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RESEARCH ARTICLES

Spatially Specific Changes in Infants' Muscle Coactivity as They Learn to Reach

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Infants first reach out and touch objects between the ages of 3 and 5 months. This article reports changes in muscle coactivity associated with this transition. A group of 4 infants were observed weekly from 3 to 30 weeks and every 2 weeks from 30 to 52 weeks. Hand kinematics of both prereaching and reaching movements were collected, as was electromyographic activity from the trapezius, deltoid, biceps, and triceps. Before infants first reached for toys presented at midline, they used biceps and triceps to move their hands near the toy in front of them and 45° to the side of midline. After the transition, they used trapezius and deltoid to move the hand toward the toy and combinations of multiple muscles when their arms were high and extended near the toy. Thus, infants showed a dramatic change in which muscles worked together across the transition to reaching, even though their hands moved in similar spatial regions.

Human infants first learn to reach out in front of them and grasp objects they see at about 3 to 4 months of age. Before that time, young infants may sometimes grasp

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onto objects placed in their hands or bring their hands to their mouths and faces. Nevertheless, infants' early arm and hand activity is generally uncoordinated and not directed toward visible targets. How do infants acquire control of their arms to perform well-aimed reaches? This question is important for two reasons. First, the onset of reaching is a major developmental transition in which a new behavior—reaching—emerges from ongoing movements that are themselves not reaching. The mechanisms underlying such behavioral shifts are not well understood. Second, studying improvements in arm and hand control at a time when control is first being established may shed light on how the central nervous system coordinates the many joints and muscles involved in even simple reaching movements. In an unskilled motor system, the various processes that influence how joints and muscles are coordinated may develop at different rates. If this is the case, it may be possible to tease apart how changes in each component process contribute to the control and coordination of arm movements.

In a previous report, we described the kinematic and kinetic changes in infants' arm movements around the transition to reaching (Thelen et al., 1993). In this article, we focus on the neuromuscular mechanisms that underlie infants' improving control of their hands. This issue is central to the study of reaching because muscles generate the forces that propel the hand through space toward the desired object. Thus, through a detailed understanding of the patterns of muscle activity before and after infants learn to reach, we help clarify precisely how infants make this transition in manual skill. Moreover, by relating muscle patterns to the three-dimensional (3D) position of the hand, we address the more general issue of how multiple arm muscles become "spatially tuned" during the first year.

PATTERNS OF MUSCLE ACTIVITY IN INFANCY

Although this study is the first to detail neuromuscular changes as infants learn to reach, previous investigators have used electromyographic recording (EMG) to describe the muscle patterns infants use to move their limbs. Hadders-Algra and colleagues (Hadders-Algra, Nakae, Van Eykern, Klip-Van den Nieuwendijk, & Prechtl, 1993; Hadders-Algra, Van Eykern, Klip-Van den Nieuwendijk, & Prechtl, 1992) looked at the spontaneous wiggling, waving, and kicking movements typical of infants in their first months of life. Thelen (1985; Thelen & Fisher, 1982, 1983) and Forssberg (1985; Forssberg & Wallberg, 1980) described early spontaneous kicking and "stepping" movements. These investigators all found that early arm and leg movements, seemingly not directed toward an obvious goal, were characterized by high degrees of coactivation between antagonist muscles as well as synchronous activation of muscles in the same limb (see also Gatev, 1972). For instance, when young infants were either supine or held upright, their leg movements showed characteristic synchronous flexions and extensions of hip, knee, and ankle. EMG patterns were varied but highly coactive, usually showing a large coactive burst at the onset of flexion during which the four major leg muscles (quadriceps, hamstrings, tibialis anterior, and gastrocnemius) fired in unison. In addition, there was often a second coactive burst at ground contact when infants were stepping (Forssberg, 1985; Forssberg & Wallberg, 1980; Thelen & Fisher, 1982).

There is also general agreement that with age, the pervasive coactivity of the first few months decreases. For example, Hadders-Algra et al. (1992) saw examples of reciprocal activity of the deltoid and pectoral muscles during rapid arm movements ("swats") in the third month. Supine leg kicks also became less coactive: By 5 months of age, leg kicks showed an increase in reciprocal muscle patterns (Thelen, 1985). Finally, although EMG patterns are still variable and predominantly coactive when infants take their first supported and independent steps at about 8 months, reciprocal activation develops gradually during the weeks and months that follow (Berger, Horstmann, & Dietz, 1990; Berger, Quintern, & Dietz, 1985; Forssberg, 1985; Okamoto & Goto, 1985; Sutherland, Olshen, Cooper, & Woo, 1980).

In summary, previous work has demonstrated that as infants become more skilled in using their arms and legs, their initially coactive muscle patterns become organized into more specific sequences of activity involving fewer coactive muscles. There are two reasons this may be the case. First, it may be that in the immature neuromotor system, inhibitory networks are poorly developed such that activity in one muscle irradiates to nearby muscles. Indeed, in studies of limb and orofacial reflexes, investigators found widespread reflex irradiation, especially in the newborn period (Barlow, Finan, Bradford, & Andreatta, 1993; Myklebust, Gottlieb, & Agarwal, 1986).

However, muscle coactivity may be more than just neuromotor noise; it may also be adaptive in early skill learning. Muscle coactivity could serve to stiffen joints, making them more resistant to perturbation from both external forces—a bump on the shoulder as an infant reaches for a toy—and internal forces—forces created by the motion of other body segments that are poorly controlled. In addition, coactivity may simplify the control of complex movements by freezing out possible "degrees of freedom" (Bernstein, 1967). For instance, Berthier, Clifton, McCall, and Robin (1999) reported that infants largely used shoulder and torso rotation—without elbow flexions and extensions—to move their hands to toys in the first few weeks after reaching onset. These researchers proposed that infants simplified the reaching movement by freezing out the elbow joint via cocontraction of the muscles around this joint. Thus, within the general developmental trend from coactive to more differentiated muscle patterns, several processes may be occurring: both the decline of general muscle hyperactivity and the specific use of coactivity to help control unskilled movements.

QUANTIFYING NEUROMUSCULAR CHANGES AS INFANTS LEARN TO REACH

What neuromuscular patterns do infants use in the particular case of learning to reach? How do activation patterns during reaching differ from patterns during prereaching movements? Does the development of reaching conform to the more general trend of declining coactivity with increasing skill? To answer these questions, we used two new methods to characterize patterns of muscle activity as infants learned to reach: a multimuscle state analysis and an analysis of the relation between muscle states and the spatial position of the hand.

Conventionally, researchers analyze changes in muscle patterns over development by describing qualitative changes in the activity of individual muscles. However, to understand natural movements, single muscle activity may not be enough because most movements require the use of many muscles working in concert. Indeed, one of the foundational principles of the contemporary study of motor control is that every movement uses multiple muscles and every muscle can participate in many different movements (Bernstein, 1967). Thus, developmental changes may reside in the combinations of muscles used rather than whether any individual muscle is active during a movement or at a particular age.

In this study, we looked at changes in coactivity across multiple muscles by identifying coactivity states (see also Spencer & Thelen, 1999). To do this, we identified, for every sample of EMG data, a state vector that indicated whether each muscle was "on" or "off." This provided an operational definition of coactivity, indicating which muscle combination occurred at each moment in time. We then compared the states infants used at different ages relative to the different ways they moved their arms across the first year. Hadders-Algra, Brogren, and Forssberg (1996) used a related method to identify patterns of coactivity in postural muscles in sitting infants. Our state analysis differs from theirs in its improved temporal resolution: Hadders-Algra et al. (1996) identified only one predominant coactivity pattern per trial, whereas we quantified all coactivity patterns.

The second innovation in this study is that we related patterns of muscle state activity to the space through which infants moved their hands. This is particularly critical when studying infant reaching because recent studies of adult reaching movements have demonstrated that adults' muscle activity shifts relative to the space through which the hand moves (Flanders, 1991; Flanders, Pellegrini, & Soechting, 1994; Flanders & Soechting, 1990). In particular, Flanders and colleagues (Flanders, 1991; Flanders et al., 1994) reported that adults' arm muscles show maximal activation for movements of the hand in particular "preferred" directions, with decreasing activation as the direction of movement diverges from these directions. Although the preferred direction for a given muscle is related to its anatomical pulling direction, the spatial tuning of arm muscles is quite broad—muscles generally contribute to force generation across a broad array of movement directions (Buchanan, Almdale, Lewis, & Rymer, 1986; Flanders 1991; Flanders et al. 1994; Flanders & Soechting 1990). This has two important implications. First, muscle activation patterns for a given movement will depend on movement direction and the spatial orientation of the arm. Nevertheless, these spatial variables will not completely determine which muscles are active at any given time during a movement.

In this study, we used the location of the hand in the 3D task space as an index of the spatial orientation of the arm. Although this index is imperfect and, therefore, places limitations on the conclusions that can be reached from this study, it allowed us to examine which muscle combinations infants used when they moved their hands through different spatial regions. Spatially tuned muscle activity is an especially interesting issue in studies of infants' arm movements, because infants start reaching movements from a variety of starting positions and move through many different spatial regions en route to a target object (Berthier et al., 1999; Corbetta & Thelen, 1995; Thelen, Corbetta, & Spencer, 1996). Furthermore, early spontaneous movements are even less constrained because they do not end with contact at a particular location.

SPECIFIC GOAL

The goal of this study was to quantify how infants' muscle coactivity changed as they learned to reach and to relate these changes to the spatial regions through which they moved their hands. To accomplish this goal, we used the state analysis to quantify the muscle coactivity states infants used across the first year. Then, we examined which muscle states infants used when their hands were in different spatial regions. This is important because infants may use different muscles early versus late in the year for at least two reasons: (a) because they are moving their hands in very different regions of space, or (b) because they are moving through similar regions of space but using different muscle combinations. It is important to note that there is a key distinction between different regions of space and very different regions of space. By definition, infants move in different regions of space after they learn to reach—before the transition, they do not move their hands to the exact location of the toy; after the transition, they do. The critical question is whether infants move near the toy before the transition. If this is the case, then the broad spatial tuning of adults' muscles implies that it is possible that infants could use the same muscles across the first year, but do they?

METHOD

Participants

Four healthy, full-term infants participated in this study—1 girl (HR) and 3 boys (GS, NQ, and JA). Data collection began when infants were 3 weeks of age and continued until they were 52 weeks of age. Families were recruited either through local prenatal classes before the infants were born or through published birth announcements after the infants were born. All infants were from White, middle-class families. Parents were paid $15 for each observation session.

Apparatus

Infants were secured in a specially designed infant chair with a broad torso strap that allowed free arm movement yet provided secure postural support. The chair had a removable head support and could be slightly reclined to stabilize infants' heads during early data collection weeks. Position–time data of infants' arm movements were recorded at 150 Hz using a Watsmart motion analysis system (Northern Digital, Inc.). The four-camera Watsmart system records the two-dimensional (2D) position of infrared emitting diodes (IREDs) within a calibrated volume. One IRED was attached to the hand (third metacarpal), wrist, elbow, and shoulder joints of both arms of each infant; 3D coordinates were calculated from these 2D data using the direct linear transformation technique (see Horn, 1987). The average measurement error of the IREDs in the calibrated volume was less than 1 mm.

In addition to the position–time data, EMG data were collected using a Grass Model 7D polygraph. The EMG signals were sampled at 750 Hz and synchronized with the position–time data using a Watscope A/D data acquisition system (Northern Digital, Inc.). Pediatric silver–silver chloride surface electrodes were taped to the bellies of the following muscles on one side of the body: upper trapezius (Trap), anterior deltoid (Delt), biceps (Bi), and triceps (Tri). All trials of a reaching session were videotaped from the side and either a frontal or overhead view. Both views were simultaneously recorded using a split-screen generator with an added frame counter and synchronized with the EMG and position–time data.

Procedure

Each infant was observed weekly from 3 to 30 weeks and every 2 weeks thereafter until 52 weeks of age, for a total of 39 weeks. When the infants arrived at the laboratory each week, their shirts were removed and eight IRED markers were attached to their arms. Next, we determined which arm was more active when a toy was presented to the infants at midline. The four EMG electrodes were attached to this side of the body. Thus, during some weeks, we recorded the activity of muscles in the left arm; during other weeks, we recorded the activity of muscles in the right arm. After the IREDs and electrodes were in place, electrode resistances were checked. The infants were then secured in the infant chair.

Data were collected in a series of 14-sec trials. Trials began by triggering the Watsmart and EMG data collection systems. During most trials, toys were offered to the infant at midline, shoulder height, several seconds after the recording equipment was triggered. Toys were presented either by the parent, an experimenter, or by an apparatus with the toy attached to a dowel. These different toy presentation types were used to keep the infants engaged in the reaching task. Consequently, the order of presentation shifted depending on what each infant seemed most interested in. We conducted as many toy trials as possible before the infant became fussy. In general, 8 to 12 trials were conducted within each session. On some trials, we did not present a toy, but instead recorded infants' arm movements while they interacted with their parents (for further details, see Thelen et al., 1993). At the end of each session, anthropometric measurements of the infants' arm and body dimensions were recorded. Details of the anthropometric models and measurements are reported in Schneider, Zernicke, Ulrich, Jensen, and Thelen (1990) and Schneider and Zernicke (1992). Here, we used the measured distance between the shoulder and elbow to help subdivide the space through which infants moved their arms (see the following spatial analysis).

For this report, data were used from both the prereaching weeks (Pre) prior to the first week when infants began reaching out and touching toys on multiple trials, and the reaching weeks (Reach) following this transition in reaching skill. For all infants, the transition to reaching was quite sudden. The infants made one or two extended arm movements in the vicinity of the toy the week before the onset of reaching. One week later—the transition week—all infants repeatedly reached out and contacted toys. During the Pre period, data for both toy and interaction trials were analyzed. During the Reach period, only data from the trials during which a toy was presented and contact with that toy occurred were analyzed. Data from at least 47 trials across 5 weeks were included in the analyses of each period (see Table 1 for details on the number of trials and weeks analyzed per infant for each period). Data from several weeks were excluded due to noisy EMG channels. Overall, 6 weeks of data were excluded for this reason for GS, 7 weeks of data were excluded for NQ, 14 weeks of data were excluded for HR, and 3 weeks of data were excluded for JA. Data from several Reach weeks were also excluded because the infants did not reach with the arm to which the EMG electrodes were attached. Six weeks of data were excluded for this reason for GS, 5 weeks of data were excluded for NQ, and 4 weeks of data were excluded for both HR and JA.

Method of Analysis

Kinematic analyses. The data for each IRED marker and each coordinate (8 IREDs × 3 coordinates) were interpolated and filtered. Missing data were interpolated using a linear spline function. Cutoff frequencies for filtering were deter-

TABLE 1
Amount of Electromyographic and Kinematic Data Analyzed per Infant for Each Period

Infant	Period	*EMG* Trials	*EMG* Weeks	*Kinematics* Trials	*Kinematics* Weeks	*EMG + Kinematics* Trials	*EMG + Kinematics* Weeks
GS	Pre	47	5	75	11	34	5
	Reach	117	21	185	26	116	21
NQ	Pre	52	5	41	8	33	5
	Reach	85	18	183	29	32	18
HR	Pre	49	5	102	15	24	4
	Reach	95	15	156	21	95	15
JA	Pre	108	12	82	14	60	12
	Reach	75	17	136	21	75	17

Note. EMG = electromyographic recording.

mined through spectral analysis. A spectral density profile was constructed for each IRED and coordinate, resulting in an integral for each of the 24 curves. The cutoff frequency used for each dimension was 97% of the integral's value. After these cutoff frequencies were computed, each coordinate for each IRED was smoothed individually using a fourth-order Butterworth filter (for further details, see Thelen et al., 1993).

Next, the videotapes from each session were coded to identify segments of the 14-sec trials that were "behaviorally interesting" (for a detailed review of this segmentation process, see Thelen et al., 1993). Segments of data were considered behaviorally interesting if they contained either spontaneous activity (e.g., rhythmical movements) or goal-directed movements (e.g., reaching to objects or hand-to-mouth behaviors). These segments were then further constrained by the following IRED visibility criteria: (a) IREDs had to be visible for at least 70% of the behaviorally interesting segment, and (b) gaps of missing data had to be smaller than 50 samples (one third of the sampling frequency). All analyses of hand kinematics were based on either the hand (third metacarpal) or wrist IRED, depending on which IRED had better visibility.

Spatial analysis. To investigate where infants moved their hands during the first year, the 3D space around the infants' arms was divided into 11 mutually exclusive and exhaustive regions (see Figure 1). The first two regions (sphere-lateral, sphere-midline) were located within a sphere centered at the shoulder with a radius equal to the measured distance between the shoulder and elbow. This sphere was divided in half by a vertical front-to-back plane running through the shoulder joint perpendicular to the line connecting the two shoulders. Thus, one half of this sphere was away from the body (lateral), whereas the other half was toward the body midline. Two vertical planes defined side, 45°, and front areas of the 3D space: the vertical plane through the shoulder joint described previously and a plane through the shoulder rotated 45°. These regions were further subdivided by two horizontal planes, creating low, mid, and high regions. One horizontal plane ran through the shoulder, and a second was located below the shoulder at a distance equal to the shoulder–elbow distance.

EMG data analysis. The EMG data were filtered using a band-pass filter with cutoff frequencies set at 75 Hz and 300 Hz. The band-pass filter eliminated small amounts of low-frequency noise present in some of the channels on a few weeks. After band-pass filtering, the data were rectified. Finally, boxcar averaging with a window size of seven samples was used to eliminate the high-frequency components added by rectification.

EMG analyses commonly used to study adult movements tend to examine both the timing and amplitude (intensity) of muscle activity. Unfortunately, the fat-to-muscle ratio around each arm muscle changes considerably during the first year, differentially affecting EMG amplitudes. In addition, as infants' arms grow, it is very difficult to position electrodes consistently over the bellies of different arm muscles. This adds to amplitude variability. Due to these difficulties, we did not analyze changes in EMG amplitudes across the first year. Instead, all EMG analyses reported here were based on an on–off transformation of the EMG data. To transform the data, we used a 50-msec moving window shifted sample by sam-

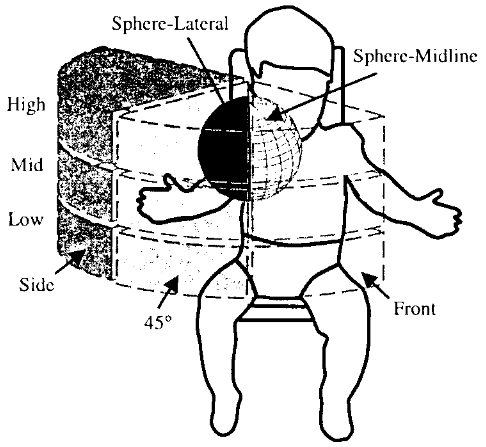

FIGURE 1 Illustration of the 11 mutually exclusive and exhaustive regions used for the spatial analysis of the hand kinematics. The high, mid, and low side regions are shown in dark gray; the 45° regions are shown in gray; and the front regions are shown in light gray. The inner sphere centered at the shoulder was divided into two halves: a lateral half and a midline half.

ple to scan through the EMG signals. If an EMG signal was, on average, above a signal-to-noise threshold within a given window, then the central sample of that window was considered on.

In adult research, the signal-to-noise threshold is generally identified visually using an interactive graphics program (e.g., Walter, 1984). Although this approach may be effective with adult EMG signals, it would be subjective with infant EMG due to the many sources of amplitude variability over development. Thus, we developed a set of criteria for determining the signal-to-noise threshold that could be systematically applied to EMG data across the first year.

During a typical 14-sec trial, infants exhibited bouts of activity and inactivity. Thus, the EMG signal alternated between high-amplitude bursts and low-amplitude baseline activity. Due to the length of a trial, the low-amplitude baseline activity generally dominated. Thus, the modal amplitude on any given trial was clearly in the noise range, whereas amplitudes much greater than the mode were clearly in the signal range. The goal, then, was to select some amplitude value greater than the modal amplitude that would distinguish signal from noise. To do this, we computed a frequency histogram (interval width = 5 mV) of the amplitudes for each EMG signal across each 14-sec trial and normalized the histograms to the modal amplitude (amplitude/modal amplitude). A sample histogram for one EMG signal from one trial is shown in Figure 2. The first amplitude greater than the mode that occurred with a frequency less than 0.15 of the modal frequency (see line labeled "Cutoff Prop #1" in Figure 2) was selected as the trial threshold. The trial threshold for the histogram shown in Figure 2 is at the intersection of cutoff line #1 and the histogram (see line labeled "Threshold Amplitude #1" in Figure 2). The cutoff value of 0.15 was selected via visual inspection after applying this method to EMG signals from different infants collected at different points across the first year. To compute the signal-to-noise threshold for each muscle, the trial thresholds for each EMG signal were averaged across the trials of a data collection session. The trial thresholds were averaged because the goal of this technique was to determine the level of noise in the recording equipment, which we assumed to be relatively stable across trials.

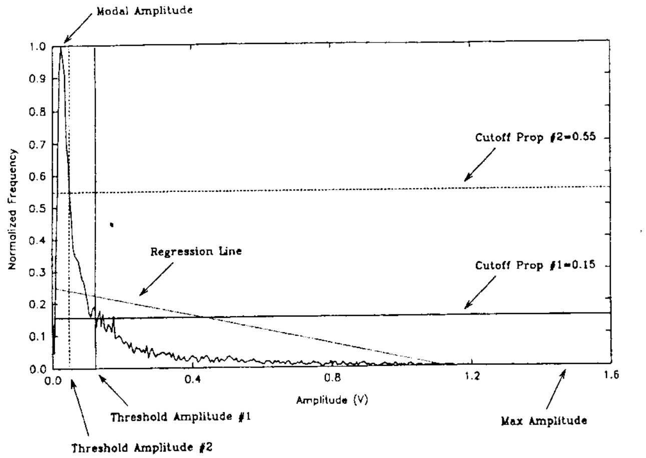

FIGURE 2 Example histogram of EMG amplitudes for one muscle from one 14-sec trial. Histograms were normalized to the modal amplitude. On most trials, the threshold amplitude corresponding to the first cutoff proportion was used. If the slope of the regression line was greater than –0.5, however, the second threshold amplitude was used.

This technique successfully differentiated on–off activity when compared to the judgments made by an independent experimenter with several years of experience working with EMG signals. This person judged the on–off activity of twenty-eight 2-sec EMG traces, seven traces from each muscle. The computer and human rater agreed on 89% of the 1,120 50-msec intervals judged, with systematic error on the part of the computer in a conservative direction (less activity).

Although the signal-to-noise algorithm performed well on most trials, on trials with very frequent high-amplitude activity, the computer technique was too conservative. Thus, on these trials, we increased the 0.15 criterion previously described to 0.55 (see line labeled "Cutoff Prop #2" in Figure 2). Once again, the 0.55 criterion was selected based on visual inspection. To identify high-activity trials, a linear regression was computed on the portion of the amplitude histogram between the modal amplitude and the maximal amplitude (see regression line in Figure 2). The slope of this regression line will approach zero (become less negative) as the amount of high-amplitude activity in an EMG signal increases. A slope of –0.5 was selected as the high-activity cutoff value—high-activity trials had a slope greater than –0.5.

During some weeks, the infants spent several trials completely inactive. This tended to bias the signal-to-noise threshold toward lower amplitudes and, in some cases, pulled the threshold down to an unacceptably low level. To counteract this effect, a low threshold criterion was used: The threshold for an EMG signal was set to 75 mV if the computed threshold went below this level for any data collection session. We selected the 75 mV criterion based on visual inspection of trials during which the infants remained completely inactive. Although four criteria were used in this study to identify on–off EMG activity, subsequent analyses of EMG signals from a study of infant locomotion only required the first criterion to adequately detect signal from noise (Ulrich, Angulo-Kinzler, Chapman, & Thelen, 1996).

To evaluate the effectiveness of the signal-to-noise threshold criteria, one of us judged via visual inspection if the threshold computed for each data collection session missed segments of muscle activity for each EMG channel of each trial analyzed. One of three judgments was made: (a) A burst of EMG activity was clearly missed, (b) a portion of an EMG burst may have been missed, or (c) no EMG activity was missed. Trials with one or more EMG channels with "clearly missed" activity were excluded from further analyses. This occurred on 5 trials for GS, 3 trials for NQ, 13 trials for HR, and 10 trials for JA. On average, 7.9% of the Pre EMG channels and 4.6% of the Reach EMG channels were judged to be in Category 2. Thus, based on visual inspection, the threshold algorithm successfully identified all EMG bursts on more than 90% of the trials across the first year.

Unlike adults, infants reach from a variety of starting positions and often initiate reaches from ongoing movement. Thus, to identify the start of on activity for each reach, a two-step process was used. First, the kinematic onset of each reach was identified using a combination of video coding, hand displacement, and hand speed (for details, see Corbetta & Thelen, 1995). Next, a computer program selected the first segment of on activity lasting more than 50 msec after the kinematic onset. The duration of on activity was summed across small segments of activity if the period of inactivity between segments was less than 50 msec. The user had the option to either accept the computer's choice or select a different segment that exceeded the onset duration criterion. On average, a new EMG onset was selected for 2.6% of the reaches across the first year.

Finally, to examine patterns of muscle coactivity, we used a muscle state analysis (see Spencer & Thelen, 1999; for a similar method, see Cocatre-Zilgien & Delcomyn, 1993). This analysis technique assigns a state vector to each EMG sample consisting of a 0 (off) or 1 (on) for each muscle. Data from four muscles were recorded in this study; thus, there were 2^4 or 16 possible muscle states ranging from [0000]—no muscles active—to [1111]—all muscles active. For example, if the Trap and Delt were both on for a particular EMG sample and the Bi and Tri were not, the state vector would be [1100]. After transforming the on–off data in this manner, we analyzed the frequency of occurrence of each state and the timing and ordering of state sequences, revealing which muscles worked together and when they worked together during the first year.

RESULTS

Spatial Analysis of Hand Kinematics

The transition to reaching occurred at different ages for the four infants studied: GS, 15 weeks; NQ, 12 weeks; HR, 20 weeks; JA, 20 weeks. Prior to these transition weeks (Pre period), infants were unable to reach out and contact the toy. From the transition week forward (Reach period), infants could reach out and touch, grasp, and later manipulate the toy. Our first question focused on this transformation in reaching skill: Did infants fail to reach for the toy during the Pre period because they were unable to generate the forces needed to move their hands into the regions of space in which the toy was located?

To address this question, we conducted a spatial analysis to determine where infants were moving their hands during the Pre and Reach periods. We computed the mean proportion of time that infants' hands were in each of 11 spatial regions. For this analysis, we included all available kinematic data from the Pre period (from both the right and left hands) and kinematics from the reaching segments of the Reach period (see Table 1). As shown in Figure 3, infants generally spent a comparable proportion of time in each spatial region across the two periods. This was true even in the 2 regions in which the toy was most commonly positioned. The toy was presented at midline, shoulder height (see the Method section). At this position, the toy would be in 1 of 2 regions—front mid or front high. Infants spent a comparable amount of time in both spatial regions before and after they learned to reach. Nevertheless, there were some significant differences across periods. A two-way repeated measures analysis of variance (ANOVA) with period and region as within-subject factors revealed a significant main effect of region, $F(10, 30) = 14.69, p < .05$, and a significant Period × Region interaction, $F(10, 30) = 12.47, p < .05$. Post hoc Tukey honestly significant difference (HSD) tests ($\alpha = .05$) showed that the interaction was due to a significant decrease in the proportion of time spent in the front low region during the Reach period and significant increases in the amount of time spent in the 45° low and 45° mid regions (see Figure 3).

These data demonstrate that infants moved their hands within all areas of the 3D space during the Pre period, even within the regions in which the toy was located. Thus, although they did not contact the toy, the infants did get their hands near the toy before the transition to reaching. Learning to reach, therefore, is not simply a matter of getting the hand in the vicinity of the toy.

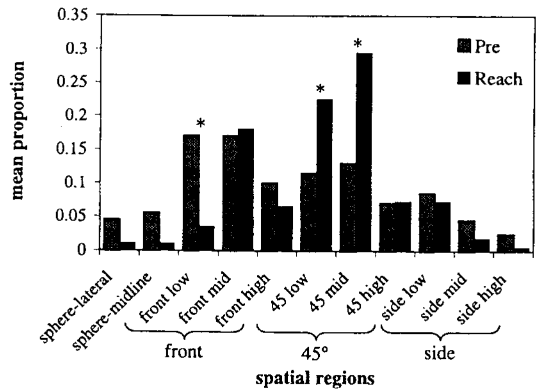

FIGURE 3 Mean proportion of time infants' hands were in each of 11 spatial regions during the Pre and Reach periods. The regions are labeled as in Figure 1. Asterisks indicate significant differences in mean proportions across the Pre and Reach periods ($p < .05$).

Spatial Analysis of Muscle State Activity

Next, we examined which muscle states infants used during the Pre and Reach periods. We calculated the proportion of time each muscle state occurred during each data collection session. Then we calculated the mean proportion of time each state occurred across the Pre and Reach weeks for each infant. The zero state—[0000]—was excluded because there was a disproportionate amount of muscle inactivity during the Pre and Reach periods due to the differential amount of movement sampled: 14-sec trials in the Pre period and about 2-sec reaches in the Reach period.

The mean proportions across the Pre and Reach periods for nine states are shown in Figure 4. Data from six states—Bi/Trap, Tri/Trap, Bi/Tri/Trap, Bi/Tri/Delt, Bi/Delt/Trap, and Bi/Tri/Delt/Trap—were not included in this figure because they occurred infrequently across the first year. Excluded states had a mean proportion across the 4 infants ≤ 0.05 and a maximum proportion for any one infant < 0.10. As can be seen in Figure 4, three states that were frequent during the Pre period—Tri, Bi, and Bi/Tri—decreased during the Reach period. By contrast, five states that were infrequent during the Pre period—Delt, Delt/Trap, Delt/Tri, Delt/Bi, and Delt/Trap/Tri—increased during the Reach period. These data indicate that infants used a lot of triceps and biceps activity in the absence of deltoid and trapezius activity early in the first year. However, once they began reaching for toys, infants relied more heavily on patterns of deltoid-related muscle activity.

The state data were analyzed using a two-way repeated measures ANOVA with state and period as within-subject factors. There was a significant main effect of state, $F(14, 42) = 11.52, p < .05$, and a significant State × Period interaction, $F(14, 42) = 13.37, p < .05$. Post hoc analyses revealed that the Tri and Bi states decreased significantly across the Pre and Reach periods, whereas the Delt and Delt/Trap states increased significantly across these periods (see Figure 4).

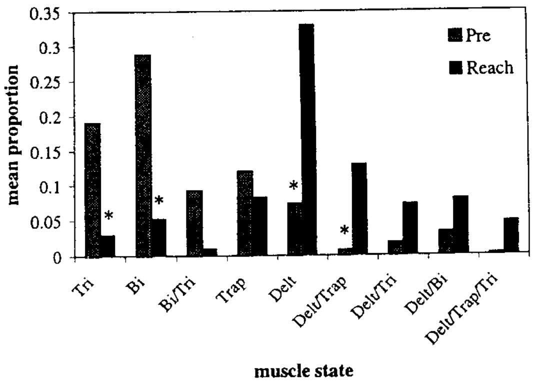

FIGURE 4 Mean proportion of time nine muscle states occurred relative to the total amount of nonzero state activity for the Pre and Reach periods. Asterisks indicate significant differences in mean proportions across the two periods ($p < .05$).

The next question was how these changes in muscle state activity related to where infants were moving their hands during the Pre and Reach periods. To examine this issue, we computed the proportion of time each state occurred in each spatial region for each data collection session. Then these proportions were averaged across the Pre and Reach weeks. The data in each region were analyzed using two-way repeated measures ANOVAs with state and period as within-subject factors. There were significant state main effects in all spatial regions, and significant State × Period interactions in the mid and high subsections of the front regions, across all 45° regions, and in the mid and low subsections of the side region—for all, $Fs(14, 42) > 2.30, ps < .05$.

Post hoc analyses of the State × Period interactions showed significant changes in Pre versus Reach for the same four states that changed significantly in the overall state analysis described previously: Tri, Bi, Delt, and Delt/Trap. The proportion of time these four states occurred across the side (45°) and front regions is shown in Figure 5. As can be seen in this figure, there was a significant decrease in Bi state activity during the Reach period across the mid and high subsections of the 45° and frontal regions. Delt state activity increased during the Reach period in both the mid and low subsections of the 45° region, whereas the significant changes in Delt/Trap and Tri were confined to one spatial region.

Spatial Analysis of Deltoid-Related State Activity

In the state spatial analysis, there were significant increases in Delt or Delt/Trap state activity in two spatial regions. This is consistent with recent data from Berthier et al. (1999) that show that infants use primarily shoulder rotations when they first learn to reach. Given the congruous results across these studies, we conducted a follow-up analysis to investigate the activity of the deltoid muscle in more detail. Visual inspection of the data in Figure 4 shows that the deltoid muscle was active in conjunction with several other muscles. Sometimes, the deltoid muscle was active alone (Delt) or with the trapezius (Delt/Trap). Other times, the deltoid was active with both the trapezius and the triceps (Delt/Trap/Tri). Consequently, there may have been a more general increase in the activation of the deltoid muscle than what was detected in the previous analysis. More specific, it is possible that if all deltoid activity was pooled across states, we would find a significant increase in the activity of this muscle across more spatial regions than just the mid and low subsections of the 45° region. Thus, we conducted a follow-up analysis in which the proportion of all deltoid-related state activity in each spatial region was summed.

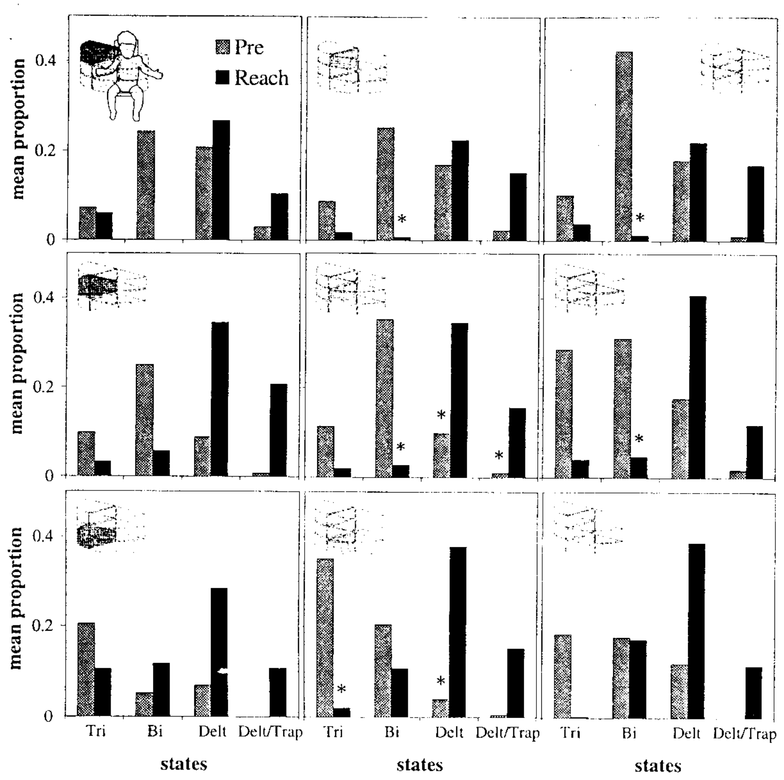

FIGURE 5 Mean proportion of time four muscle states occurred within the side (left column), 45° (center column), and front (right column) regions across the Pre and Reach periods. The inset in each graph indicates from which spatial region the data originate (see Figure 1). Asterisks indicate significant differences in mean proportions across the Pre and Reach periods ($p < .05$).

Specifically, for each data collection session, we summed the proportion of time that the following states occurred: Delt, Delt/Trap, Delt/Tri, Delt/Bi, Delt/Trap/Tri, Delt/Trap/Bi, Delt/Tri/Bi, and Delt/Trap/Tri/Bi. We then averaged these proportions across the Pre and Reach weeks.

Figure 6 shows the mean proportion of time all deltoid-related states occurred across the side, 45°, and frontal regions. As in the state spatial analysis, there was an increase in deltoid-related state activity during the Reach period. To analyze these data in more detail, we conducted a paired t test within each spatial region, comparing deltoid-related state activity across periods. Figure 6 shows the results of these analyses: There was a significant increase in deltoid-related state activity across seven spatial regions, all $ts\ (3) < -3.25, ps < .05$. Thus, there was an increase in the activity of the deltoid muscle during the Reach period above and beyond the increase in Delt and Delt/Trap state activity reported previously.

Spatial Analysis of Muscle Coactivity

In the state spatial analysis, there was only one significant change in a state that involved the coactivity of multiple muscles (Delt/Trap). This is rather surprising

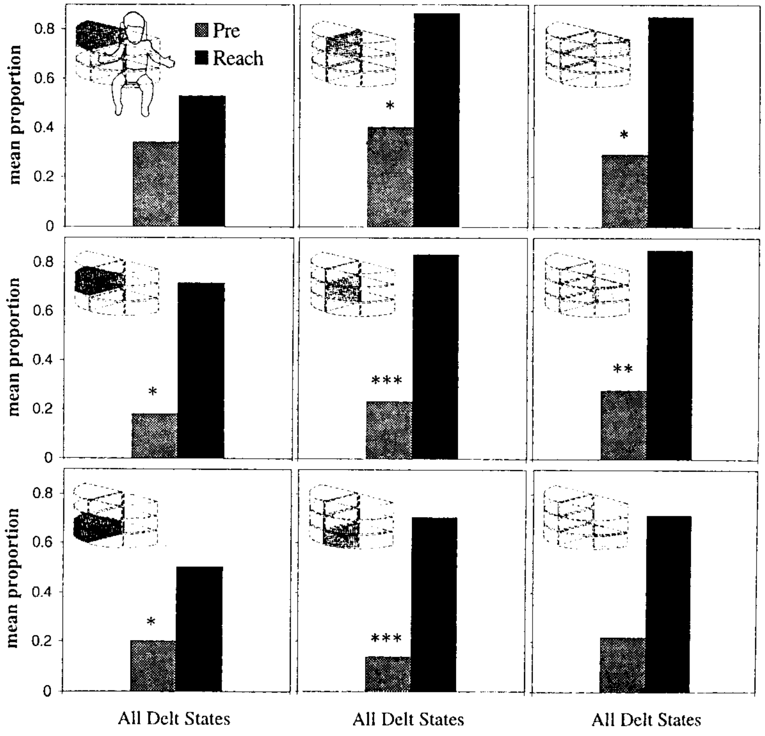

FIGURE 6 Mean proportion of time deltoid-related state activity occurred within the side (left column), 45° (center column), and front (right column) regions across the Pre and Reach periods. The inset in each graph indicates from which spatial region the data originate. Asterisks indicate significant differences in mean proportions across the Pre and Reach periods (*$p < .05$; **$p < .01$; ***$p < .005$).

given that data from other studies of neuromuscular development suggest that early skills are associated with a high degree of coactivity. To investigate muscle coactivity in more detail, we conducted a follow-up analysis in which the proportion of all two-muscle and three- or four-muscle coactivity states in each spatial region was summed. Specifically, for each data collection session, we summed the proportion of time that all two-muscle states occurred (Bi/Tri, Delt/Trap, Delt/Tri, Delt/Bi, Trap/Tri, and Trap/Bi) and the proportion of time that all three- or four-muscle states occurred (Delt/Trap/Tri, Delt/Trap/Bi, Delt/Tri/Bi, Trap/Tri/Bi, and Delt/Trap/Tri/Bi). Then, these proportions were averaged across the Pre and Reach weeks.

There was an increase during the Reach period in both two-muscle and three- or four-muscle coactivity across the mid and high subsections of the front and 45° regions. These data are shown in Figure 7. Across these four regions, single muscle activity dominated during the Pre period. During the Reach period, there was a decrease in single muscle activity and an increase in coactivity. This was particularly apparent in the high subsections in which there was a roughly equal proportion of one-, two-, and three- or four-muscle coactivity after the transition to reaching. The coactivity data in each spatial region were analyzed using a two-way ANOVA with coactivity type and region as within-subjects factors. Of particular importance was the pattern of Coactivity × Period interactions across the spatial regions. There were significant interactions across the mid and high subsections of the front and 45° regions, all $Fs(2, 6) > 8.5$, $ps < .05$. Post hoc analyses indicated that the proportion of single muscle activity decreased significantly in the Reach period across all four spatial regions shown in Figure 7. In addition, there were significant increases in multimuscle coactivity in both subsections of the 45° region and in the high subsection of the front region.

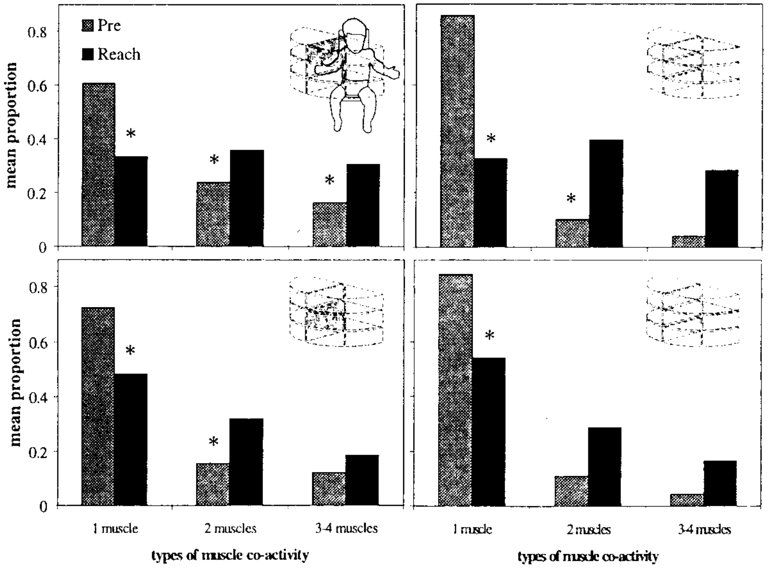

FIGURE 7 Mean proportion of time three different types of muscle coactivity occurred within the 45° (left column) and front (right column) regions across the Pre and Reach periods. The inset in each graph indicates from which spatial region the data originate.

These results indicate that infants did increase muscle coactivity during the Reach period when their hands were extended from the body in the mid and high regions. Given that the toy was often located in one of these regions—the high frontal region—these data may indicate that infants used multimuscle coactivity to help move the hand toward the toy from the mid and high 45° regions and then stabilize the hand at the toy location.

Week-to-Week Changes in Muscle State Activity

The results from the muscle state analyses demonstrate that infants used different muscle combinations before versus after they learned to reach, even though they moved their hands through similar regions of space. Nevertheless, because these analyses examined changes in state activity averaged across several Pre and Reach weeks, it is unclear how tightly linked the state changes were to the onset of reaching.

To investigate this issue, we returned our focus to the states that met the inclusion criteria (see Figure 4). Our goal was to examine whether changes in the proportion of time these states occurred was synchronized with the transition week (i.e., was there a consistently high proportion of some states leading up to the transition, a consistently low proportion of other states leading up to the transition, and an abrupt switch in these proportions at the transition week). Based on visual inspection of the data in Figure 4, three of the included states decreased across the transition to reaching,—Bi, Tri, and Bi/Tri—whereas five states increased—Delt, Delt/Trap, Delt/Tri, Delt/Bi, and Delt/Trap/Tri. Thus, for each infant, we identified the first 5 weeks of available data immediately before the transition and the first 15 weeks of available data from the transition week onward. Next, we summed the proportion of Bi and Tri state activity (Bi, Tri, Bi/Tri) and deltoid-related state activity (Delt, Delt/Trap, Delt/Tri, Delt/Bi, Delt/Trap/Tri) for each selected week and averaged these proportions across the four infants. These data are shown in Figure 8.

As can be seen in Figure 8, the proportion of Bi and Tri states decreased at the transition week, and the proportion of deltoid-related states increased at the transition week. Each type of state activity was analyzed using a one-way ANOVA with weeks as a within-subjects factor. There was a significant decrease in Bi and Tri

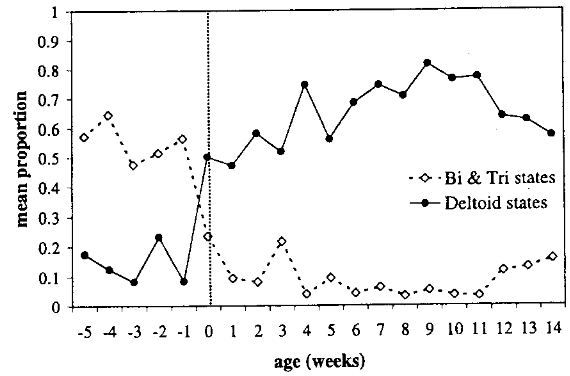

FIGURE 8 Week-by-week changes in the mean proportion of time three bicep and tricep states occurred (dashed line) and five deltoid-related states occurred (solid line). Week 0 is the transition week. Negative weeks indicate the number of weeks before the transition, and positive weeks indicate the number of weeks after the transition.

state activity across the 15 weeks examined, $F(19, 57) = 7.77, p < .05$, and a significant increase in deltoid-related state activity, $F(19, 57) = 5.19, p < .05$. It is important to note that the abrupt transition shown in Figure 8 was linked to the onset of reaching and not age per se. Recall that the four infants reached at different weeks during the first year: 15 weeks, 12 weeks, 20 weeks, and 20 weeks. The transition in state activity shown in Figure 8 was not abrupt when we aligned the data by age. Thus, it appears that changes in muscle state activity were well synchronized with the onset of reaching. This conclusion must remain tentative, however, because three of the infants had no usable data for either 1 week or 2 weeks immediately before or after the transition.

DISCUSSION

Before infants can perform accurate goal-directed reaches, they often hold their arms flexed toward their bodies, put their hands in their mouths or on their faces, grasp their clothes or blankets, or wave their arms in a more extended manner. After they successfully reach for distal objects, they may continue these earlier movements, but they can also reach out and grasp objects. Our analysis of infants' movements through several body-centered spatial regions revealed that this behavioral transition was not simply a matter of being able to move into new regions of personal space. Indeed, infants moved their hands within all spatial regions across both periods, and in approximately the same proportions in most of the delineated areas. In principle, therefore, the onset of reaching need not have required a fundamental change in muscle coactivity patterns. What we found, however, was a shift of the muscle patterns infants used that coincided with the week of reach onset. In the Pre period, infants used predominantly Bi and Tri state activity. After reaching onset, these states were less frequent, whereas Delt and Delt/Trap state activity increased in frequency.

At a more detailed level of analysis, we discovered that the shifts in infants' muscle patterns were specific to movements generated when the hand was in particular spatial regions. There was a significant decrease in Bi state activity across the transition to reaching when the hand was in the mid and high subsections of the front and 45° regions. This change can be mapped onto behavioral observations. Consider first what type of movement would result from the activation of the biceps muscle alone when the hand was in these four regions. Although the location of the hand provides incomplete information about the configuration of the arm, Figure 9a shows a sketch illustrating a likely possibility. Activation of the biceps alone when the hand was in the front and 45° regions would rotate the elbow and shoulder, bringing the hand toward the mouth. It is important to note that such biceps activity could move the hand near the toy. However, without concurrent stabilizing forces produced by the coactivity of other muscles, the end result would be to move the hand near and then past the toy. Consistent with Figure 9a, all four infants made frequent hand-to-face and hand-to-mouth actions when gazing at the toy, but before they could reach and grasp it (Thelen, in press; for related observations, see Lew & Butterworth, 1997; Rochat, 1993).

We also found a significant decrease in the Tri state when the hand was in the 45° low spatial region. Figure 9b shows a sketch of what effect such state activity may have on the motion of the hand: Tri state activity would likely extend the hand

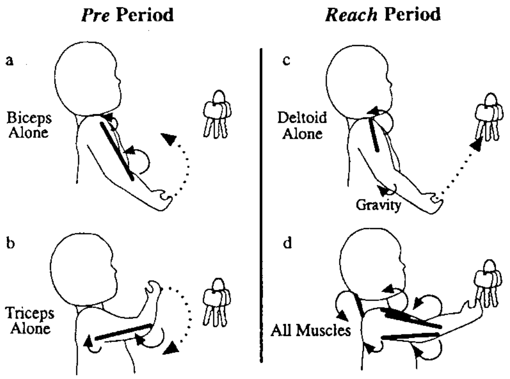

FIGURE 9 Schematic summary of muscle state results from the Pre and Reach periods.

away from the toy and mouth. Thus, once again, an early pattern of muscle activity was appropriate for a very common prereaching action—bringing the hands away from the face and mouth.

The week infants first contacted the toy, they began using deltoid-related muscle combinations to both lift the arm and stabilize the hand near the toy. Recall that during the Reach period, there were significant increases in Delt or Delt/Trap activation in two spatial regions—the low and mid subsections of the 45° region. What may be the effect of using these Delt states within the 45° region? Data from Flanders (1991) showed that the anterior deltoid is a primary agonist for movements from a side or 45° low position to front mid and high positions in adult reaching movements. Based on these data, Figure 9c shows a sketch illustrating how activation of the deltoid from the 45° low and mid regions would likely move the hand: This state in combination with gravitational effects would move the hand toward the toy. Thus, at the transition to reaching, infants appear to have learned an effective way to move their hands toward the toy—start from a 45° low or mid region and use the deltoid muscle to get the hand moving in the right direction. Consistent with this interpretation, infants' hands spent proportionally more time in these two spatial regions during the Reach period.

However, a subsequent analysis of all deltoid-related states revealed that the significant increase in the activity of the deltoid muscle was not confined to the 45° regions. Instead, there were significant increases in deltoid-related activity across side, 45°, and frontal regions. Thus, infants may have learned the specific pattern of using deltoid activation alone in the 45° low and mid regions, and the more general pattern of using deltoid activation in conjunction with other muscles when moving toward the toy from the side and frontal regions.

A final spatial analysis added an important element to the view of what infants learned at the transition to reaching. As infants approached the toy from the mid and high 45° and front regions, they showed a general increase in two- and three- or four-muscle coactivity. What would be the function of such coactivity? As shown in Figure 9d, this may have helped infants achieve a stable, extended arm posture near the toy in the face of gravitational torque and muscle and reactive torques generated during the active braking of arm extension (for related results, see Schneider, Zernicke, Schmidt, & Hart, 1989; Spencer & Thelen, 1999). The increase in muscle coactivity after the transition to reaching is consistent with other studies of neuromuscular development. It is important to note, however, that the infants did not show a general increase in the amount of coactivity across all regions of the work space. Instead, the increase in coactivity was specific to when their hands were extended toward the toy in the front and 45° regions. Thus, coactivity in early reaching is not a general process. It was specifically used to meet the demands of reaching for toys at midline.

The deltoid-related and muscle coactivity changes in this article may shed new light on results reported by Berthier et al. (1999). These researchers found that infants used primarily shoulder and torso rotations to move their hands toward toys in the first few weeks after reaching onset. This is consistent with the increase in deltoid-related activity during the Reach period reported in this article. These researchers also proposed that infants cocontracted the muscles around the elbow joint to prevent flexions and extensions of the elbow. The data suggest that when infants move from a 45° low or mid region, they use gravity—not active cocontraction—to maintain arm extension. In other spatial regions, however, infants do cocontract multiple muscles, particularly when their hands move within the high subsections of the front and 45° regions. We did not directly examine if this cocontraction prevented flexions and extensions of the elbow joint, although it is certainly possible this was the case.

To summarize the results sketched in Figure 9, data from our spatial analyses revealed systematic differences between infants' movements during the Pre and Reach periods. Early in the first year, infants moved through many spatial regions, including regions in which the toy was located. However, many of these early movements involved the activation of Bi and Tri alone. Such muscle state activity likely served to flex and extend the elbow and shoulder joints, moving the hand toward or away from the mouth. After infants first learned to reach for toys at midline, these early patterns of muscle activity were replaced by deltoid-related states. These states likely served to move the hand toward the toy. Finally, infants increased the amount of muscle coactivity when their hands were near the spatial regions in which the toy was located. Thus, across the transition to reaching, infants learned which muscles served to get their hands moving toward the toy and which muscle combinations served to keep their hands near the toy's location.

In a final analysis, we asked if changes in muscle state activity were temporally linked to the transition to reaching. This was indeed the case. When we looked at week-to-week changes in Bi and Tri state activity and deltoid-related state activity, we saw a change in the frequency of these state types synchronized with the transition week. Thus, the deltoid–coactivity strategy appears to emerge at, or very near, the transition week. These data are consistent with behavioral data collected during week-to-week play sessions with the same four infants (Spencer, Vereijken, Diedrich, & Thelen, 2000). In this study, infants were placed in different postures each week—supine and in a slightly reclined infant seat—and videotaped as they interacted with their parents. Behavioral coding of these videotapes revealed that all infants could consistently control their heads and upper torsos and extend their arms toward toys a week or two before the transition week (for related results see Butterworth & Hicks, 1977; Rochat, 1992). Head and upper torso control would require reliable activation of the Trap, whereas arm extensions away from the body would likely use activation of the Delt. Thus, data across these different observation periods reveal a consistent pattern of results closely synchronized with the transition.

Although the summary of results sketched in Figure 9 is consistent with data from our naturalistic play sessions, these results need further elaboration. It is not clear, for instance, how the deltoid–coactivity pattern developed. One possibility is that infants' own attempts to grab the toy resulted in a variety of possible muscle combinations during the Pre period and those combinations that worked (i.e., that moved the hand close to the toy) were selectively strengthened (Edelman, 1987, 1993; Sporns & Edelman, 1993; Thelen & Smith, 1995). If this is the case, then successful reaching should be dependent on infants' amount of experience moving the arms and attempting to contact the target. Previously reported data from these four infants indirectly support this possibility: The two highly active infants, who generated more and faster arm movements, first successfully reached 5 to 8 weeks earlier than the two less active infants (Thelen et al., 1993). However, the rather sudden change in EMG patterns at the transition week suggests that selection may be working on a faster time scale than 1 week. Thus, recording changes in infants' muscle activity day by day just prior to the transition may reveal the process that leads to the deltoid–coactivity pattern. An alternative possibility is that deltoid activity emerges through infants' other related improving skills such as head and upper torso control. As we mentioned previously, there is a close correspondence between the onset of reaching and these postural milestones. Finally, our data do suggest that the reaching transition involved more than just suppression of early reflex irradiation. Rather, we saw that muscles were "tuned" to the spatial and force demands of the task.

Conclusions from the trends sketched in Figure 9 must be tentative, however, due to several limitations of this study. First, we were missing data from several weeks before and after the transition to reaching for all of the infants. Thus, it is possible that changes in muscle state activity were more gradual than we were able to detect. More important, however, due to data limitations we were not able to examine changes in muscle activity relative to two parameters closely related to the neuromuscular control of reaching: movement direction and arm configuration (see, e.g., Buneo, Soechting, & Flanders, 1994; Caminiti, Johnson, Galli, Ferraina, & Burnod, 1991; Flanders, 1991; Georgopoulos, Kettner, & Schwartz, 1988). Although we assumed that the location of the hand in space would be related to these two parameters, a more explicit account of the mapping between muscle state activity and these parameters may reveal more subtle changes in the spatial tuning of muscles across the first year.

Despite these limitations, the muscle state analysis provided a coherent picture of changes in muscle coactivity as infants learned to reach. This method successfully moved beyond the analysis of individual muscle activity and allowed us to measure changes in the specific muscle patterns infants used and relate these changes to the demands of the movement task. To examine how robust this method is, we are currently using the state analysis to quantify changes in infants' muscle activity as they learn to walk (Angulo-Kinzler, Ulrich, Chapman, & Thelen, 2000; Ulrich et al., 1996).

Finally, it is important to note that our results differ from previous descriptions of early muscle activity in that global coactivity was not the dominant muscle pattern during the Pre period. Rather, the Pre period was dominated by single muscle activity—Bi, Tri, and Trap—and the Bi/Tri state. There are several possible reasons for these differences. First, we used a task that minimized the postural requirements of upright reaching. Infants were given upper body support by a torso strap and their heads were stabilized by pads on both sides. Studies of postural and balance control in infancy and studies of locomotion demonstrate that when infants need to maintain a stable base from which to move, coactivity is common (e.g., Berger et al., 1990; Berger et al., 1985; Ulrich et al., 1996; Woollacott & Sveistrup, 1992). By reducing such postural requirements, we may have reduced the need for coactivity. A second factor that may account for infants' infrequent use of coactivity during the Pre period is the amount and variety of spontaneous movement sampled. Trials were 14 sec long and included a diversity of movements: fidgeting, waving, banging, hand-to-mouth movements, and so on. It is possible that a more detailed analysis may reveal that coactivity is specific to particular types of movement early in the first year.

The data presented here illustrate how infants modified their muscle activity while learning to reach for toys at midline. Despite the variability between and within infants in their prereaching movements and in their reaches, a consistent pattern of changes emerged: a dramatic increase in the activation of the deltoid muscle by itself and in combination with other muscles, and the specific use of muscle coactivity to stabilize the hand near the toy. The mechanisms generating these shifts in muscle patterns are yet unknown. However our new methods can facilitate more detailed studies of this important skill transition.

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