

## RESEARCH ARTICLE

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# The development toward stereotypic arm kinematics during reaching in the first 3 years of life

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**Abstract** We recorded reaching movements from nine infants longitudinally from the onset of reaching (5th postnatal month) up to the age of 3 years. Here we analyze hand and proximal joint trajectories and examine the emerging temporal coordination between arm segments. The present investigation seeks (a) to determine when infants acquire consistent, adult-like patterns of multijoint coordination within that 3-year period, and (b) to relate their hand trajectory formation to underlying patterns of proximal joint motion (shoulder, elbow). Our results show: First, most kinematic parameters do not assume adult-like levels before the age of 2 years. At this time, 75% of the trials reveal a single peaked velocity profile of the hand. Between the 2nd and 3rd year of life, “improvements” of hand- or joint-related movement units are only marginal. Second, infant motor systems strive to obtain velocity patterns with as few force reversals as possible (uni- or bimodal) at all three limb segments. Third, the formation of a consistent interjoint synergy between shoulder and elbow motion is not achieved within the 1st year of life. Stable patterns of temporal coordination across arm segments begin to emerge at 12–15 months of age and continue to develop up to the 3rd year. In summary, the development toward adult forms of multijoint coordination in goal-directed reaching requires more time than previously assumed. Although infants reliably grasp for objects within their workspace 3–4 months after the onset of reaching, stereotypic kinematic motor patterns are not expressed before the 2nd year of life.

**Key words** Learning · Motor control · Multijoint movement · Human infant

## Introduction

Human motor systems are redundant at muscular and joint level. The nervous system overcomes this inherent redundancy by applying coordinative constraints which in turn will lead to acceptable and unique movement solutions (Flash 1990). During the execution of goal-directed arm movements, these movement solutions yield stereotyped kinematic patterns (i.e., straight hand paths with a bell-shaped velocity profile; Morasso 1983). Recent findings indicate that these stereotyped arm kinematics are not the expression of prewired or inborn motor patterns, but the result of learning during ontogenesis (Corbetta and Thelen 1996; Hofsten 1991; Konczak et al. 1995). It is not known when this learning process finally leads to adult-like stereotyped motor responses and what proximal joint configurations underlie the manifestation of stable endpoint kinematics. (We refer to *endpoint* as the distal part of the human arm, i.e., the hand. With respect to the endpoint, we refer to shoulder and elbow as *proximal joints*.)

Although infants dramatically improve their kinematic performance within the first months after the onset of reaching, the developmental process toward the expression of stereotypic joint kinematics continues beyond the 1st year of life. Previous data from our ongoing longitudinal study indicate that, at 15 months of age, infants have not acquired the degree of kinematic or dynamic “invariance” observable in adult motion (Konczak et al. 1995). Since then we continued to follow these children up to their 4th year of life. The focus of the present paper is to map the developing patterns of proximal joint and endpoint kinematics during reaching. We ask two questions: When do infants achieve consistent kinematics comparable with adults, and what are the corresponding patterns of interjoint coordination that are the basis for efficient endpoint motion?

Most previous studies investigated the kinematic properties of the endpoint, focusing on the spatial layout of the hand path and its derivatives. Our study measured both hand- and joint-space parameters, allowing us to relate

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the development of the hand trajectory to the formation of proximal joint patterns. If one subscribes to the notion that stereotypic kinematic responses are a sign of an established control system, a developmental comparison of endpoint and proximal joint motion should yield unique insights into underlying planning mechanisms and how they constitute themselves during ontogenesis.

## 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 4, 5, 6, 7, 9, 12, 15, 24, and 36 months. Two families moved within that time period, so at 24 months we collected data of only eight children, and observed seven infants at the age of 36 months. In addition, we recorded reaching movements of four healthy adults (mean age 34.9 years, SD 5.9 years).

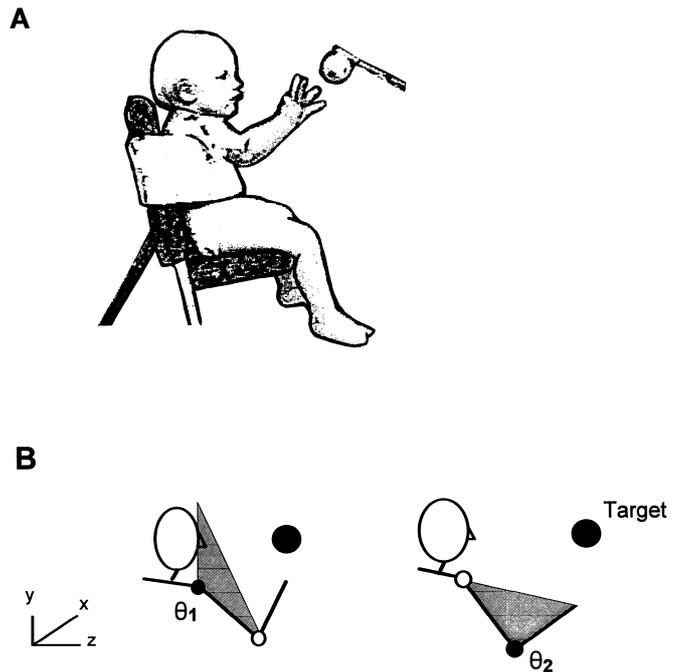
### Procedure

Infants sat in a specially designed chair with their trunk stabilized by a foam-coated seat belt (see Fig. 1). The experimenter or the parents presented small toys at shoulder height and to the right side of the infants. To contact the target object infants had to perform right-handed reaches with a large vertical and small coronal displacement. Infra-red 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 adult movements, markers were attached to the shoulder, elbow, wrist joint, and 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 we had 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.

### Data reduction

A total of 1099 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).

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



**Fig. 1** **A** Scanned video image of a 12-month-old infant reaching for a ball. Infants were sitting in a custom-made chair with no arm rests, allowing free movement of the arms. A foam-coated belt was fastened around the trunk to avoid falling and to minimize trunk translation during reaching. **B** Definition of the planar angles reported in the study.  $\theta_1$  is the 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 ( $z$ ) coordinates of this phantom 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  $\theta_2$  is the planar angle between humerus and ulna. Time-position data of shoulder, elbow, and hand marker were used to calculate  $\theta_2$ .

at shoulder height and to the right side of the infant. Horizontal 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 value of the shoulder angle ( $\theta_1$ ) had to exceed  $125^\circ$  and the initial elbow angle ( $\theta_2$ ) had to be greater than  $85^\circ$ . The shoulder angle  $\theta_1$  is the planar angle enclosed by the upper vertical of the shoulder joint and the humerus. The elbow angle  $\theta_2$  is the planar angle between humerus and ulna. Time-position data of shoulder, elbow, and hand marker were used to calculate  $\theta_1$  and  $\theta_2$ . Both angles determine a plane defined by three markers (see Fig. 1). We choose to report planar angles instead of sagittal projection angles, because these angles more closely reflect actual joint motion when infants moved their arms out of the sagittal plane<sup>1</sup>. Third, at the time of ob-

<sup>1</sup> A drawback of this moving-plane approach is that the planar shoulder angle does not determine a unique position of the upper arm, because this joint has three degrees of freedom. To account for this, we also compared  $\theta_1$  to the sagittal projection angle of the shoulder. The differences for each infant are only marginal. Thus based on this analysis and on our video recordings we can be reasonably sure that the selected reaching movements were largely performed within the sagittal plane.

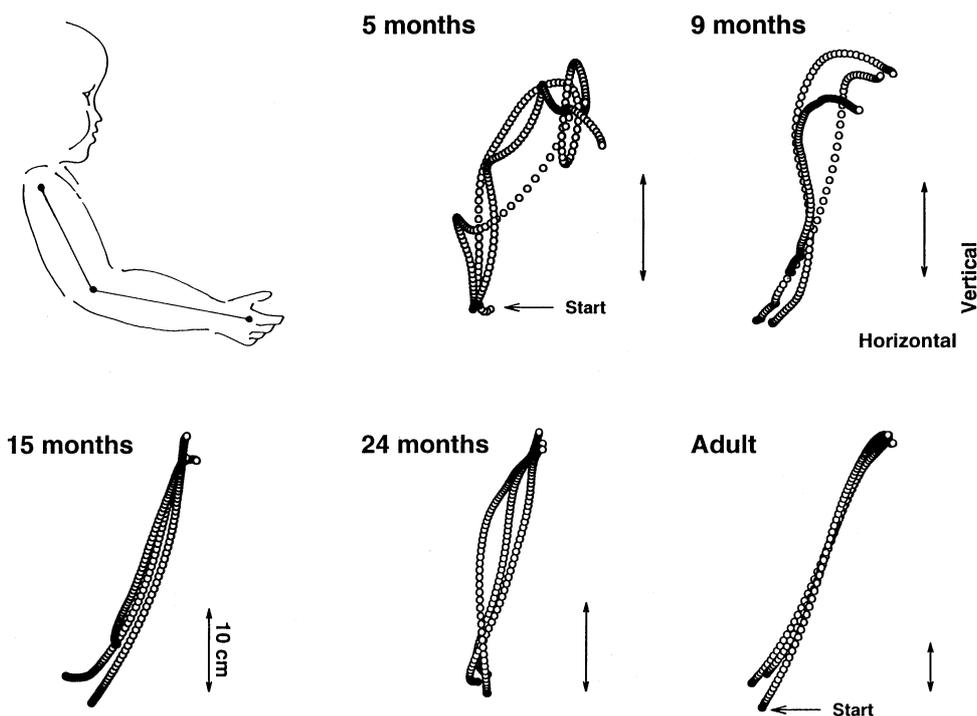
ject contact, the distance between shoulder and hand marker in the sagittal and transverse plane was not allowed to drop below 70% of the infant's total arm length. Arm length was measured as the distance between shoulder and hand marker when the arm was fully extended. This procedure assured that only reaching movements showing a large vertical and small coronal displacement to the periphery of the infants' workspace were analyzed. A total of 537 reaches out of 1099 recorded movements fulfilled the above criteria and also had sufficient visibility of all three joint markers. They were the subject of further analysis.

#### Data analysis

Based on the filtered time-position data, we derived angular and endpoint velocity and acceleration using a three-point differentiation technique. We then determined the *number of movement units of the hand* (MU), representing a measure of how smoothly the hand moved toward the target. A movement unit is defined as the time of one acceleration and one deceleration (or the time of its corresponding velocity peak; Brooks et al. 1973). To assure that only substantial movement reversals were classified as a movement unit, we introduced the following inclusion criterion: If a particular velocity peak exceeded 20% of maximum resultant hand velocity during that trial, we considered this velocity peak a movement unit. We also computed movement units for the elbow and shoulder joint based upon their respective angular accelerations. Infants initiated their movements not necessarily from rest and often did not have zero acceleration at object contact. In those cases we determined the next closest point of zero acceleration and included it for calculation of the number of movement units in that particular trial.

Next, we determined *total length of the hand trajectory* (TL) and *three-dimensional distance* (DIS) between the positions of the hand marker at movement onset and object contact. In order to obtain a measure of straightness of the hand path, we computed the ratio between TL and DIS. As parameters of proximal joint motion, we determined *angular amplitude* as the absolute difference between the angular positions at start and object contact ( $AMP_{\text{Elbow}}$ ,  $AMP_{\text{Shoulder}}$ ) and the *total path length in joint space* ( $PL_{\text{Elbow}}$ ,  $PL_{\text{Shoulder}}$ ). In analogy to the TL/DIS quotient, the ratios between length of joint path and angular amplitude for both proximal joints (i.e.,  $PL_{\text{Elbow}}/AMP_{\text{Elbow}}$ ) represent indirect measures of joint path "straightness."

**Fig. 2** Exemplar sagittal hand paths of one infant at four different developmental times, illustrating the progression toward the "smoothing" of endpoint motion. Time interval between successive data points is 10 ms. The impression that kinematic performance "worsened" between 15 and 24 months is not warranted. Although intertrial variability seemed larger at 24 months in the shown trials, hand paths at both ages had a unimodal velocity profile (no movement reversals). This further argues for the notion that producing "straight" hand paths may not be the first priority of the system during movement planning

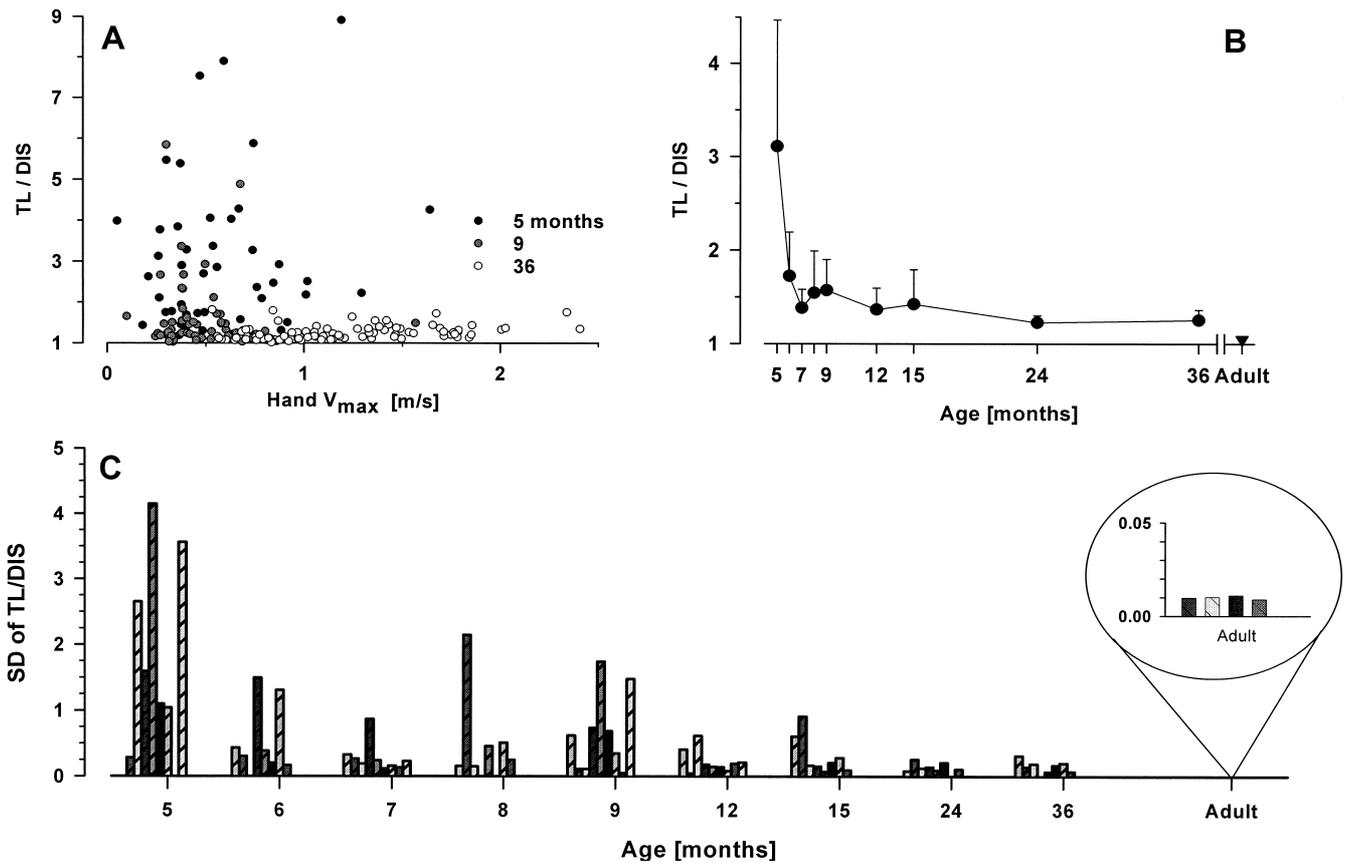


Human adults perform vertical reaching movements with a simple, temporal interjoint synergy. Movements are initiated by shoulder flexion and followed by elbow extension. To document how infants form this temporal synergy between proximal arm segments, we calculated the *relative timing of peak angular velocity at the shoulder* ( $rt_{\text{SHVMAX}}$ ) *during flexion*, and the timing of *peak angular velocity at the elbow* ( $rt_{\text{ELVMAX}}$ ) *during extension* (see Fig. 7). The difference ( $\Delta t$ ) between  $rt_{\text{ELVMAX}}$  and  $rt_{\text{SHVMAX}}$  indicates the temporal relationship between these two events, thus providing a way to assess the degree of temporal coupling between elbow and shoulder motion. To complement this analysis we also calculated the relative timing of peak resultant hand velocity ( $rt_{\text{HDVMAX}}$ ). Each relative timing variable was computed as the quotient of one of these particular temporal events, divided by total movement time (MT).

## Results

### Measures of displacement and velocity

In Fig. 2, exemplar time-position data of one infant illustrate how hand motion is "smoothed" during the 3-year observation period. For five different ages, typical hand paths projected to the sagittal plane are shown. To assess the straightness of the hand path, we computed the quotient of hand path length and distance covered (TL/DIS). An ideal straight-line hand path would result in a TL/DIS ratio of 1. We previously reported (Konczak et al. 1995) that the largest decrement in TL/DIS happened during the first 4 weeks after the onset of reaching. After that time, the quotient of TL/DIS declined only in small increments to 1.2 (SD 0.07) by the age of 2 years and remained at that level for the 3-year-olds (mean 1.3, SD 0.1). With respect to its initial value at the age of 5 months, mean TL/DIS was reduced by over 90% in our infant sample by 24 months of age, indicating the



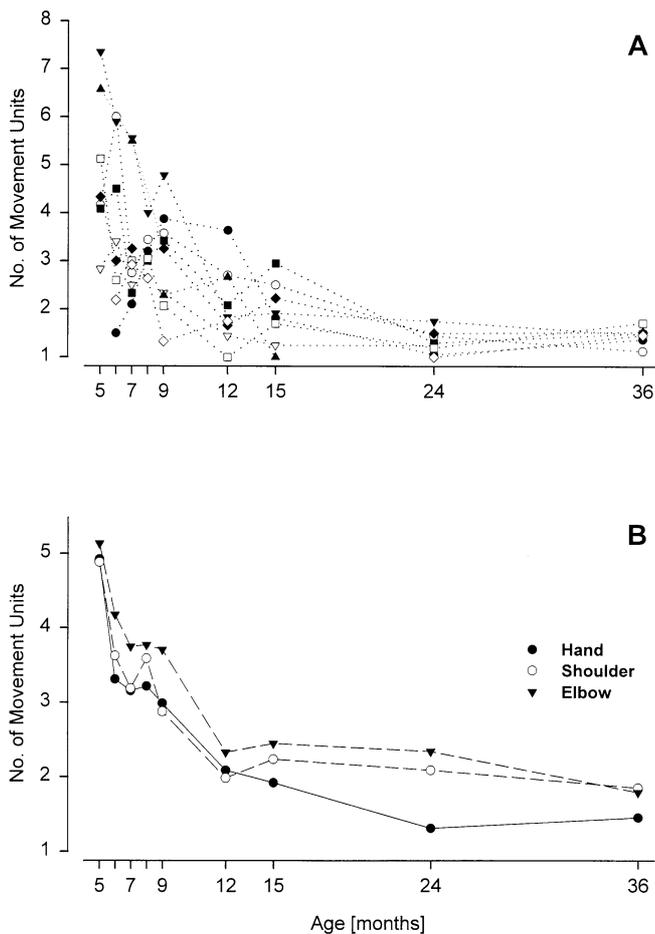
**Fig. 3A–C** Ratio of hand trajectory length ( $TL$ ) and three-dimensional distance ( $DIS$ ) covered by the hand from start to object contact. A ratio of 1 would yield an ideally straight path. **A** Individual trial means of  $TL/DIS$  ratios as a function of peak hand velocity. Velocity units are meters per second. Note how trial variability was reduced during the 3-year period. **B** Group means of  $TL/DIS$  are based on individual subject means computed over the number of trials at a particular age. Mean  $TL/DIS$  for the adult group was 1.1 (SD 0.01). By 2 years of age, infants had essentially achieved a straightness in their hand path that was comparable with adult performance. **C** Individual standard deviations of  $TL/DIS$  for all infants. Each *black bar* represents the standard deviation of a single infant at a particular age and provides an indirect measure of the stability of the observed motor pattern. Note the large degree of interindividual difference after the onset of reaching. Largest decrements are obtained up to the 9th month. By 24 months all infants revealed a similar degree of consistency. However, between-trial variability was still up to 10 times higher at 36 months when compared with adult performance. Reasons for missing SD values are (a) a missed session, or (b) that less than two trials met the inclusion criteria

progressive straightening of the hand path.  $TL/DIS$  ratios of individual trials are shown as a function of peak hand velocity in Fig. 3A and as a function of age in Fig. 3B. How the individual variability of  $TL/DIS$  changed during our observation period and how all infants ultimately reduced their between-trial variability is demonstrated in Fig. 3C.

Another measure of path smoothness, the number of velocity-based movement units per reach, continued to decline until 36 months of age. By the age of 24 months, infants exhibited an average of 1.3 MUs (SD 0.2) per

reach (for data before 24 months, see Konczak et al. 1995). At 36 months of age, mean MU was 1.5 (SD 0.2) – a value not significantly different from the mean performance at 2 years of age ( $P > 0.05$ ). Figure 4 plots the individual means of MU for the infant sample, illustrating the inter- and intra-individual variability that was substantially reduced by the age of 2 years. Table 1 reveals how many trials in each age group were performed with a single movement unit. Trials with a single peaked velocity profile of the hand were observable through all phases of development. Yet not before 2 years of age did unimodal endpoint velocity patterns become predominant. [Following Nelson (1983), we use the term *unimodal* to denote a single peak time-velocity curve].

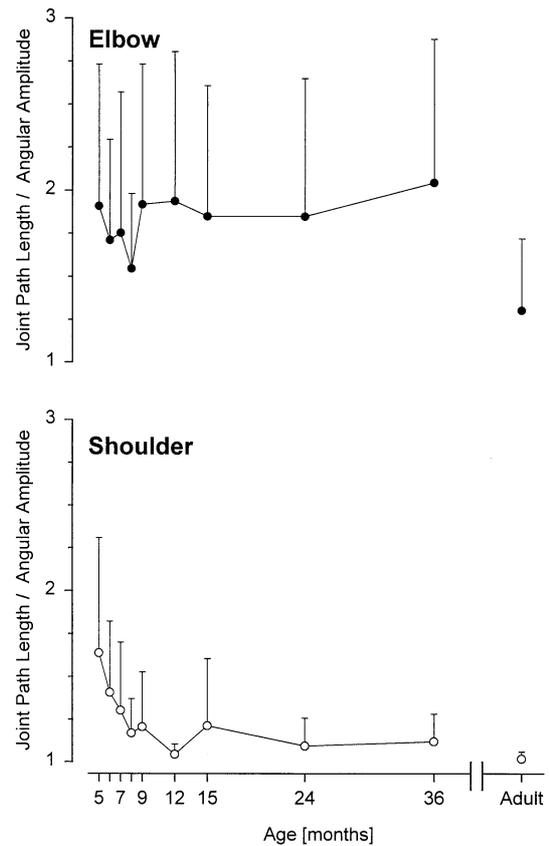
In analogy to determining the straightness of the hand path, we assessed the straightness of the proximal joint trajectories by calculating the *path length/angular amplitude ratios* (i.e.,  $PL_{Shoulder}/AMP_{Shoulder}$ ). If a joint segment moves the shortest possible path, its path length is equal



**Fig. 4A, B** Development of joint and endpoint movement units. **A** Number of endpoint movement units across age. Values are individual subject means. A complete set of nine means could not be obtained for all age groups, because (a) the onset of reaching had not occurred at that time (5 months), (b) there were missed sessions of an infant (6, 7, 8, 24, 36 months), or (c) data did not fulfill inclusion criteria (15 months). Largest reduction in movement units was observed between 5–8 months. By 24 months, 75% of the recorded reaches showed a single velocity peak. **B** Group data for hand, shoulder, and elbow. Values are means of individual subject means. Note the concurrent reductions in movements units at hand and both proximal joints within the 1st year of life

to the angular amplitude between start and contact and the resulting ratio is 1. Our data in Fig. 4 reveal that the elbow path length remained approximately twice as long as the corresponding amplitude until the end of our observation period (36 months) with no appreciative decrease in variability. In contrast, we observed a progressive straightening the shoulder joint path. The largest decrement occurred in the first 3 months after the onset of reaching, from 1.6 (SD 0.7) at 5 months to 1.2 (SD 0.2) at 8 months of age. After that time the quotient of  $PL_{Shoulder}/AMP_{Shoulder}$  ranged between 1.04 and 1.2. The adult mean was computed as 1.01 (SD 0.04).

Mean peak tangential hand velocity steadily increased from an initial 0.56 m/s (SD 0.15) at 5 months to 1.17 m/s (SD 0.32) at 3 years of age. This increase

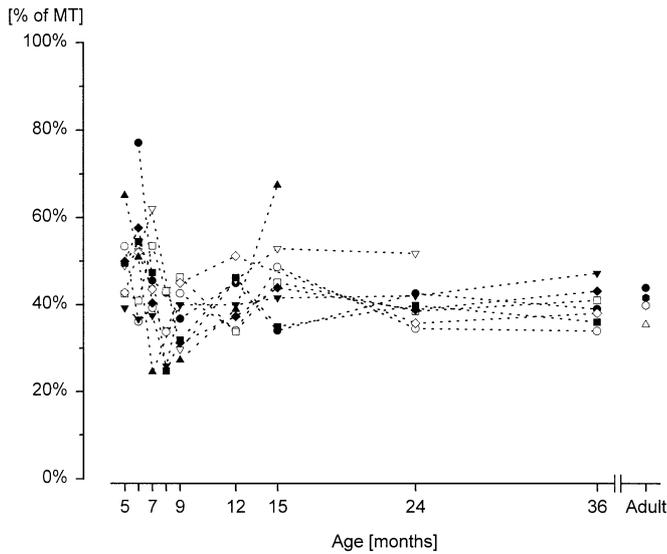


**Fig. 5** Ratios of joint path length and angular amplitude for both proximal joints. Values are group means computed for each developmental age. Units are dimensionless. Note that only the shoulder joint shows a reduction in the path length-amplitude ratio during development

in absolute peak hand velocity is associated with the lengthening of the arm ( $r = 0.59$ ), indicating that development of hand speed was partially influenced by bio-mechanical changes. For the angular velocities that are independent of arm anthropometrics, we found no developmental trend in peak elbow velocity, while shoulder peak velocity during flexion increased steadily from 104°/s (SD 29.9) at 7 months to 186°/s (SD 60.9) at 36 months of age.

#### Measures of temporal coordination

To investigate the temporal organization of hand and proximal joint motion we computed the relative timing of their respective peak velocities during each reach. Adults produced their reaching movement in a stereotyped temporal pattern. Mean peak hand velocity was 40.4% of MT (SD 4.8%), implying that the velocity profile was skewed, giving rise to a slightly longer deceleration phase. Individual standard deviation ranged between 2.1% and 4.6% of MT. This low temporal variability of the endpoint was reflected in the proximal kinematics, with  $rt_{SHVMAX}$  occurring at 46.4% of MT (SD 4.6%)



**Fig. 6** Relative timing of peak hand velocity. Units are percentages of movement time. Values are individual subject means. By 12 months, all infants performed within or near the adult temporal range. The reasons for the missing values are explained in the legend to Fig. 4

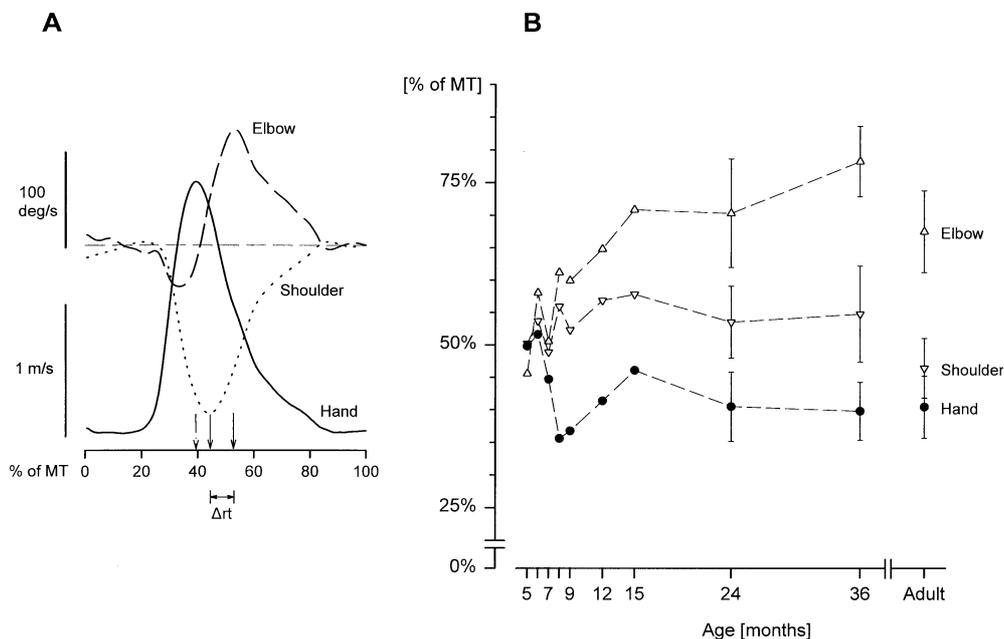
and  $rt_{ELVMAX}$  following later at 67.5% (SD 6.3). These mean values also describe the preferred adult interjoint synergy in this task – shoulder flexion is followed by elbow extension.

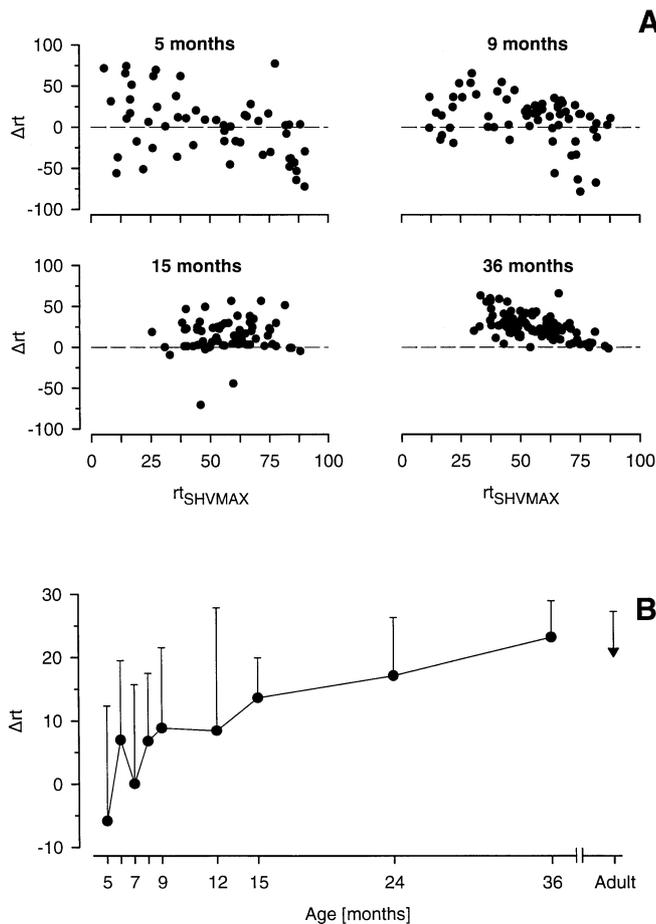
At 5 months of age, mean  $rt_{HDVMAX}$  was 49.8% (SD 8.3%) for our infant sample, indicating that, on average, their hands spent about equal time in acceleration and deceleration. In the months following the onset of reaching,  $rt_{HDVMAX}$  varied considerably intra- and interindividually. By 2 years of age, the infants' mean performance stabilized and assumed values around 40% of MT – effectively lying in the same range as the four adults (see Fig. 6). The

corresponding age group means of  $rt_{HDVMAX}$  next to the corresponding means of the proximal joint peak velocities ( $rt_{SHVMAX}$ ,  $rt_{ELVMAX}$ ) are shown in Fig. 7.

In order to determine the degree of temporal coupling between elbow and shoulder motion in this multijoint task, we computed the difference ( $\Delta rt$ ) between  $rt_{ELVMAX}$  and  $rt_{SHVMAX}$ . Mean  $\Delta rt$  for the adult group was 21.0% (SD 6.3), documenting again that adult reaching movements are characterized by a basic temporal pattern of shoulder flexion followed by elbow extension. Individual adult standard deviations of  $\Delta rt$  ranged from 3.8 to 6.2% of MT. This temporal relationship was not observed at the onset of reaching. At 5 months of age, mean  $\Delta rt$  was  $-5.8\%$  (SD 18.2), indicating that early reaches also showed a pattern of elbow extension preceding shoulder motion. In general, the way elbow and shoulder motion was coupled fluctuated largely during the 1st year. We could not identify a preference for a particular temporal pattern in that time period (see Fig. 8A). Not before 15

**Fig. 7A, B** Relative timing of peak endpoint and proximal joint velocity. **A** Velocity profile of individual adult trial. Resultant peak hand velocity ( $rt_{HDVMAX}$ , *first lefthand arrow*) is closely associated with the peak of shoulder velocity during flexion ( $rt_{SHVMAX}$ , *second arrow*). A decrease in angular velocity corresponds to joint flexion (joint angle gets smaller); an increase in angular velocity corresponds to joint extension (joint angle gets larger). Thus, the local minimum of the velocity curve represents peak angular shoulder velocity during flexion. Elbow extension succeeded shoulder flexion ( $rt_{ELVMAX}$ , *third arrow*).  $\Delta rt$  represents the temporal difference between peak shoulder velocity during flexion and peak elbow velocity during extension. *Dashed horizontal line* represents  $0^\circ/s$ . **B** Mean relative timing of the three temporal events specified in **A**. Values are means of individual subject means. Temporal onset of peak shoulder and hand velocities remained stable between 24 and 36 months of age. *Error bar* represents 1 SD. For sake of readability, error bars for ages 5–15 months are omitted. For that period, SDs ranged:  $rt_{HDVMAX}$  5.9–13.7%;  $rt_{ELVMAX}$  9.2–20.3%; and  $rt_{SHVMAX}$  7.6–17.4% of MT. *Filled circles*,  $rt_{HDVMAX}$ ; *empty triangles*,  $rt_{ELVMAX}$ ; *empty inverted triangles*,  $rt_{SHVMAX}$





**Fig. 8A, B** Temporal difference in the relative onset of shoulder and elbow peak velocity ( $\Delta r_t$ ). **A** Individual trial means at four different ages. *Abscissa* is peak shoulder velocity during flexion ( $r_{tSHVMAX}$ ). A negative value of  $\Delta r_t$  implies that elbow extension preceded shoulder flexion. Across infants a common timing pattern emerges, with negative  $\Delta r_t$  values substantially diminished by 15 months and no longer occurring at 36 months. See Fig. 7A for the computation of  $\Delta r_t$ . **B** Development of  $\Delta r_t$  across age. Values are means of individual subject means. *Error bar* represents 1 SD. A temporal pattern of elbow flexion following shoulder extension that was comparable with adult movements was not achieved before 24 months

months of age did mean  $\Delta r_t$  fall within in the adult range, indicating that a firm temporal sequence of successive shoulder flexion and elbow extension was then realized in the majority of the infant trials (see Fig. 8B).

## Discussion

Infants attempt their first goal-directed reaches around 4–5 months of age. The kinematics of these reaching movements have an ataxic appearance with segmented hand paths and multiple velocity peaks. At the onset of reaching, interindividual differences in hand trajectory and intersegmental coordination are substantial. Shape and velocity of the selected trajectories vary greatly. During development infants converge to a common basic

pattern of intralimb and endpoint organization, systematically reducing their between-trial variability. Up to now it has been unclear when the developmental process toward the expression of stereotyped kinematic patterns is actually completed. Concerning the period of early reaching, our data corroborate the results of previous studies (Hofsten 1991; Konczak and Thelen 1994; Mathew and Cook 1986; Thelen et al. 1993), showing that after 4–8 weeks of practice infants have found movement solutions that satisfy their objective of grasping the presented toy object. Yet, even after this initial practice period, the kinematic features of their arm movements are far from resembling the efficiency and consistency seen in adult reaching. We found that consistent unimodal endpoint kinematic patterns do not begin to emerge before the age of 12–15 months. By 2 years of age, unimodality of tangential hand velocity is basically achieved, and many other spatial and temporal endpoint and proximal joint parameters exhibit a variability close to or within the adult range. Yet, differences in spatial layout and precision of velocity control may still exist between 3-year-old children and adults.

Within the first 3 years of life, endpoint and shoulder joint path lengths were shortened substantially, both following a similar developmental time course. In contrast, the straightness of the elbow joint path remained variable and was not significantly shortened throughout this observation period. The fact that only shoulder, but not elbow, joint paths were reduced in length and variability during development underlines the primary importance of the shoulder joint during vertical reaching. Although not conclusive, our data are consistent with the view that vertical arm movements are planned in *shoulder-centered* coordinates – a claim based on previous studies with human adults (Soechting and Flanders 1989a, b).

An alternative explanation for this phenomenon is that the motor system attempts to reduce redundancy by the use of a *principal joint* whose rotation can cover most of the distance between initial and target position of the hand (Haggard et al. 1995). A potential benefit of applying a *principal-joint strategy* is that it simplifies multi-joint coordination, because “secondary” joint trajectories do not need to be specified in detail through all phases of the movement. In the case of vertical reaching, the exact angular position of forearm is not critical during the transport phase of the upper arm but needs to be precise when the hand is approaching the target. The problem with this view is that the secondary joint cannot stay uncontrolled for certain parts of the trajectory, because the interaction forces of distal limb segments certainly influence the joint path of more proximal limb segments (Hollerbach and Flash 1982; Jensen et al. 1994; Virji-Babul and Cooke 1995). Thus, in the case of reaching, any multijoint controller needs to know the direction and magnitude of the interactive torque from the elbow to maintain control of the primary shoulder joint; even so, the actual elbow joint kinematics may not be important for early parts of the trajectory.

## Achieving low-modality velocity patterns

The analysis of the velocity profiles unambiguously indicates that within the infinite number of joint configurations that satisfy the objective of grasping the presented toy, infant motor systems strive to produce movement patterns yielding uni- or bimodal velocity profiles for endpoint and proximal joint motion. Unimodal velocity patterns represent a certain movement efficiency, because they are characterized by a single acceleration phase followed by a single episode of deceleration, thus requiring no intermediate force reversals (Nelson 1983). Kinematic patterns with unimodal endpoint velocity profiles are rarely observable at the onset of reaching. At 15 months of age about a third of the recorded reaches showed a single endpoint velocity peak, and by the age of 2 years over 75% of the reaching movements exhibited a unimodal endpoint velocity pattern. That is, although infants drastically reduced endpoint movement units within the first 2–3 months after the onset of reaching, it took most infants at least an additional 7 months before they predominantly produced hand trajectories with single velocity peaks (see Table 1). With respect to the proximal joints, the reductions in shoulder and elbow MU followed largely the same time course as the development of endpoint MU (see Fig. 4B).

Obviously, the mechanical coupling of arm segments mandates that an increased “smoothness” of the hand trajectory cannot be realized while proximal joint motion is jerky. The reason for jerky proximal joint motion lies in unstable control of the joint dynamics. Our infants clearly showed such signs of unstable dynamic control (Konczak et al. 1997). At the onset of reaching, infants frequently switched between producing flexor and extensor muscle torque (up to 20 joint torque reversals within a single trial). With increasing age they decreased the number of force reversals at both shoulder and elbow joint, which then resulted in a smaller number of joint-related movement units, ultimately translating into smoother endpoint motion.

## Emergence of intralimb coordination

Intralimb coordination requires that limb segments are moved within closely defined temporal relationships. The underlying synergies that are the basis of stereotypic interjoint patterns are not established when infants start to reach, but have to be acquired during ontogenesis. This study describes the developmental progression of infant motor systems to relate distal elbow motion to proximal shoulder motion in a predictable manner – a phenomenon that is also characteristic of adult arm movements (Lacquaniti and Soechting 1982; for a review, Soechting and Terzuolo 1990). We reveal how infants lock upper and lower arm movements into a distinct temporal relationship during reaching, thus forming a functional intralimb synergy. At the onset of reaching, both limb segments moved largely independent of each other – elbow exten-

sion could precede or trail shoulder flexion. With increasing age a discrete timing pattern emerged where shoulder flexion initiated the reach followed by elbow extension. By about 24 months of age this interjoint synergy had become the predominant pattern of intersegmental coordination in all of our infants. The emergence of such temporal coupling among limb segments is indicative of an internal constraint of movement execution. But to be fair, our data cannot be conclusive on this issue, because we only investigated reaches to a single target within the workspace. We do not know whether this relationship is preserved during reaching to different targets. However, assuming the same starting position, but a different target location, we would predict that similar temporal patterns of intralimb coordination evolve during development.

Our kinematic and electromyographic data (Konczak et al. 1997) provide empirical support to the notion that developing nervous systems employ synergies to reduce both the number of controlled movement parameters and the amount of afferent information necessary for the generation and guidance of goal-directed movement (Bernstein 1967, 1988). A neurobiological model of how these synergies might be formed in ontogenesis presents the theory of neuronal group selection (Edelman 1993; Sporns and Edelman 1993). In simple terms, the theory states that appropriate motor patterns are selected from a basal movement repertoire acquired by prenatal and early postnatal spontaneous movements. Basal brain circuits form functional neuronal groups during development that ultimately lead to the progressive formation of a task-related movement repertoire. Empirical findings from animal studies (Bekoff et al. 1989) support this view, and our data on human motor development are congruent with the theory.

## Summary

After human infants begin to reach, they need 10 months or more to acquire stereotypic arm kinematics. In essence, this time period is necessary to find stable solutions to the problem of matching one’s own muscular forces to changing external forces. Considering the “simplicity” of our reaching task, developmental progress might seem relatively slow on first sight. Yet, other tasks such as the force control in the precision grip follow a similar developmental time course (Forssberg et al. 1991). In our view these “long” time periods for the formation of stereotypic motor responses are not surprising considering that neural development and infant growth spurt continue well into the 3rd year of life (Barkovich et al. 1988; Kinney et al. 1988; Tanner 1981). Thus, early motor development can be viewed as a process of continuing calibration of the motor system in the presence of ongoing neural and anthropometric growth.

The exact mechanisms of how changes in central structures innervating the muscles are matched to peripheral changes are not yet known. Thus, one future task is to determine which invariants fall out of the biomechanics (pe-

ripheral constraints) and which are the result of a neural constraint. In this context experiments are needed where infants perform reaches (a) to different parts of the workspace and (b) under varying task constraints (i.e., changing loads, targets, moving around obstacles). Only if reaching under different task constraints yields similar kinematic or dynamic invariants can one be reasonably sure that these parameters are considered in a planning process.

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## References

- Barkovich AJ, Kjos BO, Jackson DE Jr, Norman D (1988) Normal maturation of the neonatal and infant brain: MR imaging at 1.5 T. *Radiology* 166:173–180
- Bekoff A, Kauer JA, Fulstone A, Summers TR (1989) Neural control of limb coordination. *Exp Brain Res* 74:609–617
- Bernstein NA (1967) *The co-ordination and regulation of movements*. Pergamon Press, Oxford
- Bernstein NA (1988) Die Koordination der Bewegungen in der Ontogenese. In: Pickenhain L, Schnabel G (eds) *Bewegungsphysiologie*. Barth, Leipzig, pp 99–137
- Brooks VB, Cooke JC, Thomas JS (1973) The continuity of movements. In: Stein RB, Pearson KG, Smith RS, Bedford JB (eds) *Control of posture and locomotion*. Plenum Press, New York, pp 257–272
- Corbetta D, Thelen E (1996) The developmental origins of bimanual coordination: a dynamic perspective. *J Exp Psychol: Hum Percept Perform* 22:502–522
- 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
- Edelman GM (1993) Neural Darwinism: selection and reentrant signaling in higher brain function. *Neuron* 10:115–125
- Flash T (1990) The organization of human arm trajectory control. In: Winters JM, Woo SL-Y (eds) *Multiple muscle systems: biomechanics and movement organization*. Springer, New York, pp 282–301
- Forsberg H, Eliasson AC, Kinoshita H, Johansson RS, Westling G (1991) Development of human precision grip. I. Basic coordination of force. *Exp Brain Res* 85:451–457
- Haggard P, Hutchinson K, Stein J (1995) Patterns of coordinated multi-joint movement. *Exp Brain Res* 107:254–266
- Hofsten C von (1991) Structuring of early reaching movements: a longitudinal study. *J Mot Behav* 23:280–292
- Hollerbach JM, Flash T (1982) Dynamic interactions between limb segments during planar arm movement. *Biol Cybern* 44:67–77
- Jensen JL, Ulrich BD, Thelen E, Schneider K, Zernicke RF (1994) Adaptive dynamics of the leg movement patterns of human infants. I. The effects of posture on spontaneous kicking. *J Mot Behav* 26:303–312
- Kinney HC, Brody BA, Kloman AS, Gilles FH (1988) Sequence of central nervous system myelination in human infancy. II. Patterns of myelination in autopsied infants. *J Neuropathol Exp Neurol* 47:217–234
- 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 force control. *Exp Brain Res* 106:156–168
- Konczak J, Borutta M, Dichgans J (1997) Development of goal-directed reaching in infants. II. Learning to produce task-adequate patterns of joint torque. *Exp Brain Res* 113:465–474
- Lacquaniti F, Soechting JF (1982) Coordination of arm and wrist motion during a reaching task. *J Neurosci* 2:399–408
- Mathew A, Cook M (1986) The control of reaching movements by young infants. *Child Dev* 61:1238–1257
- Morasso P (1983) Three dimensional arm trajectories. *Biol Cybern* 48:187–194
- Nelson WL (1983) Physical principles for economies of skilled movements. *Biol Cybern* 46:135–147
- Soechting JF, Flanders M (1989a) Sensorimotor representations for pointing to targets in three-dimensional space. *J Neurophysiol* 62:582–594
- Soechting JF, Flanders M (1989b) Errors in Pointing are due to approximations in sensorimotor transformations. *J Neurophysiol* 62:595–608
- Soechting JF, Terzuolo CA (1990) Sensorimotor transformations and the kinematics of arm movements in threedimensional space. In: Jeannerod M (ed) *Motor representation and control*. (Attention and performance XIII). Erlbaum, Hillsdale, NJ, pp 479–494
- Sporns O, Edelman GM (1993) Solving Bernstein's problem: a proposal for the development of coordinated movement by selection. *Child Dev* 64:960–981
- Tanner JM (1981) *A history of the study of human growth*. Cambridge University Press, Cambridge
- 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
- Virji-Babul N, Cooke JD (1995) Influence of joint interaction effects on the coordination of planar two-joint arm movements. *Exp Brain Res* 103:451–459