basic skills, such as reaching and stepping.

Mapping developmental systems framework principles to real (as opposed to modeled) brain activity during the acquisition or performance of functional motor skills in infants has been limited to date by the constraints of traditional neuroimaging techniques. For example, when using functional magnetic resonance imaging (fMRI) the head must be stationary and the machine is loud (Almli, Rivkin, & McKinstry, 2007). Event-related potentials (ERPs) obtained through electroencephalography (EEG) are quiet and less head stabilization is required, but still experience high attrition rates due to the dynamic nature of the stimuli which causes infants to move (Stets, Stahl, & Reid, 2012), introducing movement-related artifacts.

Recently, technological advances in the use of functional near-infrared spectroscopy (fNIRS) have enhanced its effectiveness in brain-imaging studies focused on developmental questions (Lloyd-Fox, Blasi, & Elwell, 2010; Vanderwert & Nelson, 2014). fNIRS utilizes source optodes that emit near-infrared light which is projected

through the scalp, skull and the cerebral cortex, then reflected back out of the brain and picked up by detector optodes. Changes in the reflected light intensity occur as concentrations of oxygenated (HbO) and deoxygenated (HbR) hemoglobin vary, which arise due to activation of the sampled brain tissue (Villringer & Chance, 1997). fNIRS technology offers a number of advantages over fMRI and EEG. fNIRS has a greater spatial resolution compared to EEG and the temporal resolution of fNIRS is greater than that of fMRI (Huppert, Hoge, Diamond, Franceschini, & Boas, 2006). This system is more resilient to movement-related artifacts than fMRI and EEG and is not subject to rigid head stabilization or supine posture of fMRI. Most important for our questions is that fNIRS allows participants to assume a naturalistic posture specific to a movement task while tolerating larger limb movements. (Lloyd-Fox et al., 2010; Quaresima, Bisconti, & Ferrari, 2012; Vanderwert & Nelson, 2014).

Brain imaging studies of children and adults show that the primary motor cortex activates the muscles to produce voluntary goal-directed movements and plays a role in practicing and consolidating new skills (Filimon, Nelson, Hagler, & Sereno, 2007; Indovina & Sanes, 2001; Koenraadt, Duysens, Smeenk, & Keijsers, 2012; Koenraadt, Duysens, Meddeler, & Keijsers, 2013; Nishiyori et al., 2016). These neural excitation patterns have not been tested or observed in human infants, that is, their origins are not known. Skills used in motor studies for adults involve learning a new *sequence* or *adapting to a new constraint* during a repeated goal, such as to manually control a joy-stick correcting for a force perturbation; the basic movements themselves, however, have been extensively practiced and used for years prior. Thus, we do not have direct developmental data to illustrate: (i) how the primary motor cortex becomes organized in the way we observe it to be in adults; (ii) the level of activity in the primary motor cortex when skills that are truly novel and nascent are attempted; and (iii) how primary motor cortex activation patterns change as skills improve over time.

The specific goals of our current study were to delineate the developmental changes in brain activity for two distinctly different tasks: reaching for a toy with the upper limbs while seated, and stepping with the legs while supported upright on a treadmill. Reaching represents a functional, voluntary, and self-initiated skill with a clear goal which infants produce successfully by about 4 months of age and subsequently practice many times daily. In contrast, stepping while supported over a treadmill is an elicited movement pattern with recognizable limb patterns. Infants never practiced treadmill stepping; at 6 months they have not begun to step voluntarily but by 12 months most have, at least begun to practice stepping as they start to cruise. Here, we explored the emergent patterns of motor cortex activity associated with infants' motor patterns, at two developmental time points, 6 and 12 months. At 6 months of age, infants had 1–2 months of practice reaching for toys, but minimal to no experience stepping upright or cruising. By 12 months of age, infants are very skillful reachers but are relative novices at voluntary stepping (1–2 months of gaining upright posture and cruising or walking).

Based on the developmental systems framework and previous developmental neuroscience data, we proposed that the motor cortex

neural activation change as infants discover patterns that fit their self-selected goals and then repeat cycles of practice (e.g., creating and enhancing the perception-action links) to accomplish these goals. More specifically, we hypothesized that with increased goal-directed experience, brain activity will shift from diffuse to more refined and focal activity. That is, 6 month-old infants will exhibit a dispersed area of motor cortex activity (nascent reaching) compared to 12 month-old infants during reaching when the skill is well established. During stepping, 6 month-old infants will exhibit reduced areas of cortical activity because it is not voluntary or "goal-directed", compared to 12-month old infants, who will show a dispersed area of motor cortex activity because they are nascent "walkers," similar to the 6 month-old brain activity during reaching.

2 | METHODS

2.1 | Participants

We consented 34 infants, 14 in the younger and 20 in the older age groups. Of these, one of the younger infants and three of the older infants became too fussy during preparation for testing to allow us to collect data. In addition, two of the younger infants and three of the older infants' data were unusable due to extensive noise, motion artifacts, or too few usable channels. This resulted in 11 of the younger infants and 14 of the older infants for whom we had usable data for reaching and/or, stepping. Not all infants' data were usable from both tasks, thus the final numbers, ages, and gender for each task and age group were: reaching = 11 younger ($M = 26.2$ weeks, range = 23.2–29.9 weeks, seven females) and 11 older ($M = 52.2$ weeks, range = 50–56 weeks, seven females); stepping = 11 younger ($M = 27.12$ weeks, range = 23.3–29.9 weeks, seven females) and 11 older ($M = 52.1$ weeks, range = 49.3–56.6 weeks, six females) infants. Table 1 presents a summary of the participants' characteristics.

2.2 | Session overview

Upon arrival to the lab, we allowed infants to acclimate to our space and interact with the research team. During this time, a research team member explained the study to parents and answered any questions with the parents, who read and signed the informed consent. Next, we removed infant's clothing except their shirt and diaper to allow infants to move freely. We measured the infant's head circumference, distance between inion and nasion, and left pre-auricular to right pre-auricular point to identify the vertex of the head, or Cz according to the 10–20 international system (Jasper, 1958). After we placed the infant into the customized infant seat, we secured the headgear on the infant's head. Floor to ceiling curtains were approximately 60 cm away from both sides of the table on which the infant seat rested, which minimized the amount of distraction due to open space. We began testing with the reaching task, followed by a brief break and then tested the stepping task. During the break, we re-arranged the lab to prepare for the stepping task. After completion of the stepping task, we took photographs of the headgear on the infants to ensure the

TABLE 1 Average (*M*) and standard deviation (*SD*) for anthropometric measurements and the motor scale of the Bayley scale of infant development (MS-BSID-III) for each group by task

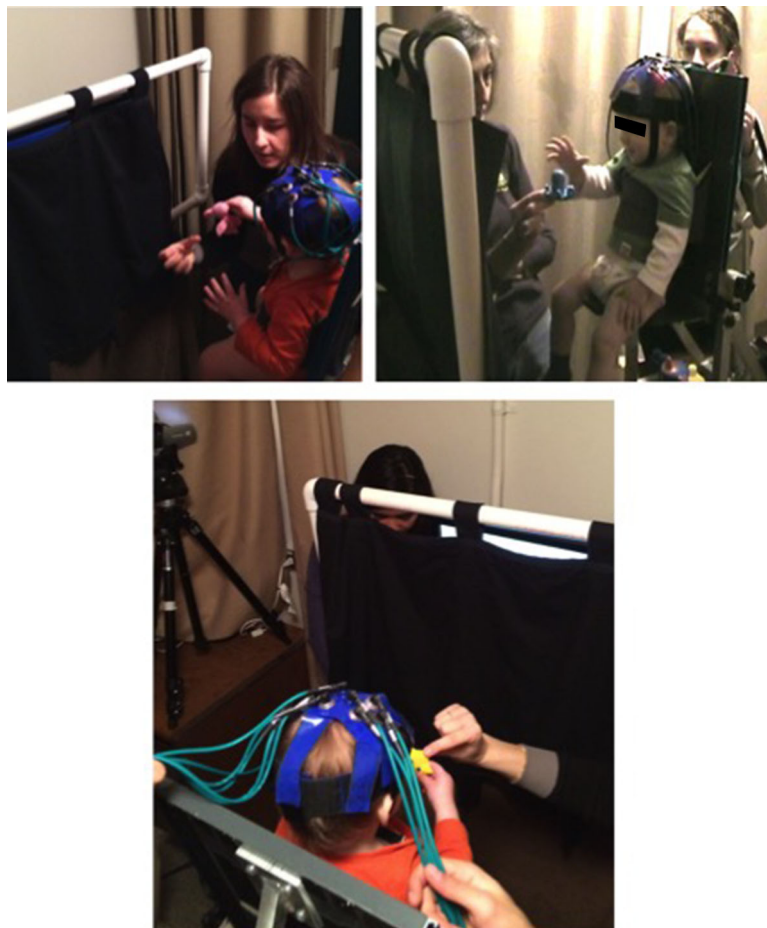
	Younger				Older			
	Reaching		Stepping		Reaching		Stepping	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Age (weeks)	26.22	2.24	27.12	3.86	52.2	1.63	52.1	1.80
Weight (kg)	8.24	0.82	8.24	0.85	9.69	1.28	9.93	1.32
Length (cm)	66.54	2.48	68.12	2.63	76.58	2.66	75.23	2.61
Head circumference (cm)	43.62	1.40	44.21	1.33	47.12	0.72	47.21	1.08
Inion-Nasion (cm)	26.02	0.93	25.93	0.91	27.34	1.12	27.83	1.83
A1–A2 (cm)	25.89	0.91	25.87	0.99	27.66	1.71	27.48	1.53
BSID-III (raw score)								
Fine	20.13	3.00	20.14	3.24	27.75	0.46	27.10	1.29
Gross	25.13	1.89	25.00	2.00	44.13	4.05	41.50	5.56
Total	45.25	4.33	45.14	4.63	71.88	4.29	68.60	6.54

optodes/headgear had not moved from the target areas, as this could affect the quality and precision of our fNIRS measurements. We then removed the headgear and took basic anthropometric measurements (e.g., weight, total body length, leg length and circumference, and thigh and umbilicus skinfold). Finally, we administered the Motor Subscale of the Bayley Scales of Infant Development III (BSID-III, Bayley, 2006).

2.3 | Tasks

2.3.1 | Reaching

For the reaching task, infants were secured in a customized infant seat (seat pan was 32 cm above the table top, backrest: 75 cm long, and reclined approximately 10° from the vertical) with a chest strap. The infant seat was secured on top of a table [117.4 (L), 59.5 (W),

**FIGURE 1** Set up for reaching task

79.5 cm (H)], so that infant's head would be at eye level with the video monitor. We positioned a video monitor (23" LCD, Phillips, Andover, MA) on a cart in front of and approximately 80 cm away from the seat. We hung a thick black curtain in front of the monitor that could be opened and closed to hide the monitor during reaching trials and revealed videos playing during the rest phase (Figure 1). For reaching trials, a variety of age-appropriate small grip-sized toys [5 (L) × 5 (W) × 5 cm (H), Figure 2] were presented to elicit reaching and maintain interest.

For the task phase, an experimenter presented the toy at the infant's midline within reach, followed by a rest phase. The experimenter first retrieved the toy from the infant then unveil the monitor playing an infant entertainment video (e.g., Baby Einstein) intended to keep the infant calm and still for a minimum of 20 s (rest phase). If after 10 s from toy presentation, the infant did not reach for the toy we presented, we began a rest phase then started a new trial with a new toy. We repeated the cycle of reaching and rest for a minimum of 10 successful trials.

2.3.2 | Stepping

We placed our custom-designed treadmill [frame: 93.5 (L) × 43.7 (W) × 21 cm (H); belt: 81.5 (L) × 30.6 cm (W)] on top of and near the front edge of the same table used for reaching, in the center of the room (Figure 3). Each trial consisted of a rest-phase followed by a stepping phase. We started with a 30 s rest phase. During the rest phase, the experimenter held the infant who rested against the experimenter's chest. From pilot sessions, we determined that this was the best position to keep the infant calm and minimize movements thus optimizing rest phase status and values. Following the rest phase, each stepping phase lasted 30 s. During the stepping phase, an experimenter supported the infant under the arms so they were upright with feet touching the belt surface. Infants were encouraged to support as much of their weight as they could; experimenter provided supplemental weight support and posture control. The treadmill belt speed was set at .20 m/s for both younger and older infants based on previous research which showed this to be the most effective speed to elicit alternating steps in infants across the first year of life (Teulier et al., 2009). If infants did not respond to the moving belt with any leg movements during a trial, that is they allowed their legs to drag and

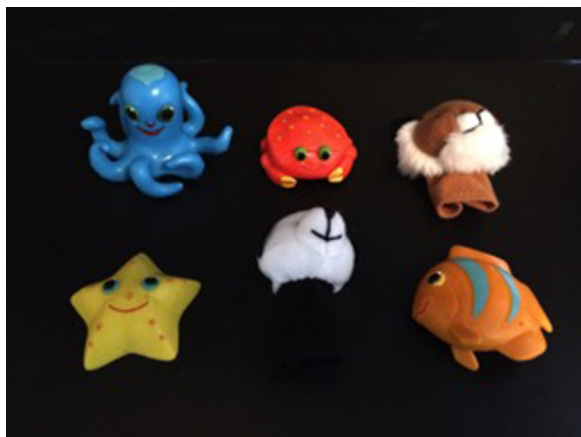


FIGURE 2 Exemplar toys used for reaching



FIGURE 3 Set up for stepping task

extend behind them, we lifted the infant up to bring their legs forward and placed them on the belt again to encourage a motor response—stepping. We collected a minimum of 10 successful stepping trials.

2.4 | fNIRS data acquisition

To record the hemodynamic responses of the primary motor cortex (M1) during reaching and stepping tasks, we used a continuous wave fNIRS system (CW6; TechEn Inc., Milford, MA) which utilized two wavelengths (690 and 830 nm) and sampled at 50 Hz. Near-infrared light was delivered via fiber optic cables that terminated into a customized headgear (Figure 4). The base of the headgear was an adjustable headband (Velcro, Manchester, NH) with a panel with extensions, both made of blue Dycem. In this panel, we embedded the base for the optodes (grommets, TechEn, Inc., Milford, MA). The fNIRS cables/optodes were connected to the panel prior to placing the apparatus on the infant's head. Extensions of this panel connected to the headband, which allowed us to adjust a snug fit for each infant. The headgear contained four source- and six detector-optodes placed approximately 2.5 cm apart creating a 12-channel array. We positioned the headgear on the infant's head in alignment with Cz as defined by the 10–20 International system (Jasper, 1958). Channels covered the area around the C3 and C4 landmarks, thus our configuration placed the optodes in position over the M1 or Brodmann Area (BA) 4 (Figure 4). The design of our probe array was based on a study we completed previously with adults (Nishiyori et al., 2016).

2.5 | Video recording

We used a digital camcorder (Canon, Melville, NY) that sampled at 60 Hz to record both reaching and stepping tasks. During the reaching trials, the video was mounted on a tripod positioned at a 45° from midline and 100 cm away from the center of the infant seat. During stepping trials, the camcorder was repositioned perpendicular to the side of the treadmill. In these positions, we were able to identify the activity of all four limbs and the trunk. Furthermore, these views allowed us to view any gross movements of the headgear and fNIRS

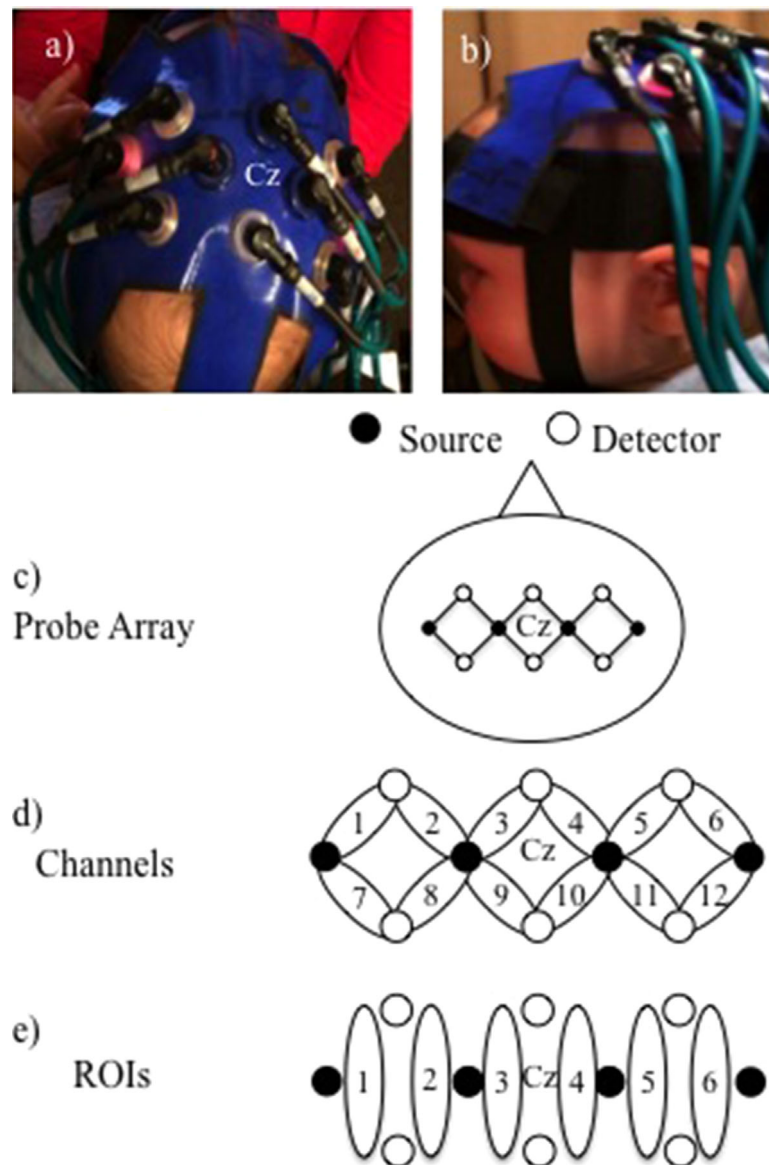


FIGURE 4 Layout of headgear from the (a) superior view and (b) lateral view of on an infant's head. Diagram and superior view of the (c) sources and detectors, (d) channels, and (e) ROIs

cables. The onset of task, rest phases, and any undesired behaviors such as crying and head turning were documented.

The camcorder and fNIRS system were synchronized via an audio signal. At the start of each condition, we inserted an audio signal simultaneously to the video and fNIRS data. We then mapped the timing of the onset of reaches and steps and the start of the rest phases onto the fNIRS data to identify functional movement-related changes in hemodynamic activity of M1.

2.6 | Motor subscale of Bayley scales of infant development

At the end of the session, we administered the Motor Subscale of the Bayley Scales of Infant Development (BSID-III). This scale allowed us to characterize the status of gross and fine motor skill acquisition between the two groups.

2.7 | Trial rejection

To determine the usability of trials, all videos were behavior-coded offline by two different researchers. For reaching, trials were valid if the infant reached for and successfully grasped the object. Trials were not considered for further analysis if infants did not reach for the object. For stepping, trials were valid if the infant stepped in response to the moving belt. Trials were not considered for further analysis if infants did not step in response to the moving belt. For instance, if the infant allowed her legs to drag behind them for a majority of the trial, we did not code this as a stepping trial.

2.8 | Data processing

fNIRS data were processed using the Homer2 (Huppert, Diamond, Franceschini, & Boas, 2009) Matlab toolbox (Mathworks, MA). Data were low-pass filtered at .8 Hz and then motion-corrected using a

wavelet-based filtering (Molavi & Dumont, 2012). The optical density signal was then converted into concentration using the modified Beer-Lambert Law. Partial path-length factor was set at 6.0 and the known coefficients of oxygenated (HbO) and deoxygenated (HbR) hemoglobin (Cope et al., 1988; Obrig & Villringer, 2003). Concentration data were then time locked to movement onset and epoched. For the reaching task the epoch consisted of 3 s prior to and 10 s post onset of reach. For the stepping task, the epoch was 1 s prior to and 10 s post onset of stepping. Epochs were averaged for each channel, group, and task and baseline corrected to pre-movement period. Outlier trials in which task-related change in HbO and HbR exceeded two standard deviations were excluded from further analysis. With this criterion, 16% of the total 440 test trials (11 participants \times two groups \times two tasks \times 10 trials = 440 test trials) were excluded. Finally, six brain regions of interest (ROIs, Figure 4) were then defined for analysis by pairing adjacent anterior and posterior channels.

2.9 | Data analysis

Three dependent variables of interest were extracted from the data. First, in order to determine the number of functionally active ROIs, the change in HbO values from each ROI within the epoch were used. We used an independent samples *t*-test to detect any significant changes between pre- and post-onset of the movement for all trials. This test provided the number of ROIs demonstrating task-related activity, which were then compared across group for each task using separate independent *t*-tests. The dependent variable of number of active ROIs was quantified as a tally of significant ROIs for each infant in each task. The same analysis was performed for HbR. Second, percent signal change were calculated based on the change of concentrations for both HbO and HbR compared to rest values within an epoch. We then determined group differences in peak activity by comparing percent signal change in the ROI demonstrating peak HbO change from each participant. Separate independent samples *t*-tests were performed for reaching and stepping. Finally, we summed the percent signal change of the active ROIs to calculate the volume of activity during a task. The volume of each HbO (sum of percent signal change across active ROIs) across groups was compared for each task using separate independent samples *t*-tests for each task. Volume derived in the manner provides an indication of percent signal change across significant ROIs. In conjunction with the number of active ROIs and peak signal change, it can provide information about the focality of cortical activity that neither the number nor peak signal change alone can provide.

3 | RESULTS

3.1 | Motor subscale of the Bayley scales of infant development

The Bayley data, revealed that younger infants, as expected, achieved fewer items, 47, than older infants, 74 items. The scores were tightly clustered for each age group, therefore we could not make meaningful comparisons with the fNIRS data.

3.2 | Reaching

An average of 10.4 (SD = 2.1) and 11.0 (SD = 3.0) reaching trials were considered valid and included in the data analysis for younger and older groups, respectively.

The independent samples *t*-test on the number of active ROIs for HbO during reaching revealed that younger infants ($5.1 \pm .25$ ROIs) showed significant activity in a larger number of ROIs compared to older infants ($2.7 \pm .38$ ROIs, $t(10) = 5.221$, $P < .01$). There were no differences across groups in the number of ROIs demonstrating significant change in HbR (Younger = $1.09 \pm .21$ ROIs, Older = $.64 \pm .15$ ROIs, $t(10) = .65$, $P = .27$). Despite differences in the number of ROIs for HbO, the percent signal change in HbO for the peak ROI was not different between younger ($.72 \pm .20 \mu\text{M}$) and older infants ($.72 \pm .08 \mu\text{M}$, $t(10) = .21$, $P = .98$). A comparison of the volume of activity revealed that younger infants ($.32 \pm .25 \mu\text{M}$) demonstrated lower volumes of activity compared to older infants ($1.37 \pm .24 \mu\text{M}$, $t(10) = 2.531$, $P = .03$). Overall, while percent signal change was similar at the peak ROI, younger infants tended to demonstrate lower levels of reaching related activity distributed across a larger number of ROIs compared to older infants (Figures 5 and 6).

3.3 | Stepping

An average of 8.8 (SD = 2.6) and 7.2 (SD = 2.7) stepping trials were considered valid and included in the data analysis for younger and older groups, respectively. These trials consisted of bouts of alternating steps. Trials in which infants dragged their feet or did not respond with leg movements, were not included in this analysis.

In contrast to reaching, during stepping younger infants ($2.6 \pm .15$ ROIs) demonstrated fewer ROIs showing significant HbO change compared to older infants ($3.5 \pm .24$ ROIs, $t(10) = 3.1$, $P = .01$). There were no differences between groups in the number of ROIs demonstrating significant change in HbR (Younger = $1.73 \pm .24$, Older = $2.28 \pm .33$ ROIs, $t(10) = .21$, $P = .42$). While older infants demonstrated a greater number of active ROIs during stepping, activity in the peak ROI was significantly lower for younger infants ($.30 \pm .05 \mu\text{M}$) compared to older infants ($.84 \pm .17 \mu\text{M}$, $t(10) = 2.78$, $P = .02$). A comparison of the volume of activity across group revealed that younger infants ($.59 \pm .13 \mu\text{M}$) demonstrated lower levels of activity across all active ROIs compared to older infants ($1.8 \pm .45 \mu\text{M}$, $t(10) = 2.37$, $P = .04$). Overall, motor cortex activity was lower across all three measures in younger infants compared to older infants during stepping (Figures 5 and 6). Summary of the number of active ROIs can be found in Table 2 (HbO) and Table 3 (HbR).

4 | DISCUSSION

The goal of our current study was to take the first step in identifying the emergent patterns of cortical activation in infants as they produce and practice early motor patterns. We hypothesized, based on the developmental systems approach (Gottlieb et al., 1998) and TNGS (Edelman, 1987; Sporns & Edelman, 1993) that as infants explore and perform repeatedly, goal-directed actions, such as reaching for an

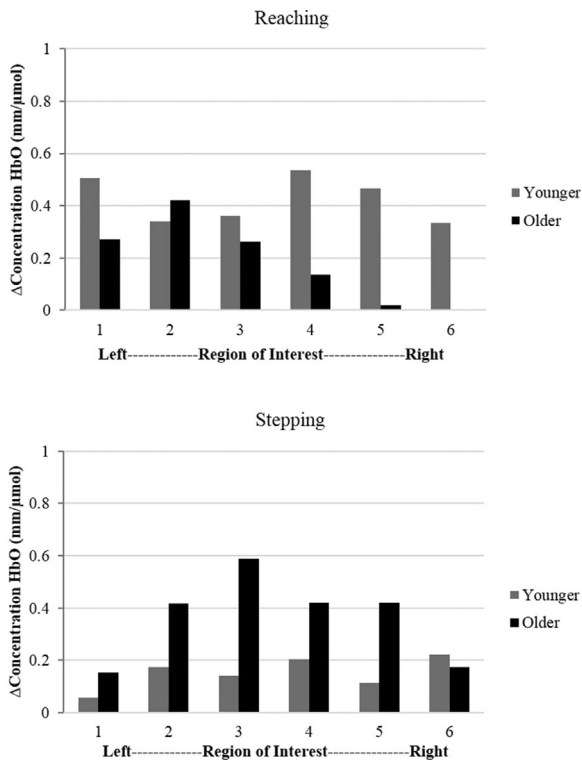


FIGURE 5 Change in concentration of HbO for reaching (top) and stepping (bottom) comparing younger and older infants in the respective ROIs

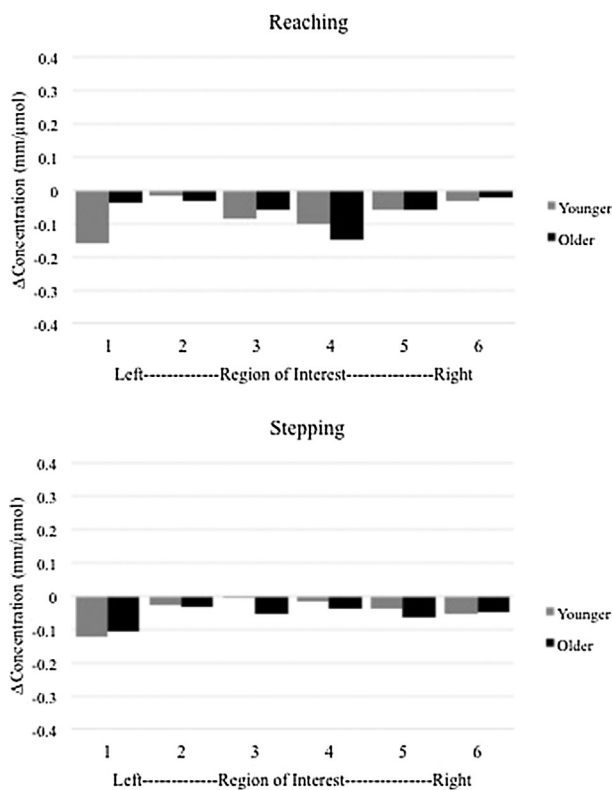


FIGURE 6 Changes in concentration of HbR for reaching (top) and stepping (bottom) comparing younger and older infants in the respective ROIs

TABLE 2 Sum of active ROIs (HbO) for each group

Participant ID	Reaching		Stepping	
	Younger	Older	Younger	Older
1	5	1	3	3
2	5	2	2	4
3	5	1	3	4
4	4	4	3	3
5	6	3	3	4
6	6	2	2	3
7	4	4	3	3
8	6	3	2	2
9	4	2	2	4
10	6	5	3	5
11	5	3	3	3
Mean (SEM)	5.09 (0.25)	2.73 (0.38)	2.64 (0.15)	3.46 (0.25)

object or moving their bodies through space, they activate large numbers of redundant neural circuits. Therefore, we predicted larger areas of activity in the primary motor cortex during early attempts leading to smaller areas of activity as skills improved. Results of our present study supported these predictions, particularly true when infants demonstrate clear goal-directed efforts. More broadly and consistently, our results demonstrated significant changes in activation patterns, that is, the dynamic nature of cortical activation, across ages and tasks. Together, these data suggest that neural responses underlying motor outcomes are associated with both the specific motor goal and experience pursuing it.

4.1 | Motor cortex activity during reaching

Both younger and older infants showed similar amplitudes in peak activity at their respective ROIs with the largest change in

TABLE 3 Sum of active ROIs (HbR) for each group

Participant ID	Reaching		Stepping	
	Younger	Older	Younger	Older
1	1	0	2	1
2	1	0	0	2
3	3	1	2	4
4	1	1	2	1
5	1	0	2	3
6	1	1	2	1
7	1	1	1	2
8	1	1	2	2
9	1	1	2	4
10	0	1	3	3
11	1	0	1	2
Mean (SEM)	1.09 (0.21)	0.64 (0.15)	1.73 (0.24)	2.28 (0.33)

concentration. However, younger infants demonstrated activity across a wider area of the cortex compared to older infants, as indexed by the number of ROIs activated. Further, the broader cortical activity is characterized by smaller task-related activity, as indexed by the volume of activity. This pattern of results is consistent with less refined neural activity during skilled reaching. Reaching is functional but not fully stable by 6 months of age. At this age, there is co-activation muscle activity when infants reach for an object in a similar setup to ours (Thelen et al., 1993). This means that younger infants recruit increased resources (e.g., area), explained by their necessity for postural control, in addition to co-activating more muscles than needed to reach for an object. Interestingly however, younger infants had comparable peak activity to older infants. Younger infants are able to drive the target muscles to reach but also activate other muscles (co-activation) that they have not learned to inhibit or control. As reaching skill develops towards 12 months of age, it appears that development is characterized by refined movement patterns rather than increased activity of task-relevant motor cortical representations. This is captured by previous reports of improved postural control, kinematics and dynamics in 12 month olds (Dusing, Thacker, Stergiou, & Galloway, 2013; Konczak, Borutta, Topka, & Dichgans, 1995; Thelen & Spencer, 1998) as well as the more focal activity in M1 observed here.

4.2 | Motor cortex activity during stepping

During stepping, younger infants activated a smaller area of motor cortex activity with both a lower peak and lower volume of activity compared to those of older infants. Stepping is an unexplored behavior for infants at 6 months of age, and is only observed when we create this unique context of supporting them over a moving belt. They were only able to achieve the stepping behavior at this age because we provided them with postural and body weight support.

Findings from animal studies show that higher brain centers, such as the cerebral cortex, are vital for the initiation of walking and to balance and support one's weight, but the alternative activations of muscles when supported on a treadmill to produce stepping patterns is controlled at the spinal level. Cortical contributions also appear to be integral for the modulation of gait patterns, for example in obstacle avoidance (Drew, Prentice, & Schepens, 2004). Therefore, stepping at this point in development, may not elicit significant or unique motor cortex activity during treadmill stepping in the absence of a volitional context or at least practice. More specifically, 6 month olds have not yet developed the volitional will to walk or step, especially in our context of treadmill stepping, in which the goal is not clear.

By 12 months of age, our infants when stepping, showed the kind of diffused activity in the motor cortex that we observed for 6 month-olds as they reached. At this age, infants have had 1–2 months of experience being upright as well as a practice producing volitional goal-directed behavior like cruising along furniture, and many have taken their first independent steps. Thus, compared to younger infants, these older infants understand the requirements to maintain their balance when the belt moves their legs from under them, which they accomplish by initiating continuous and alternating steps. Older

infants activate a diffused area of the M1 to drive the activation of muscles to voluntarily step on the treadmill. We hypothesize that, much like in reaching, continued experience with walking would result in refinement of the motor cortical activity observed at 12 months.

There is an alternative explanation that must be considered, one that could potentially reflect a maturationalist approach to the nature of stepping. That is, when younger infants stepped when we supported them on the moving belt of the treadmill, the neural drivers are those pre-designed neuronal step pattern generators located in the spinal cord and not neurons located in the primary motor cortex. At this point in time, maturation of the higher brain centers should inhibit this spinal reflexive activation (Forssberg, 1985; Lamb & Yang, 2000). However, while this strictly maturational approach would argue the brain should inhibit the spinal activity, the fact is infants are moving their legs in patterns we categorize as stepping. Perhaps the richness of the supported treadmill context (researcher providing postural support and balance, movement of the treadmill belt stretching muscles and joints and the gravity assisting with swing phase and momentum carrying the leg forward in a step) overcomes the inhibitory tendencies of the higher brain centers. Clearly, by the end of the first year, both theoretical approaches, maturation and developmental systems with TNGS, expect the primary motor cortex to be extensively engaged in controlling stepping and walking. What is unclear from the maturational approach is how to explain the initially highly diffuse activation during early walking (stepping on the treadmill in this experiment) that is inefficient, showing parallels to early reaching. The practice involved to become skillful and efficient with this functional motor skill seems to follow the trajectory observed here for reaching, clearly not attributed to an innate pattern generator.

5 | CONCLUSION

To summarize, we have demonstrated the viability of fNIRS technology to document the activity of cortical motor neurons activated during the emergence of neuromotor control as infants perform functional motor skills. Moreover, we have shown that characteristics of cortical activation patterns parallel changes in the skill levels of infants across at least two motor skills and goals. Specifically, when self-initiated motor patterns occur as skills are nascent and have minimal practice, cortical activity is dispersed. Conversely, when infants are highly efficient and the skill is well practiced, as in our reaching task, neural activity reduces and is more specific to the production of the skill. Finally, when skills are unexplored in a goal-directed manner, activity in the primary motor cortex may be undetectable or severely limited. Future research is needed to extend the ages of observation and levels of practice to strengthen and confirm these arguments. In addition, because our data capture were limited to the primary motor cortex, it will be important to expand the regions of interest to include areas deemed critical to establishing control of goal-directed movements, especially the prefrontal cortex and cerebellum. The parallel or prescient activity in these areas may help understand the roles of volition and adaptation in the early development of neuromotor control.

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