RESEARCH ARTICLE

Jürgen Konczak · Maike Borutta · Johannes Dichgans

The development of goal-directed reaching in infants
II. Learning to produce task-adequate patterns of joint torque

Abstract Nine young infants were followed longitudinally from 4 to 15 months of age. They performed multi-joint reaching movements to a stationary target presented at shoulder height. Time-position data of the hand, shoulder, and elbow were collected using an optoelectronic measurement system. In addition, we recorded electromyographic activity (EMG) from arm extensors and flexors. This paper documents how control problems of proximal torque generation may account for the segmented hand paths seen during early reaching. Our analysis revealed the following results: first, muscular impulse (integral of torque) increased significantly between the ages of 20 (reaching onset) and 64 weeks. That is, as infants got older they produced higher levels of mean muscular flexor torque during reaching. Data were normalized by body weight and movement time, so differences are not explained by anthropometric changes or systematic variations in movement time. Second, while adults produced solely flexor muscle torque to accomplish the task, infants generated flexor and extensor muscle torque at shoulder and elbow throughout a reach. At reaching onset more than half of the trials revealed this latter kinetic profile. Its frequency declined systematically as infants got older. Third, we examined the pattern of muscle coordination in those trials that exhibited elbow extensor muscle torque. We found that during elbow extension *coactivation* of flexor and extensor muscles was the predominant pattern in 67% of the trials. This pattern was notably absent in comparable adult reaching movements. Fourth, fluctuations in force generation, as measured by the rate of change of total torque (NET) and muscular torque (MUS), were more frequent in early reaching (20–28 weeks) than in the older cohort (52–64 weeks), indicating that muscular torque production became increasingly smoother and task-efficient. Our data demonstrate that young infants have problems in generating smooth profiles of proximal joint torques. One possible reason for this imprecision in infant force control is their inexperience in predicting the magnitude and direction of external forces. That infants learned to consider external forces is documented by their increasing reliance on these forces when performing voluntary elbow extensions. The patterns of muscle coordination underlying active elbow extensions were basically the same as during the prereaching phase, indicating that the formation of functional synergies is based on a basal repertoire of innervation patterns already observable in very early, spontaneous movements.

Key words Arm movement · EMG · Motor learning · Torque · Human

J. Konczak (✉) · M. Borutta · J. Dichgans
Department of Neurology, University of Tübingen,
Hoppe-Seyler-Strasse 3, 72076 Tübingen, Germany;
Fax: +49–7071–296504, e-mail: konczak@uni-tuebingen.de

Introduction

We previously found that the multisegmented trajectories seen during early reaching (von Hofsten 1979) are not explained by a failure of infant motor systems to produce sufficient peak amplitudes of muscular torque (Konczak et al. 1995). However, we did observe that infants initially had difficulties in timing task-adequate sequences of torque bursts. While adult movers gained peak muscle torque to flex upper and forearm well within the first third of the reaching motion, 5-month-old infants achieved the equivalent maximum torque after the second half of the reach. However, by the age of 15 months, the relative timing of peak muscle torque was, on average, within the performance range of adults. This result demonstrates that the coordination of goal-directed reaching is not solely a problem of torque generation but also a problem of temporal force control.

Notwithstanding that changes in the temporal control of proximal joint motion are associated with improvements in endpoint kinematics, it is unlikely that the appropriate relative timing of peak force production alone determines the expression of an adult-like hand trajectory. (We use *endpoint* to refer to the distal end of the human arm, i.e., the hand.) At least two other scenarios are pos-

sible: first, reaching for an object at the outer edge of personal workspace requires sufficient generation of muscular flexor torque to counterbalance the effect of gravity (which tends to pull the arm down). In this context, it seems possible that infants cannot maintain high enough levels of flexor torque throughout the reaching motion. If this is true, the kinematic improvements in endpoint control during ontogenesis should be accompanied by a systematic increase in mean flexor torque. This hypothesized increase should occur independent of changes in anthropometrics and inertial load. An analysis of the integrated torque curve (angular impulse) ought to provide an answer to this question, because it provides a measure of the mean torque applied throughout a reach. Second, the jerky hand paths often observed in early reaching are due to the imprecise generation of proximal joint torque. In biomechanical terms, neither torque amplitude nor mean joint torque per reach are the sole limiting factors, but also the inability of the motor system to generate a smooth torque output. An adequate measure to assess the smoothness of a torque curve is to analyze the number of zero-crossings in rate of change of torque (derivative of torque over time). Many zero-crossings throughout a reach indicate an unsteady generation of torque.

At this point one can only speculate about the underlying physiological reasons for this imprecision. One working hypothesis is that infant motor systems have not yet learned to adjust their muscular force output to the external forces encountered during movement execution (Bernstein 1988; Sporns and Edelman 1993; Thelen 1995) and lack the necessary forms of anticipatory force control (Forssberg et al. 1992). We set out to examine these two potential control problems in infant motor behavior by analyzing the development of angular impulse and the rate of change of torque during goal-directed reaching between the ages of 5 and 15 months. In addition, we attempt to relate torque production to patterns of muscle activity. Specifically, we investigated early forms of muscle coordination during elbow extension.

Materials and methods

Subjects, experimental procedures, and the various steps of data reduction are described in detail in a preceding paper (Konczak et al. 1995). Here we provide a summary of the participants and the experimental setup.

Subjects

We report longitudinal data of nine healthy, full-term infants, six girls and three boys. Infants were recorded at the ages of 16, 20, 24, 28, 32, 36, 52, and 64 weeks. In addition, we collected data on reaching movements of four healthy adults (mean age 34.9 years, SD 5.9 years).

Procedure

Infants sat in a specially designed chair with their trunks stabilized by a foam-coated seat belt. The experimenter or the parents presented small toys at shoulder height and to the right side of the in-

fants. To contact the target object infants had to perform right-handed reaches with a large vertical and small coronal displacement. Infrared light-reflective markers were attached to the shoulder, elbow, and hand. Movements of the markers were recorded with an optoelectronic camera system yielding three-dimensional time-position data for each joint marker at a rate of 100 frames per second. Because the start of an infant's reach was not predictable, we recorded for a total duration of 15 s in each trial. To record the adult movements, markers were attached to the shoulder, elbow, and wrist joint, and to the hand (2nd metacarpal). Adults sat on a normal chair and were instructed to rest their hand comfortably on their thigh at the beginning of a trial, a position that met the inclusion criteria that we applied to the infant reaches. On an auditory signal, the adult movers reached for a stationary target presented at shoulder height at their preferred movement speed.

Electromyograms (EMG) were recorded from the biceps, triceps, anterior deltoid, and brachioradialis muscles in all participants, with a sampling rate of 500 Hz, using standard silver chloride surface electrodes (ARBO 2–60) with a diameter of 5 mm. Electrodes were placed on the respective muscle bellies to minimize the possibility of crosstalk. All EMG data were digitized on-line (12-bit) and then stored for later analysis.

Data reduction

A total of 852 trials with infant movements and 60 trials with adult reaches were collected. Based on video recordings, a 4-s segment containing the reaching movement was identified. Subsequently, the visibility of each marker within such a 4-s segment was determined. If the segment contained missing time-position data of one or more markers, we checked whether the total amount of missing data exceeded 10% of the total segment (40 out of 400 frames) and whether the gap was larger than 20 consecutive frames. A trial that violated any of the two criteria was discarded. We then applied a linear spline to those trials that had met these inclusion criteria and that had showed missing data. After applying this interpolation where necessary, the time-position data of all markers were filtered using the automatic model-based band-width selection procedure by D'Amico and Ferrigno (1992). The EMG signals were filtered with a 3- to 100-Hz bandpass filter for the total trial duration, subsequently rectified and smoothed with a 21-point moving-average filter.

Working with infants in an experimental setting does not allow the application of rigorous constraints that otherwise might be desirable from the experimenter's point of view. In our paradigm we could control the endpoint of the movement by placing the object at shoulder height and to the right side of the infant. Movement distance was approximately 85% of the infant's arm length. However, we could not completely control the initial position of the arm, because placing or holding the arm prior to movement onset could have resulted in unnatural trajectories. We therefore applied a set of post hoc criteria to obtain a sample of infant reaching movements that were comparable in terms of initial and final position: first, we only included those trials where the infant actually made contact with the presented object; second, the initial shoulder angle θ_1 had to exceed 125° and the initial elbow angle θ_2 had to be greater than 85°. (The shoulder angle θ_1 is the planar angle enclosed by the upper vertical of the shoulder joint and the humerus. To compute this angle we used the time-position data of the shoulder and the elbow marker. The elbow angle θ_2 is the planar angle between humerus and ulna. Time-position data of shoulder, elbow, and hand marker were used to calculate θ_2; see Appendix.) These joint angles determined a position of the hand near and lateral to the infant's right thigh. Third, at the time of object contact, the distance between shoulder and hand marker in the sagittal (D_{xy}) and transverse plane (D_{xz}) was not allowed to drop below 70% of the infant's total arm length (D_{arm}). D_{arm} was measured as the distance between shoulder and hand marker when the arm was fully extended. This way we assured that only those reaching movements were analyzed that showed a large vertical and small coronal displacement and were performed to the periphery of the infants' workspace.

Table 1 Number of movement trials included in the analysis. Empty cells are either due to a missed session or because recorded trials did not fit the inclusion criteria

Subject	Age (weeks)							
	20	24	28	32	36	52	64	Total
AG	–	2	6	10	8	10	11	47
AW	3	5	4	8	8	5	9	42
DHA	10	–	9	7	7	3	6	42
ES	9	5	2	–	6	9	8	39
JS	12	6	6	1	6	7	9	47
LS	9	5	4	10	7	2	10	47
SS	6	6	10	–	4	3	11	40
TD	–	8	12	11	9	4	2	46
UK	7	–	7	–	7	6	1	28
Total	56	37	60	47	62	49	67	378

A total of 378 reaches out of 852 recorded movements fulfilled the above criteria and also had sufficient visibility of all three joint markers (see Table 1). They were subject of further analysis. For this sample of reaching movements, the mean of D_{xy}/D_{arm}, the ratio between shoulder-hand distance in the sagittal plane and total arm length, was 84.9% (SD 7.5%), for D_{xz}/D_{arm} the mean ration was 85.1% (SD 7.6%). That is, in the selected trials, final hand positions at object contact were closely grouped around 85% of an infant's arm length. This assured that infants had indeed performed reaches toward the periphery.

Data analysis

We performed inverse dynamics computations using algorithms developed by Schneider and Zernicke (1990) to calculate the joint torques for shoulder and elbow. To allow comparisons between age cohorts, joint torques were normalized by body weight. We obtained measures for net joint torque (NET), and the residual muscular torque (MUS), also called "generalized" muscle torque. Net joint torque is the sum of all torque components (gravitational, interactive, and muscle). A detailed description of the equations of motion is given in Schneider and Zernicke (1990). Additional information on torque partitioning and its use in motor development research is found in Konczak and Thelen (1994) and Schneider et al. (1990). Because torques are vectors, they have a magnitude and direction. In our analysis, the torque direction is indicated by a plus or a minus sign. All positive torque values indicate a flexor force, all negative values imply an extensor influence.[1]

To obtain a measure of the applied joint torque throughout the whole reaching motion, we calculated angular impulse for net (L_{NET}) and muscular torques (L_{MUS}) for all reaches included in the analysis. Angular impulse for each torque variable was obtained by integrating the respective torque-time curve. Before integration we split each torque-time series into sections containing either flexor (positive) or extensor (negative) torque (see Fig. 2 for examples of torque-time data). Each section was integrated separately. Subsequently we added all the values of the negative and the values of the positive integrals for each reach to obtain a measure of mean flexor or extensor angular impulse.

---

[1] Because the shoulder joint has three degrees of freedom, upper arm orientation can also be described in terms of abduction/adduction and/or rotation. The applied moving plane algorithm does not allow us to distinguish between torques that are exclusively used for flexion/extension or are solely responsible for joint ab/adduction. In agreement with Schneider and Zernicke (1990) and for the sake of brevity, we simply label all positive torques *flexor* and all negative torques *extensor* torques. However, the reader should keep in mind that the computed shoulder torques were responsible for *flexion/extension* as well as for *ab/adduction* of the upper arm.

Further, we computed the first derivative of the torque-time curve for MUS and NET using a three-point differentiation method, thus measuring the rate of change of torque over time. We denote torque derivations with T', e.g., elbow T'_{MUS} represents the rate of change of elbow muscle torque. With custom-made, digital signal-processing software, we determined the number of zero-crossings in T'_{MUS} and T'_{NET} for both proximal arm joints. The total number of zero-crossings per reach indicates how often during a reach a particular torque changed direction (i.e., the number of "torque peaks" and "torque valleys"), thus providing an indirect measure of the smoothness of the applied torque.

Onsets of EMG activity in the recorded arm muscles were marked by hand with interactive signal-processing software. For the assessment of the muscular activation pattern (*coactivation* versus *reciprocal*), we could not apply criteria based upon a global EMG amplitude value for the following reasons: first, infants seldomly were completely at rest, thus, their muscles often showed some degree of tonic activity prior to the start of a reach. Even within the whole trial duration of 15 s, episodes of "silence" were rather rare. Second, reaching movements did not necessarily have identical starting positions. That is, the performed movements were similar, but not identical. Third, considering the changes in body composition and anthropometrics, we could not guarantee identical skin resistance and electrode placement between successive sessions, although we took great care in preparing the skin and in placing the electrodes. Given these difficulties, we therefore opted for trial-specific criteria. For each muscle we determined its maximal recorded amplitude of all trials in a given session. If muscular activity in a particular reach dropped below 15% of this maximal activity, we coded the muscle to be "silent."

Results

The development of reaching proceeds from early reaching with its segmented hand paths toward the expression of trajectories that do resemble adult movement (roughly straight hand path, single velocity peak. We use *trajectory* to denote the displacement as well as the corresponding velocity of a given joint or limb). This progression is shown in four exemplar reaches in Fig. 1. In addition to the endpoint kinematics, the angular kinematics of elbow and shoulder joint are provided, indicating that smoothing of these proximal trajectories accompanies the emergence of a unimodal velocity profile of the hand (e.g., compare the velocity profiles of the hand, shoulder, and elbow joint). The graphs in Fig. 2 represent the corresponding time series for NET and MUS torque, and T'_{MUS} at both joints. In the example of the 20-week-old infant, MUS and NET torque production was characterized by numerous shifts in force direction. The goal of torque change analysis was to determine whether these shifts were a general feature of early reaching in our infant sample.

Changes in angular impulse

Because total movement time (MT) did decrease with increasing age (mean MT 1.19 s at 20 weeks, 0.85 s at 64 weeks) and because the value of an integral depends on the length of the integration interval, we divided all impulse variables by MT to get a measure of torque production independent of MT. Thus, in addition to body
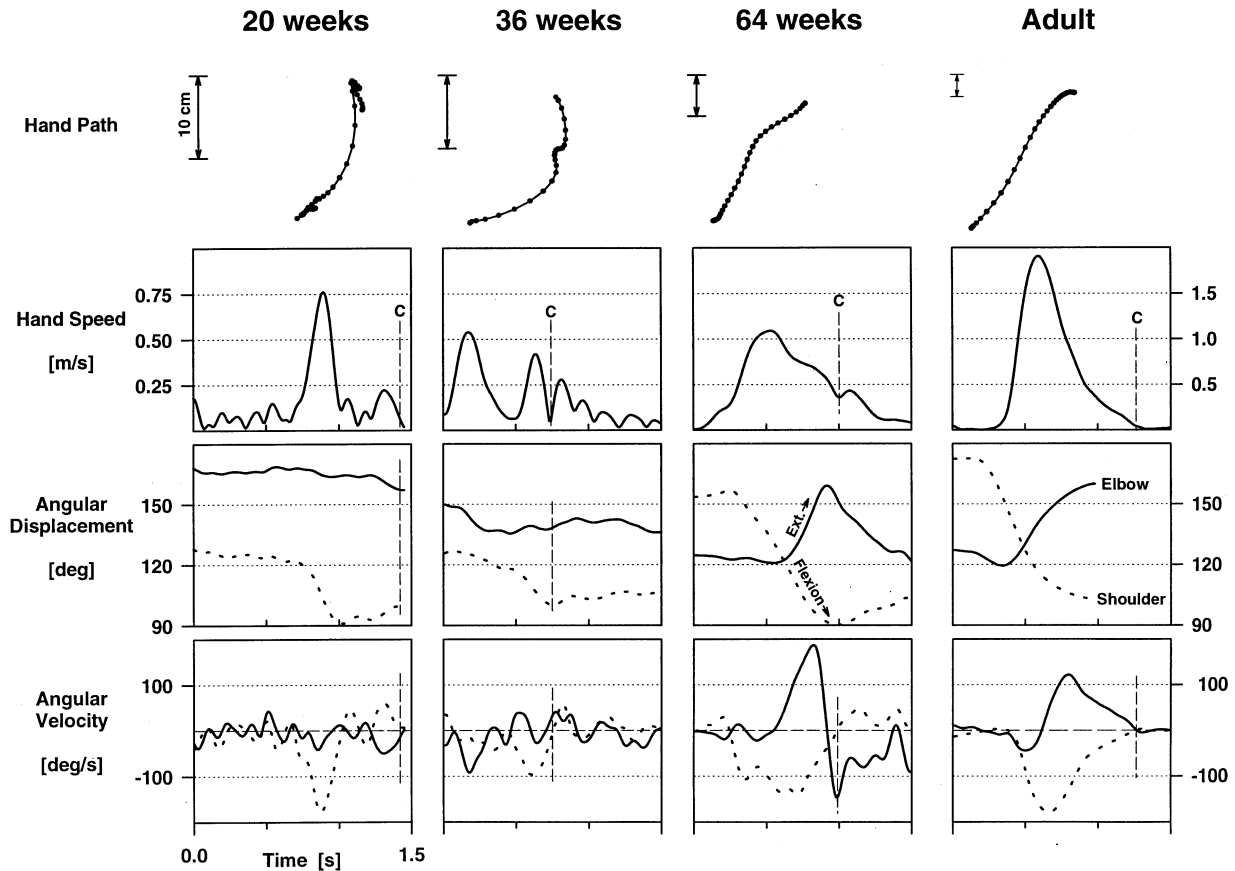
Fig. 1 Angular and endpoint kinematics of four individual reaching movements. All demonstrated infant reaches were performed by the same infant. Hand path is shown in the sagittal plane. Angular kinematics are based on sagittal projection angles. Hand path shown is the segment between movement start and contact. Time series of other kinematic variables show the same time interval. Reaching contact was indicated by a *vertical line* (*c* time of contact). Time interval between successive data points is 30 ms in the hand path graphs

weight, all reported impulse values were *normalized by movement time*. For the sake of brevity we continue to use the terms *impulse* or *angular impulse*, although we imply *normalized impulse*.

If infants indeed had problems in maintaining specific torque levels for the whole duration of the reach, one would expect that with increased competency infants should reveal a systematic increase in muscular impulse (L_{MUS}). We found that the absolute level of raw L_{MUS} (not normalized by MT) could vary substantially between sessions, as seen in the longitudinal profiles of three infants (Fig. 3A). However, when considering the age-related differences in MT by comparing the normalized data, a trend toward a systematic increase in elbow L_{MUS} is observed (Fig. 3B). This trend is substantiated when analyzing L_{MUS} for elbow and shoulder for all infants. A repeated-measures ANOVA (Age×Impulse) for the complete infant sample reveals that L_{MUS} at both proximal joints changed significantly as a function of age (elbow, $P<0.001$; shoulder, $P<0.001$). The corre-

sponding mean data are shown in Fig. 4. In comparison with adults, impulse at both joints was markedly lower in infants throughout the observation period. In adults, the individual mean range of muscular impulse at the elbow was 23.7–32.4 Nm×10⁴/N and 59.3–75.3 Nm×10⁴/N for the shoulder. The differences in L_{MUS} between adults and infants are largely due to the higher movement speed in the adult group (mean resultant hand speed, 0.5–0.75 m/s for infants, 1.6 m/s for adults).

During adult vertical reaching movements, muscle torque at the elbow exerts a flexor influence throughout the movement, even if the joint actually extends during the second part of the reach (due to the pulling action of gravitational and reactive forces). In contrast, infants may actually produce extensor MUS, although the task does not require it (see Fig. 2). To determine to what extent L_{MUS} was composed of flexor and extensor impulse, we split L_{MUS} into its two components. Figure 5 shows that, while flexor L_{MUS} increased, extensor L_{MUS} decreased at shoulder and elbow. In general, the amount of extensor L_{MUS} was smaller than flexor L_{MUS} for both joints, which can be documented by the ratio between these two impulse components. The mean ratio between flexor/extensor impulse at week 20 was 14:1 for elbow and 20:1 for the shoulder. These ratios had changed to 159:1 (elbow) and 129:1 (shoulder) by week 64, indicating that in relation to flexor L_{MUS} the expressed muscular impulse with extensor influence had dropped considerably within that time period.

Extensor MUS was not exhibited during every reaching movement. The data in Table 2 reveal that at reach-
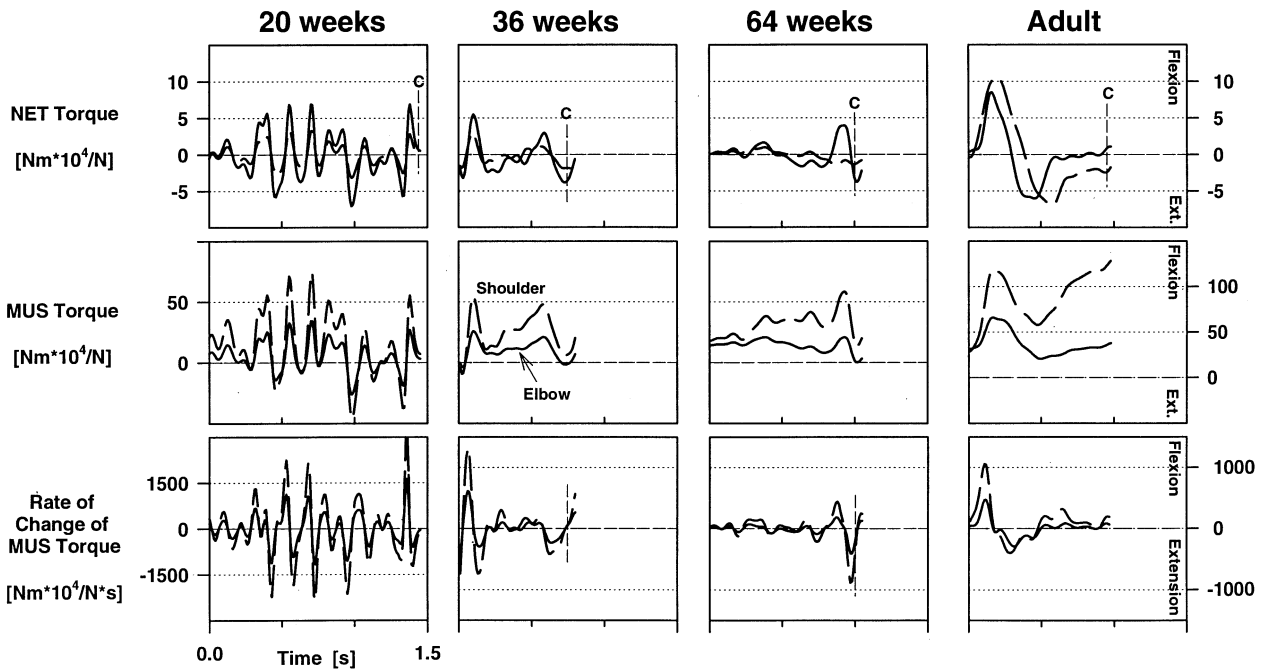
Fig. 2 Profiles of total joint torque (*NET*), muscular torque (*MUS*), and muscular torque change. Data correspond to the four reaching movements shown in Fig. 1. Owing to unpredictable changes in inertial load once infants contacted the toy, torque profiles are cut off after contact. Note that the 20-week-old infant produced muscular torque for extension, while his reach at 64 weeks, as well as the adult reach, shows only muscular torque with flexor influence

Fig. 3A, B Mean muscular impulse (L_{MUS}) at the elbow. Data show the longitudinal profiles of three infants. **A** Raw impulse, **B** impulse normalized by movement time (*MT*). Each data point represents the mean of the individual mean performance at a particular age

ing onset the frequency of trials with extensor MUS ranged between 53.9% (shoulder) and 63.4% (elbow) and did not drop substantially before 9 months of age.

### Muscle activation patterns during elbow extension

The expression of extensor muscle torque implies the activation of appropriate extensor muscles. Because we had recorded the electromyographic activity of the triceps muscle (an elbow extensor), we could analyze its firing pattern in those trials where elbow extensor MUS was present. From a total of 145 trials showing elbow extensor MUS, the EMG recordings from 109 trials could be analyzed. In the remaining trials, the EMG signals were not usable (accidental loosening of the electrodes). In 59.6% of the trials analyzed, the triceps was active at least 50 ms prior or during elbow extension. In those trials with no discernible triceps activity, the exhibited extensor MUS impulse was small (mean 0.114 Nm×10^4/N) when compared with the trials with triceps activity (mean 0.568 Nm×10^4/N). Because MUS is actually "residual" torque derived from the inverse dynamics calculations, these measurements probably reflect the contribution of other elbow extensors (anconeus muscle) or of nonmuscular forces (viscosity, bone-to-bone, bone-to-muscle).

Activation of the triceps occurred under two different patterns of muscle coordination. First, a pattern of *reciprocal innervation* (triceps active – biceps/brachioradialis silent), second a pattern of *coactivation* (triceps active – biceps/brachioradialis active). During coactivation usually either flexor muscles or the triceps were predominant. Dominance could shift within a single trial (Fig. 6A). In this example both flexors showed a higher degree of activation during elbow flexion in the beginning, while the triceps increased its activity during the final part of the reach. We found that coactivation was the predominant
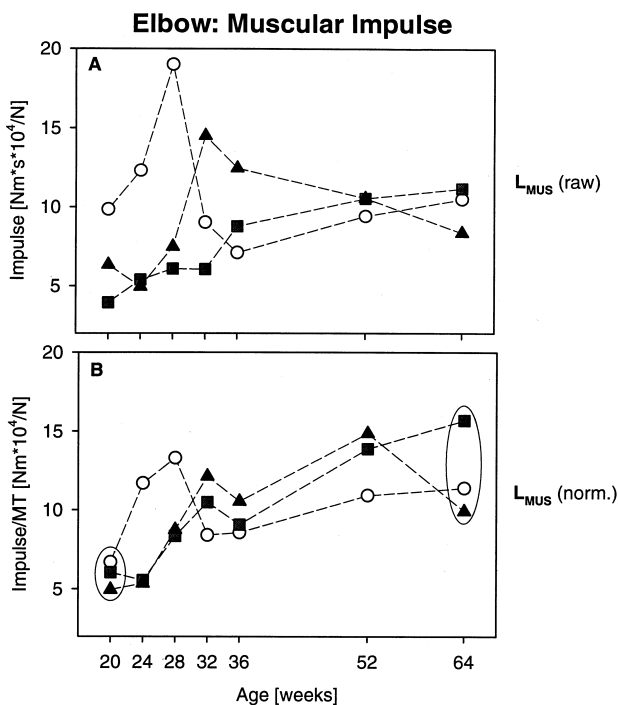
Fig. 4 Group development of mean muscular impulse at elbow and shoulder. Each data point represents the mean of the individual mean performance of all nine infants at a particular age. Length of *error bar* is 1 SD. Comparable adult means were 28.1 Nm×10^4/N (SD 3.6) for elbow, and 66.4 Nm×10^4/N (SD 6.8) for shoulder L_{MUS}
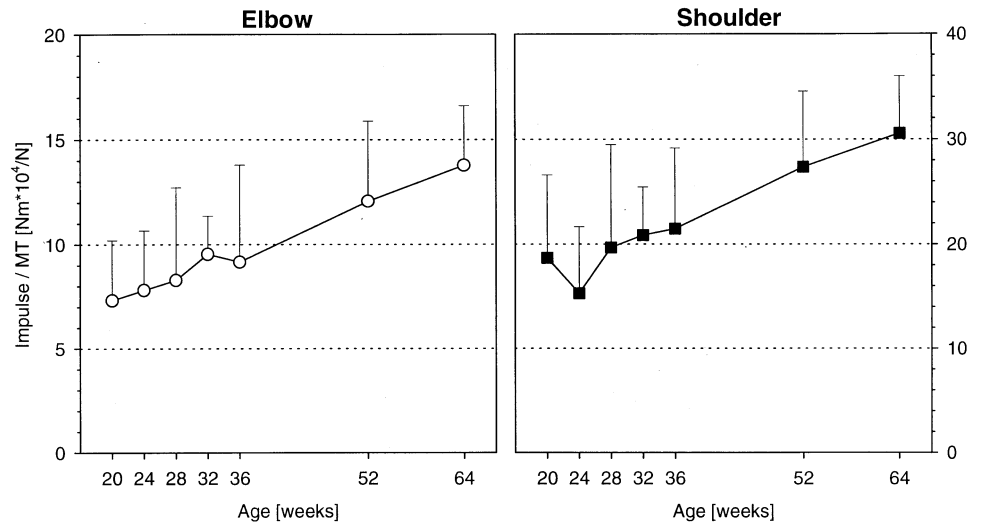
Fig. 5 Mean muscular impulse at elbow and shoulder split by extensor and flexor influence. Each data point represents the mean of the individual mean performance of all nine infants at a particular age. *Error bar* length is 1 SD. Note the differences in scale between flexor and extensor impulse. Infants clearly produced predominantly flexor torque
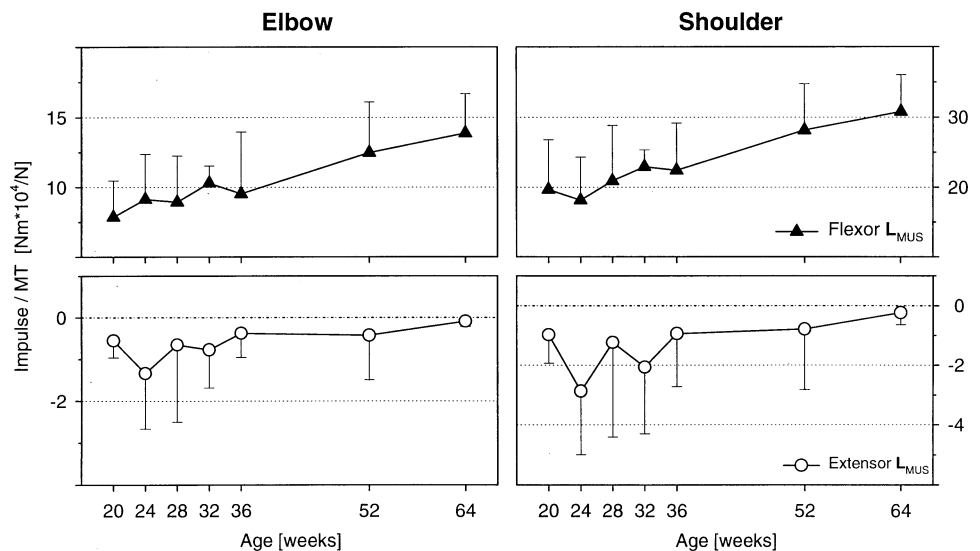
EMG pattern in over 67% of the trials, while reciprocal innervation was used in the remaining 32% of the sample (Fig. 6B). Reciprocal innervation could happen during the reaching action, but we also observed instances where the triceps was active prior to the reach, then ceased to fire as the arm flexors began to carry out the planned flexion, only to continue its activity during the manipulation of the object. Reciprocal innervation patterns were rarely characterized by a sudden drop of antagonist activity to zero-baseline. More typically, the muscle continued to maintain some background activity (see Fig. 6B). The relatively small sample size did not allow us to discern age-related changes in the selection of a specific innervation pattern. When reaching at their preferred speed, the adults in our sample showed a low-level background activity of the triceps. The primary agonist was the anterior deltoid muscle initiating flexion at the shoulder joint (Fig. 7). Subsequent elbow extension was not accompanied by increased triceps activation but occurred owing to the action of gravitational and motion-dependent forces.

Table 2 Percentage of trials exhibiting extensor muscular torque (*MUS*) at the shoulder and elbow joint. (*n* the total number of analyzed movement trials at a particular age)

Age (weeks)	(*n*)	Showing ext. MUS at shoulder (%)	Showing ext. MUS at elbow (%)
20	56	53.9	63.4
24	37	65.5	55.2
28	60	45.0	26.7
32	47	51.0	42.9
36	62	17.7	17.8
52	49	14.3	24.5
64	67	27.3	25.8

Changes in torque direction

We evaluated the number of zero-crossings for T'_{MUS} and T'_{NET}, the respective first derivatives of torque. Each zero-crossing of a torque change curve corresponded to a local maximum ("peak") or minimum ("valley") in the torque-time curve, thus providing an indirect measure of

Fig. 6A, B Two basic innervation patterns capable of generating extensor MUS at the elbow. **A** Coactivation of flexors and extensors throughout the reach. Biceps and brachioradialis were dominant during joint flexion, triceps became dominant during extension. **B** Reciprocal innervation. Flexors and extensor were both active during elbow flexion. Here the triceps probably served as a limb stabilizer. In the second part of the reach, flexor activity ceased, while triceps continued. *Dashed vertical lines* indicate movement start as coded by video (*MUS* muscle torque, *2*NET* double total joint torque). NET was multiplied by 2 for better readability. Torque units are newton-meters$\times 10^4$ per newton. Elbow angle is in degrees. Reduction in angle corresponds to elbow flexion, increase to extension. *Solid bars* indicate main activity of elbow flexors, *white bar* corresponds to main activity of elbow extensor
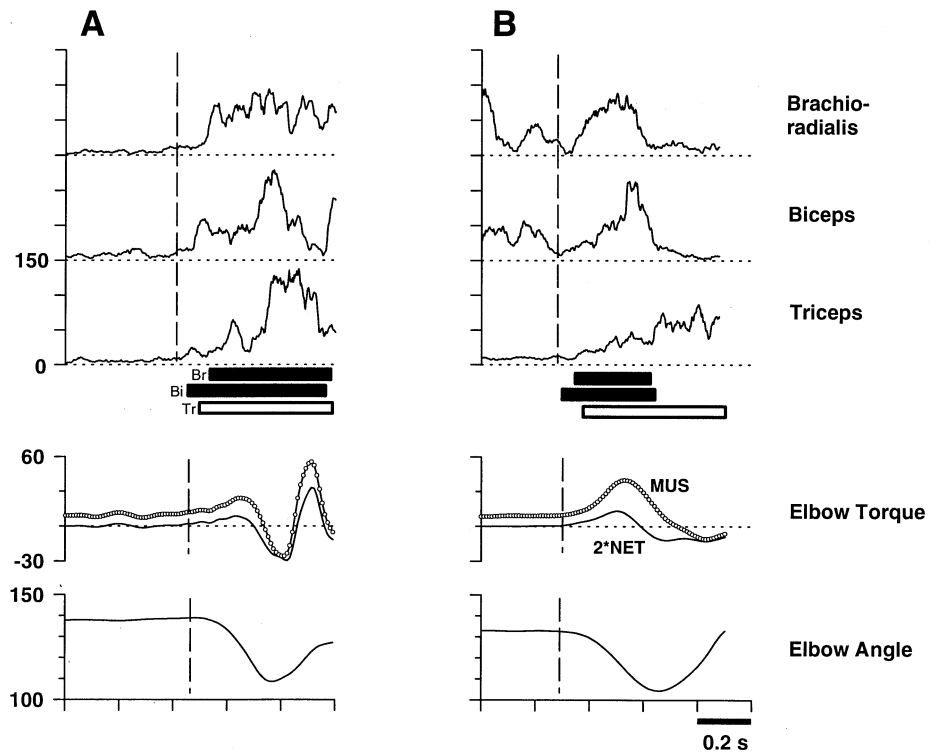
the smoothness of torque production during movement execution. Our results reveal that reaches at 20 weeks of age had, on the average, 13.2 (SD 5.3) zero-crossings in elbow MUS, a number that decreased steadily to 7.2 (SD 1.4) zero-crossings by week 64. A similar trend was observed for the torque changes of T'_{MUS} and T'_{NET} at the shoulder joint, where zero-crossings were reduced by 48% within the period of 20–64 weeks of age (Fig. 8).

A comparison of the infant with the adult data presented in Fig. 8 indicates that infants performed their reaches with a higher number of zero-crossings than adults throughout the 11-month observation period. In addition, to an age-related decrease in mean performance, the variability in the number of zero-crossings of T'MUS and T'NET also dropped as infants got older. However, the variability in torque change of MUS and NET at 15 months of age was still substantially higher than in the adult trials (see Fig. 8).

Discussion

Learning to maintain task-adequate levels of joint torque

Typically infants attempt their first goal-directed reaches around the age of 4–5 months after birth (von Hofsten 1979, 1991; Konczak and Thelen 1994; Thelen et al. 1993). Their early hand trajectories are characterized by multiple movement segments. Within 4–8 weeks after reaching onset, infants make remarkable progress in producing smoother and straighter arm trajectories. How-

ever, even at 15 months postnatally their movement patterns have not reached the smoothness and consistency of adult motion (see Fig. 1). There is still considerable debate about whether the expression of stereotypic hand trajectories observed in adults are kinematic manifestations of a control signal from the central nervous system (CNS) or are largely determined by the peripheral mechanics of the joint system (e.g., Hasan 1991; Lacquaniti 1992). This present study along with our previous publication attempts to address this issue by focusing on the relationship between peripheral and muscular forces (the only forces that are subject to CNS involvement). Here we examined how developmental changes in muscular force output of proximal limbs affected the emergence of coordinated, goal-directed arm movements. We found that at reaching onset (20–24 weeks) mean muscular impulse at both proximal joints was significantly lower than the exerted muscular impulse at 52 or 64 weeks of age (see Fig. 4). This finding suggests that early motor systems may have initial difficulties in maintaining task-adequate levels of joint torque over longer movement durations (in this study between 800 and 1200 ms). "Task-adequate" refers in our paradigm to the production of enough torque to flex the joint and maintain a joint position against the influence of gravity and reactive forces. The underlying cause of this inability to conserve levels of flexor torque is not explained by limitations in muscle metabolism of the antigravity muscles (i.e., their inability to maintain a contraction; Behrman et al. 1992; Persson and Gentz 1966), but is founded in the imprecision of early neuromotor control mechanisms. This imprecision in coordinating multijoint forces is also revealed by
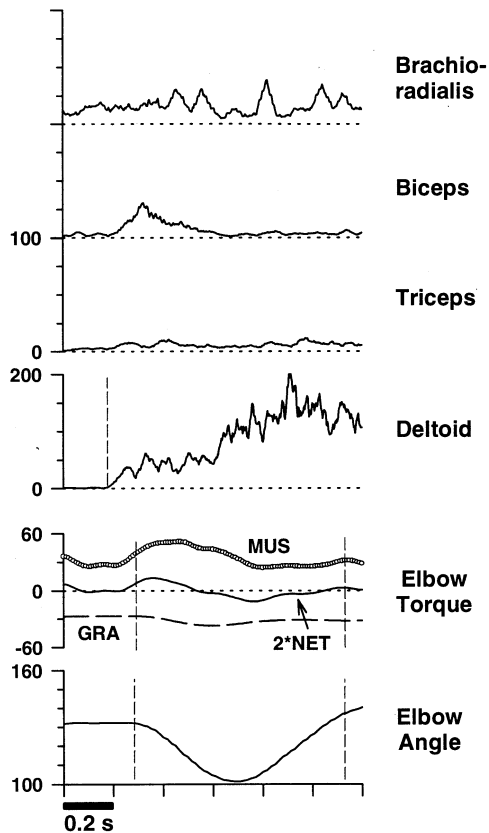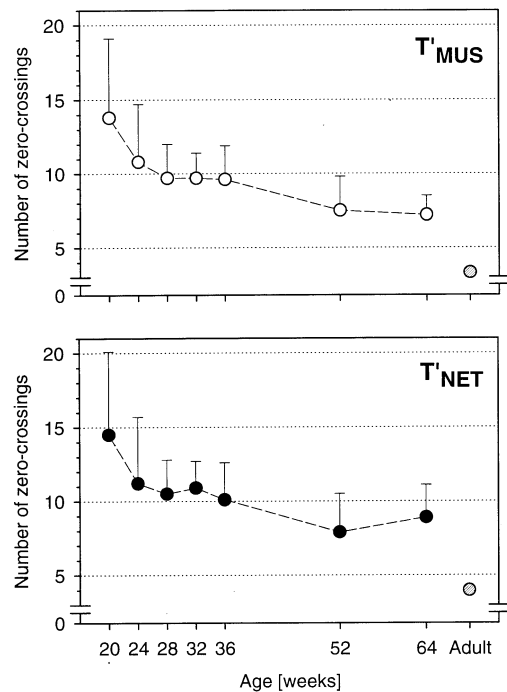
Fig. 7 Adult innervation pattern during vertical reaching movement performed at preferred speed. Anterior deltoid was the primary agonist of shoulder flexion. Triceps showed low background activity (*MUS* muscle torque, *GRA* gravitational torque, *2*NET* double total joint torque). NET was multiplied by 2 for better readability. Note that decrease in flexor MUS is sufficient to extend the forearm. Torque units are newton-meters$\times 10^4$ per newton. Elbow angle is in degrees

Fig. 8 Number of zero-crossings per reach for the rates of change of muscle torque (T'_{MUS}) and total torque (T'_{NET}) at the shoulder joint. Values are means of individual means for all infants at a particular age ($n=9$) or the adult sample ($n=4$). *Error bar* length is 1 SD. Note that the ordinate scale is too large to appreciably show adult standard deviations. With respect to T'_{MUS}, adult SD was computed as 0.1, for T'_{NET} adult SD was 0.2 zero-crossings

our finding that infants did at times produce extensor muscle torque when executing a reaching movement – a feature that was absent in comparable adult reaching motion (adults generated exclusively muscle torque with flexor influence; see Figs. 2, 7). At reaching onset (20 weeks), nearly two-thirds of all recorded reaches contained segments with elbow extensor MUS. By the age of 1 year, the percentage of reaching movements with elbow extensor MUS had dropped substantially to roughly 25% (see Table 2).

Patterns of muscle activation underlying the expression of muscular extensor torque

When extensor MUS at the elbow was exhibited, infants used *coactivation*, with the triceps being the dominant muscle in over two-thirds of the trials. One reason that might explain this preference for coactivation is that the concurrent activity of the arm flexors helps to stabilize the forearm during the intended extension (Karst and Hasan 1987) and might facilitate a more precise control in

the final phase of the reach (Ghez et al. 1983). The predominant selection of a coactivation pattern is also consistent with earlier findings showing that coactivation is the prevailing pattern of muscle coordination in spontaneous movements before reaching onset (Hadders-Algra et al. 1992). Thus, it seems plausible that infant motor systems use this already familiar muscle synergy when beginning to show goal-directed behavior.

A comparison of adult to infant motion yielded two notable differences: first, the absence of extensor muscle torque; second, the adults in our sample did not use a pattern of coactivation during elbow extension.[2] However, the movement intent to extend the forearm was the same in infants and adults. The difference between infant and adult movers lay in the way this intention to extend the limb was planned and carried out. In our paradigm, adults allowed the forearm to be pulled down passively by gravity and reactive forces, a strategy that makes use of these external forces (Hong et al. 1994; Konczak et al. 1995). In infancy, two basic movement strategies seem to coexist. During early reaching (20–32 weeks) infants used a strategy that we term "active extension." Active means that elbow extension was accompanied by epochs of extensor muscle torque (two-thirds of the reaches

---

[2] This does not imply that adults never use coactivation during a reaching task. The actual innervation pattern is a function of initial and final limb position, speed, and inertial load (Karst and Hasan 1991).

showed extensor MUS at 20 weeks). It also entails that the produced muscle flexor impulse was "low" relative to the corresponding extensor impulse (14:1 at week 20; 159:1 at week 64). Although this strategy is equally successful in getting the forearm extended, it does require extra muscular effort and hence is not as "economical" as passive extension. With increasing proficiency infants began to favor the strategy of passive extension, that is, fewer attempts were made to extend the forearm by actively generating extensor muscle torque. Instead, muscular activation served the exclusive purpose to produce flexor torque. This strategy assures that only so much muscular force is applied as is necessary to offset the effects of the gravitational and motion-dependent forces and to accomplish the task of arm flexion. An obvious benefit of "passive extension" is that it reduces muscular work during the extensor phase. Yet, because the relationship between a central impulse innervating a set of muscles and the overt limb motion is not unique (Bernstein 1967; Hasan 1991), the system has to have some a priori knowledge about the magnitude and direction of the external forces involved. Given the rapid changes in anthropometrics and limb inertia in early infancy, it is highly unlikely that infants are born with some preset "plan of action" that contains all the necessary knowledge about intersegmental limb mechanics. Therefore, it seems understandable that young infants are troubled by "reactive phenomena," when they begin to exhibit forms of goal-directed behavior that require a precise control of joint torques. In other words, they have problems in producing the right amount of muscular torque in the presence of unknown external torques, such as coriolis and gravitational forces. Consequently, the prediction of such external forces requires learning and a process of ongoing recalibration of the motor system. We here demonstrate how the appropriate calibration might ultimately lead to changes in muscular activation patterns that take these external forces into account.

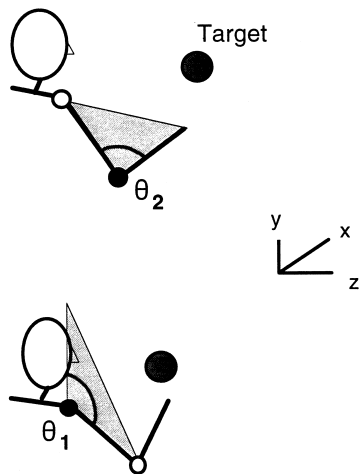### Learning to produce smooth patterns of joint torque

Additional evidence of how neuromuscular control improved during development represents our finding that the number of oscillations in the muscular torque curve did decrease as infants became more proficient in reaching. The number of zero intersections for T'_{NET} and T'_{MUS}, representing an indirect measure of the smoothness of torque generation, did decrease in absolute terms as infants got older and more experienced (see Fig. 8). That is, improvements in neuromuscular control of proximal joints led to a more regular NET output at these joints, which was ultimately reflected in the expression of a smoother hand trajectory. Our data document how the development of the hand trajectory is embedded in the dynamics of proximal limbs – a relationship naturally determined by the physical make-up of the system. Any developmental theory focusing solely on endpoint motion and disregarding this relationship will have difficulty in explaining how changes in CNS control signals will ultimately lead to multijoint coordination. Furthermore, these torque change data underline our earlier claim that the developmental process that finally leads to stereotypic kinematic responses of the hand is not completed by the age of 15 months. Although the infants in our study had similar movement times than adults by that age (infants 850 ms; adults 795 ms), the absolute number of zero-crossings for T'_{NET} and T'_{MUS} was roughly twice as high for the infant than for the adult sample (see Fig. 8). This result along with the substantially larger variability in these torque change variables warrants the conclusion that our infants had not yet achieved the consistency and smoothness of adult torque control. Our conclusion is corroborated by the results of Forssberg et al. (1991, 1992) who investigated the development of force control in a precision grip. In this fine-motor task, infants showed initially force profiles with multiple peaks when attempting to lift a small object (closely resembling the torque change profiles seen in Fig. 2). Only after 2 years of age did single-peaked force rate profiles begin to emerge, indicating a change toward anticipatory force control. The authors conclude that the coupling of grip and load force is not an innate synergy. Our data support the view that this is also true for the case of multijoint arm movements. Functional muscular synergies that are the basis of efficient endpoint motion are not developed at birth, but they have to be learned during ontogenesis.

Ample evidence suggests that the acquisition of coordination is tied to growth of the neuromuscular system and to neural development (Harbord et al. 1990; Knaap et al. 1991). However, based on the results of our data and those of others (Schneider et al. 1990; Thelen and Fisher 1982) we argue that early motor learning cannot be considered outside their biomechanical context. This study documents developmental changes in proximal joint dynamics. These dynamic changes entail that infants learned to produce smoother patterns of muscular force and to make use of external forces when elbow extension is desired. We could also show that the patterns of muscle activation that underlie active elbow extension in early infancy are basically the same as during pre-reaching and are characterized by the dominance of coactivation. How and when patterns of muscle coordination during goal-directed reaching begin to resemble adult forms of innervation needs to be subject of further study.

Appendix

Fig. 9 Angle θ_1 is the planar angle enclosed by the upper vertical of the shoulder joint and the humerus. To compute this angle we used the time-position data of the shoulder and the elbow marker and a third phantom marker. The horizontal (x) and translational coordinates (z) of this marker are identical to those of the shoulder marker. Its vertical coordinate (y) is 100 mm above the respective position of the shoulder marker. The elbow angle θ_2 is the planar angle between humerus and ulna. Time-position data of shoulder, elbow, and hand marker were used to calculate θ_2

References

Behrman RE, Kliegman RM, Nelson WE, Vaughan VC (1992) Textbook of pediatrics, 14th edn. Saunders, Philadelphia

Bernstein NA (1967) The co-ordination and regulation of movements. Pergamon, Oxford

Bernstein NA (1988) Die Koordination der Bewegungen in der Ontogenese. In: Pickenhain L, Schnabel G (eds) Bewegungsphysiologie. Barth, Leipzig, pp 99–137

D'Amico M, Ferrigno G (1992) Comparison between the more recent techniques for smoothing and derivative assessment in biomechanics. Med Biol Eng Comp 30: 193–204

Forssberg H, Eliasson AC, Kinoshita H, Johannson RS, Westling G (1991) Development of human precision grip. I. Basic coordination of force. Exp Brain Res 85: 451–457

Forssberg H, Kinoshita H, Eliasson AC, Johannson RS, Westling G, Gordon AM (1992) Development of human precision grip. II. Anticipatory control of isometric forces targeted for object's weight. Exp Brain Res 90: 393–398

Ghez C, Vicario D, Martin JH, Yumiya H (1983) Sensory motor processing of target movements in motor cortex. In: Desmedt JE (ed) Motor control mechanisms in health and disease (Advances in Neurology; Vol 39). Raven Press, New York, pp 65–67

Hadders-Algra M, Van Eykern LA, Klip-Van den Nieuwendijk AWJ, Prechtl HFR (1992) Developmental course of general movements in early infancy. II. EMG correlates. Early Hum Dev 28: 231–251

Harbord MG, Finn JP, Hall-Craggs MA, Robb SA, Kendall BE, Boyd SG (1990) Myelination patterns on magnetic resonance of children with developmental delay. Dev Med Child Neurol 32: 295–303

Hasan Z (1991) Biomechanics and the study of multijoint movements. In: Humphrey DR, Freund H-J (eds) Motor control: concepts and issues. Wiley, Chichester, pp 75–83

Hofsten C von (1979) Development of visually directed reaching: the approach phase. J Hum Mov Stud 5: 160–178

Hofsten C von (1991) Structuring of early reaching movements: a longitudinal study. J Mot Behav 23(4): 280–292

Hong D-A, Corcos DM, Gottlieb GL (1994) Task dependent patterns of muscle activation at the shoulder and elbow for unconstrained arm movements. J Neurophysiol 71(3): 1261–1264

Karst G, Hasan Z (1987) Antagonist muscle activity during human forearm movements under varying kinematic and loading conditions. Exp Brain Res 67: 391–401

Karst G, Hasan Z (1991) Timing and magnitude of electromyographic activity for two-joint arm movements in different directions. J Neurophysiol 66(5):1594–1604

Knaap MS van der, Valk J, Bakker CJ, Schooneveld M, Faber JAJ, Willemse J, Gooskens RHJM (1991) Myelination as an expression of the functional maturity of the brain. Dev Med Child Neurol 33: 849–857

Konczak J, Thelen E (1994) The dynamics of goal-directed reaching: a comparison of adult and infant movement patterns. In: Van Rossum JHA, Laszlo JL (eds) Motor development: aspects of normal and delayed development. VU University Press, Amsterdam, pp 25–40

Konczak J, Borutta M, Topka H, Dichgans J (1995) Development of goal-directed reaching in infants: hand trajectory formation and joint torque control. Exp Brain Res 106: 156–168

Lacquaniti, F (1992) Automatic control of limb movement and posture. Curr Opinion Neurobiol 2:807–814

Persson B, Gentz B (1966) The pattern of blood lipids, glycerol and ketone bodies during the neonatal period, infancy, and childhood. Acta Paediatr Scand 50(55): 353–362

Schneider K, Zernicke RA (1990) A fortran package for the planar analysis of limb intersegmental dynamics from spatial coordinate-time data. Adv Eng Software 12(3): 123–127

Schneider K, Zernicke RF, Ulrich BD, Jensen JL, Thelen E (1990) Understanding movement control in infants through the analysis of limb intersegmental dynamics. J Mot Behav 22(4): 493–520

Sporns O, Edelman GM (1993) Solving Bernstein's problem: a proposal for the development of coordinated movement by selection. Child Dev 64: 960–981

Thelen E (1995) Motor development. Am Psychol 50(2): 79–95

Thelen E, Fisher DM (1982) Newborn stepping: an explanation for a "disappearing reflex". Dev Psychol 18: 760–775

Thelen E, Corbetta D, Kamm K, Spencer JP, Schneider K, Zernicke RF (1993) The transition to reaching: mapping intention and intrinsic dynamics. Child Dev 64: 1058–1098