Training affects the development of postural adjustments in sitting infants

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1. The present study addressed the question of whether daily balance training can affect the development of postural adjustments in sitting infants.
2. Postural responses during sitting on a moveable platform were assessed in twenty healthy infants at 5–6, 7–8 and 9–10 months of age. Multiple surface EMGs and kinematics were recorded while the infants were exposed to slow and fast horizontal forward (Fw) and backward (Bw) displacements of the platform. After the first session the parents of nine infants trained their child's sitting balance daily.
3. At the youngest age, when none of the infants could sit independently, the muscle activation patterns were direction specific and showed a large variation. This variation decreased with increasing age, resulting in selection of the most complete responses. Training facilitated response selection both during Fw and Bw translations. This suggests a training effect on the first level of the central pattern generator (CPG) model of postural control.
4. Training also affected the development of response modulation during Fw translations. It accelerated the development of: (1) the ability to modulate EMG amplitude with respect to platform velocity and initial sitting position, (2) antagonist activity and (3) a distal onset of the response. These findings point to a training effect on the second level of the CPG model of postural adjustments.

Motor development results from an interaction between genetic programmes and environmental signals (Waddington, 1962; Jacobson, 1991). Some motor patterns, such as breathing and swallowing, which emerge during early fetal life (De Vries, Visser & Prechtl, 1982), develop mainly on the basis of innate information. Other motor patterns, such as writing or skating, develop only through specific training. The role of 'nature' and 'nurture' in the development of automatic motor patterns involved in postural control and walking, is a matter of debate. Thelen and coworkers, who studied infant walking, claimed that development is mainly driven by practice (Thelen, 1988; Ulrich, 1989), while others assumed that the development of gross motor functions is guided by endogenous maturation and selection of predetermined neuronal connections (Gesell, 1940; McGraw, 1943; Forssberg, 1985; Hirschfeld & Forssberg, 1994). Observational studies on the effect of training on the development of gross motor functions indicated that external stimulation can accelerate normal development (McGraw, 1935; Lagerspetz, Nygård & Strandvik, 1971; Zelazo, Zelazo & Kolb, 1972; Zelazo, 1983).

In order to improve our understanding of the contribution of 'nature' and 'nurture' in the development of automatic motor patterns, we carried out a longitudinal study of the effect of training on the development of postural control. Postural control of healthy sitting infants, aged 5–10 months, was assessed by means of external perturbations. Recently, Forssberg & Hirschfeld (1994) postulated that postural adjustments to external displacements are generated by central pattern generators (CPGs) organized in two functional levels, one dealing with the selection of the basic muscle activation pattern, the other involved in task-specific modulation of the selected pattern (e.g. Horak & Nashner, 1986; Keshner, Woollacott & Debû, 1988; Hirschfeld & Forssberg, 1991). In the preceding paper we reported the changes occurring during

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normal development without specific training (Hadders-Algra, Brogren & Forssberg, 1996). In the present study the following questions were addressed: (1) Does daily balance training facilitate the selection of the most complete response patterns? Such a facilitation of response selection would imply a training effect at the first level of the CPG model. (2) Does daily balance training affect the development of postural response modulation, i.e. the development of the circuitry at the second level of the CPG model?

Some of the present findings have already been published in preliminary form (Hadders-Algra, Brogren, Apel & Forssberg, 1994*a*, *b*; (Hadders-Algra & Forssberg, 1995).

METHODS

Subjects

Twenty healthy infants were assessed three times with an interval of 2 months at the ages of 5–6, 7–8 and 9–10 months of age. All parents gave informed consent and the procedures were approved by the Medical Ethics Committee of the Karolinska Hospital. At the first experimental session none of the infants could sit independently. At this occasion the parents of ten infants were asked to train their child's sitting balance three times a day during five minutes throughout the study period. Training consisted of toy presentation in the border zone of reaching-without-falling. Special attention was put on sidewards- and semi-backward reaches. The parents of one girl erroneously trained their daughter for only one week. This child was regarded as non-trained, resulting in a total number of eleven non-trained infants (6 girls and 5 boys, whose postural control development has been described in Hadders-Algra *et al.* 1996). The other nine infants (5 girls and 4 boys) could be trained appropriately until crawling behaviour emerged, 2–4 weeks before the final assessment, implying that the infants were trained for a period of 3–3·5 months. The assignment of the children to the training or non-training group occurred before lab entry, in order to obtain a group selection free from bias on postural control abilities and to get a similar age and sex distribution in both groups. At the first assessment session the parents were asked to note the day on which the infant was able to sit independently for about 10 s.

The protocol, recording and analyses techniques were similar to those described in Hadders-Algra *et al.* (1995). In short, procedures were as follows.

Protocol

The infants sat on a moveable platform, which produced a standard series of thirty-two random forward (Fw) and backward (Bw) translations (16 slow perturbations followed by 16 fast ones). Infants not able to sit independently were supported until 0·5–1·0 s before trial onset. The whole testing series was recorded on video, allowing selection of trials fulfilling obligatory testing conditions (non-crying, alert behavioural state; sitting as straight as possible).

EMG and kinematic recordings

Surface electromyograms (EMGs) were recorded from the sternocleidomastoideus (neck flexor, NF), rectus abdominis (RA), rectus femoris (RF), neck, thoracal and lumbar extensor muscles (NE, TE, LE) and hamstrings (Ham) on the left side of the body. TE and LE were analysed together (TE–LE), as they were usually activated in concert.

Simultaneously with the EMGs, movements were recorded by an ELITE system (Bioengineering, Technology and Systems, Milan, Italy) in a two camera configuration. Reflective markers were put on the left side of the body: (1) on the caput mandibulae, (2) 1 cm in front of the angulus mandibulae, (3) on the anterior superior iliac spine, and (4) on the trochanter major. Additionally, three markers were put on the lateral side of the platform.

Data acquisition and analysis

EMG analysis was carried out in two steps. First, muscle activation patterns were documented by describing the presence of bursts and inhibition in the recorded muscles. Second, for the analysis of EMG amplitudes, latencies and antagonistic activity, only trials were selected which had resulted in the most complete muscle activation patterns. Amplitudes and latencies were calculated as in the preceding paper. Antagonist activity was analysed during slow perturbations only, as a similar analysis during the shorter-lasting fast translations was hampered by an intermingling of responses related to platform onset and platform stop. On an empirical basis, taking into account the long duration of the EMG bursts, antagonist activity was classified as a co-activation when the onset of the antagonist occurred ≤ 100 ms after the onset of the agonist, and as reciprocal activity when the interval between agonist and antagonist onset exceeded 100 ms. Antagonist activity was expressed as rate per muscle per condition per infant.

Within each group comparisons of processed EMG data, such as mean latency and mean amplitude values per infant, were carried out with the help of Wilcoxon and Friedman tests. Differences between the two groups were calculated with the Mann–Whitney test.

Kinematic analysis. Focus was on angular values at movement onset and angular displacement (the difference between peak value and onset value) of head, pelvis and body sway. Pelvis onset angle analysis was carried out at 5–6, 7–8 and 9–10 months in 9, 10 and 4, and 4, 3 and 2 infants in the non-trained and trained group, respectively. The analysis of head rotation, body sway and pelvis displacement was performed on the two infants with the most complete kinematic recordings of each group and age. To evaluate the effect of training on angular displacements MANOVA was performed taking into account a possible effect of subject and response pattern. Pearson's correlation coefficient was used for the calculation of correlations between initial sitting position, angular displacement and functional sitting behaviour on the one hand and muscle activity on the other hand.

Throughout the study differences and correlations with a P value $< 0{\cdot}05$ were considered to be statistically significant.

RESULTS

Muscle activation patterns

At 5–6 months both groups of infants showed direction-specific postural responses with a large variation. Fw translations resulted in a variable activation of the 'ventral' muscles (NF, RA and RF) and an inhibition of the 'dorsal' muscles, whereas Bw translations elicited a variable activation of the dorsal extensor muscles (NE, TE, LE and Ham). With increasing age the variation in muscle

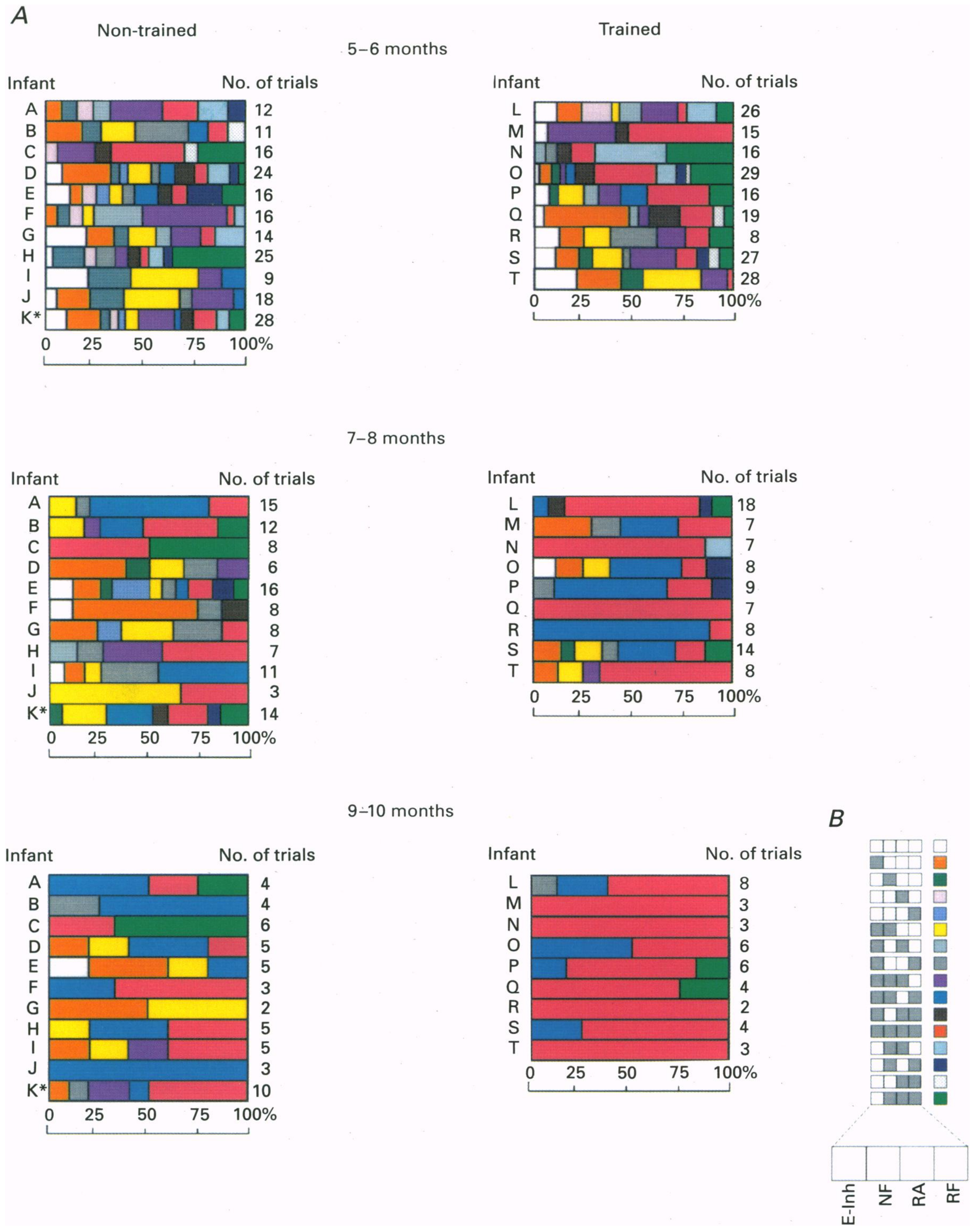

Figure 1. Effect of age and training on response variation

A, developmental changes in response pattern during slow Fw translations. In each horizontal bar the distribution of response patterns for one subject is represented. Infant K is the erroneously non-trained infant. *B*, colour codes of the response patterns in *A*. Hatching of a square indicates participation of a muscle in a particular pattern. Here and in subsequent figures: E-Inh, extensor inhibition; NF, neck flexor; RA, rectus abdominis; RF, rectus femoris.

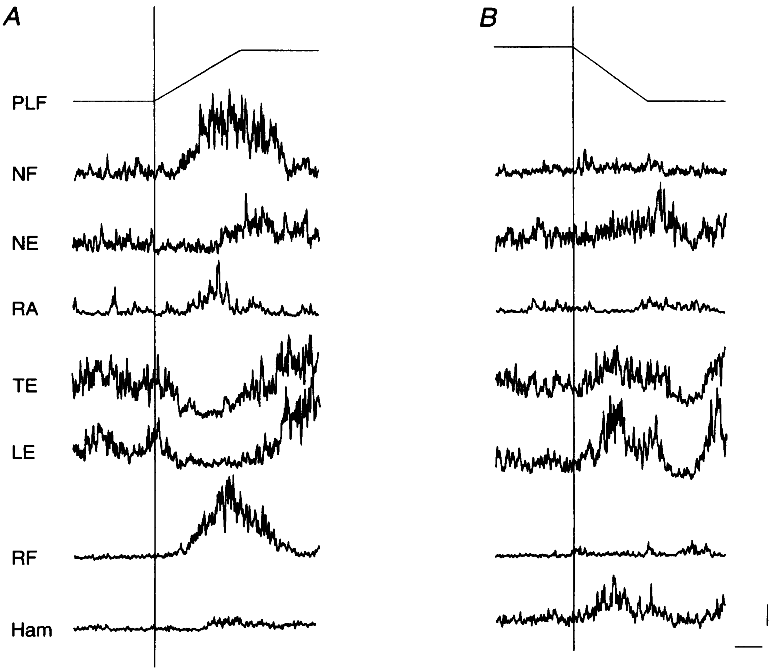

Figure 2. Complete response patterns during Fw and Bw translations

Complete response patterns of infant L of the trained group at 10 months. Average activity of 6 fast Fw trials (*A*, response: E-Inh + NF + RA + RF, the 'red' pattern) and, 6 fast Bw trials (*B*, response: NE + TE–LE + Ham). PLF, platform signal. Time calibration (horizontal bar), 100 ms; amplitude calibration (vertical bar), 0·01 mV. NF, neck flexors; NE, neck extensors; RA, m. rectus abdominis; TE, thoracal extensors; LE, lumbar extensors; RF, m. rectus femoris; Ham, hamstrings.

activation patterns decreased, resulting in selection of the most complete patterns (Fw translations: extensor inhibition (E-Inh) in combination with NF + RA + RF or NF + RF (Fig. 1); Bw translations: NE + TE–LE + Ham, see also Fig. 2). Selection was facilitated by training, especially so during slow translations (Fig. 1). A higher platform velocity also enhanced selection (see Hadders-Algra *et al.* 1996), thereby partly obscuring a training effect during fast translations. At 5–6 months the rate of occurrence of the complete patterns was low, with the non-trained infants showing a higher frequency of the complete pattern during Bw translations than the infants who were going to be trained. However, at 9–10 months the trained infants selected the complete patterns significantly more

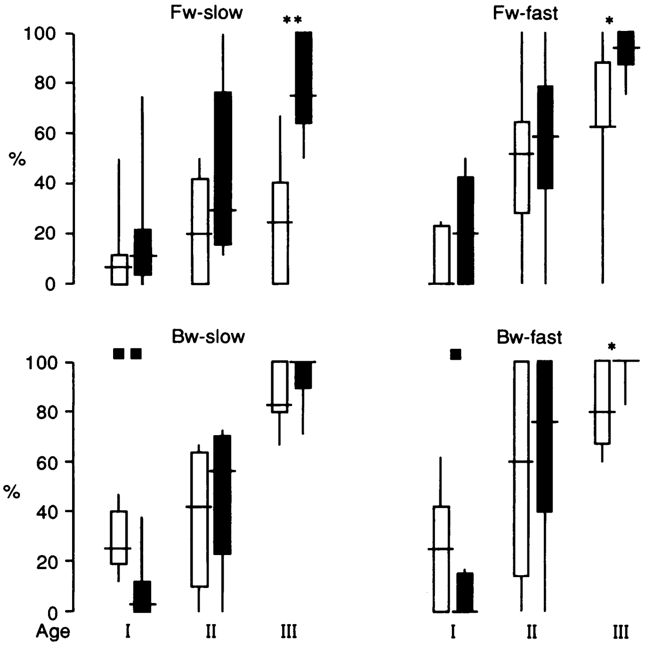

Figure 3. Developmental changes in the rate of the complete pattern during Fw and Bw translations

Group data on developmental changes in the rate of occurrence of the complete pattern during Fw translations (E-Inh + NF + RA + RF) and Bw translations (NE + TE + LE + Ham). The rate of the complete pattern was calculated for each infant and each condition by dividing the number of trials during which the complete pattern was found by the total number of trials. The data are presented as ranges (vertical bars), interquartile ranges (boxes) and median values (horizontal bars). □, the non-trained group; ■, the trained group. The absence of the interquartile box in the graph of the oldest trained infants during fast Bw translations signifies little variation with identical median and interquartile values. Asterisks indicate statistically significantly higher rates in the trained than in the non-trained group: * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; black squares denote significantly higher rates in the opposite direction: ■, $P < 0{\cdot}05$; ■■, $P < 0{\cdot}01$. I, 5–6 months; II, 7–8 months; III, 9–10 months.

often than the non-trained infants, both during Fw and Bw translations (Fig. 3).

The training effect was especially clear in the developmental trajectories of the preference pattern, i.e. the pattern the infant used most frequently in a specific condition (Fig. 4). At the youngest age both groups of infants showed a large variation in preference pattern. During slow Fw translations at 7–8 months, the trained infants preferred the two most complete response patterns (E-Inh + NF ± RA + RF, the red and blue patterns in Fig. 1), whereas the non-trained infants continued to show a large variation in preference pattern (Fisher, $P < 0{\cdot}01$). At 9–10 months all trained infants preferred the complete ('red') response pattern during slow Fw translations, whereas only four of the eleven non-trained infants did (Fisher, $P < 0{\cdot}01$). A similar effect of training on the development of preference patterns was present during slow Bw translations, but absent during fast perturbations.

The time interval between the first assessment and the age at which the child could sit independently varied from 7 to 98 days in the non-trained group and from 3 to 45 days in the trained group (median values 31 and 18, respectively; a non-significant difference). In both groups no relationship could be demonstrated between the number of days the child had experienced independent sitting and the amount of complete pattern found during Bw and Fw translations during the second or third examination.

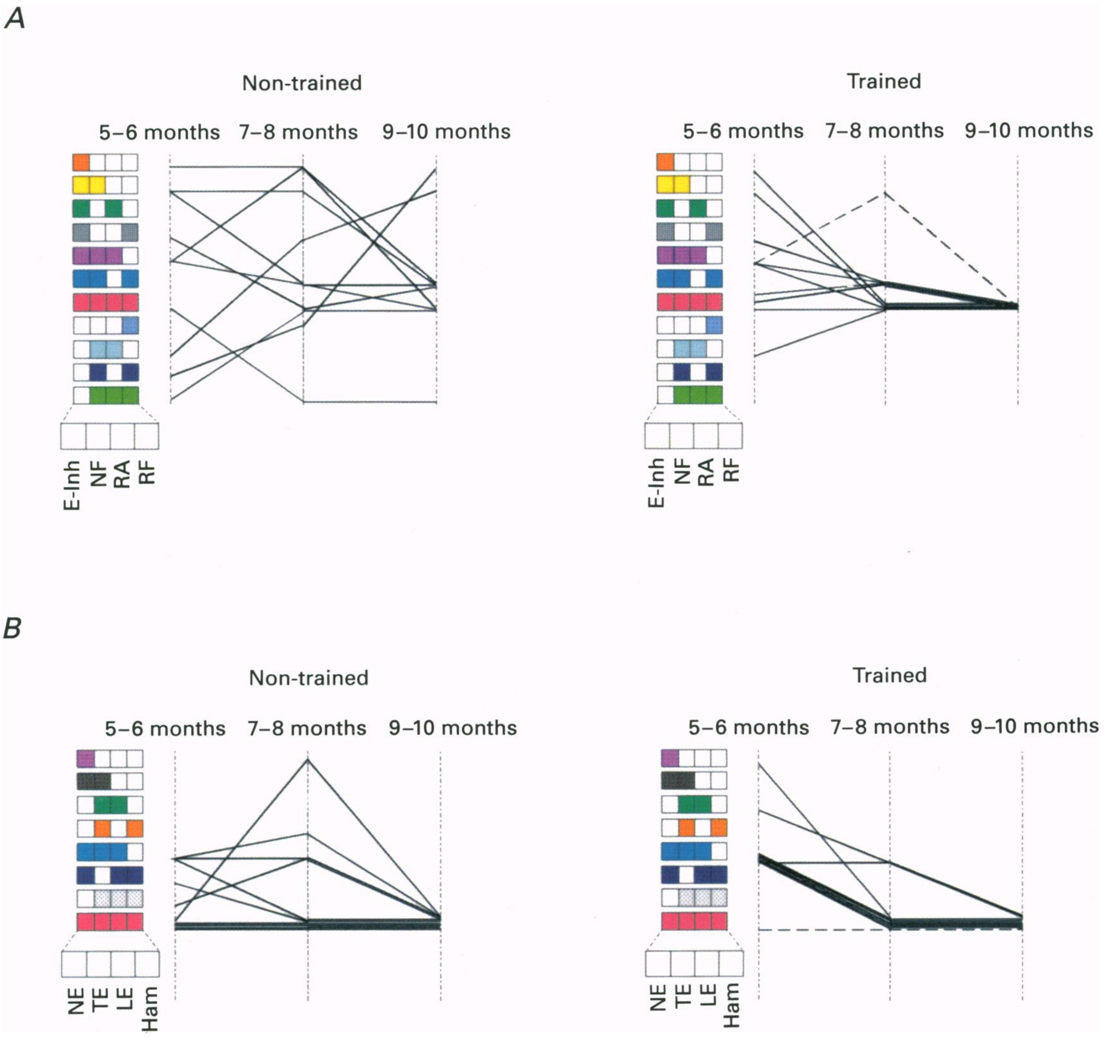

Figure 4. Development of preference patterns

Development of individual preference patterns during slow Fw (*A*) and slow Bw (*B*) translations. Each line represents one infant. The dashed line indicates the erroneously non-trained infant. Filling of a square in the code-block on the left side of the diagram indicates participation in a particular pattern. The colours correspond with Fig. 1.

EMG amplitude modulation

Previously, we demonstrated that in non-trained infants the ability to modulate EMG amplitude to the platform velocity emerged at 9–10 months (Hadders-Algra *et al.* 1996). The higher platform velocity during Fw translations was associated with a significantly larger mean flexor amplitude calculated during the first 400 ms of the response (NF_{400}, RA_{400} and RF_{400}). In the trained infants a similar modulatory effect of platform velocity on RA_{400} and RF_{400} during Fw translations was already present at 7–8 months (Fig. 5). An effect of platform velocity on extensor EMG amplitude during Bw translations was absent in both groups.

Before, we also reported that non-trained infants can modulate flexor amplitude during Fw translations to initial sitting position from 9–10 months onwards: a larger pelvis angle at perturbation onset was associated with significantly higher RA_{400} and RF_{400} values (Hadders-Algra *et al.* 1996). At 7–8 months, similar correlations were totally absent in the non-trained group, whereas in the trained group correlations were on the verge of emergence, reaching statistical significance only in the relation between initial pelvis angle and RF_{400} during fast Fw translations ($r = 0{\cdot}53$, $P < 0{\cdot}02$). In both groups initial pelvis angle during Bw translations was not related to extensor amplitude.

Antagonist activation

In the non-trained infants slow Fw translations did not elicit consistent activity in the antagonistic extensor muscles, whereas the trained infants showed activity in the antagonists at 9–10 months in more than half the slow Fw translations (Fig. 6). Antagonistic activity consisted of co-activation in the neck and leg, i.e. NE and Ham were activated within 100 ms after onset of the flexor burst, whereas TE was activated in a reciprocal way, starting > 100 ms after RA onset (see Fig. 2*A*). Antagonistic activity in flexor muscles during Bw translations was absent on all occasions.

Latencies and temporal order

In neither group were statistically significant developmental changes found in the latencies to the various EMG responses. At the youngest age, the latencies to the onset of flexor activity during Fw translations varied considerably. This variation in flexor onset latency decreased with increasing age, most clearly so in RA and RF latency of the trained infants. The latencies to the extensor responses showed little variation at any age.

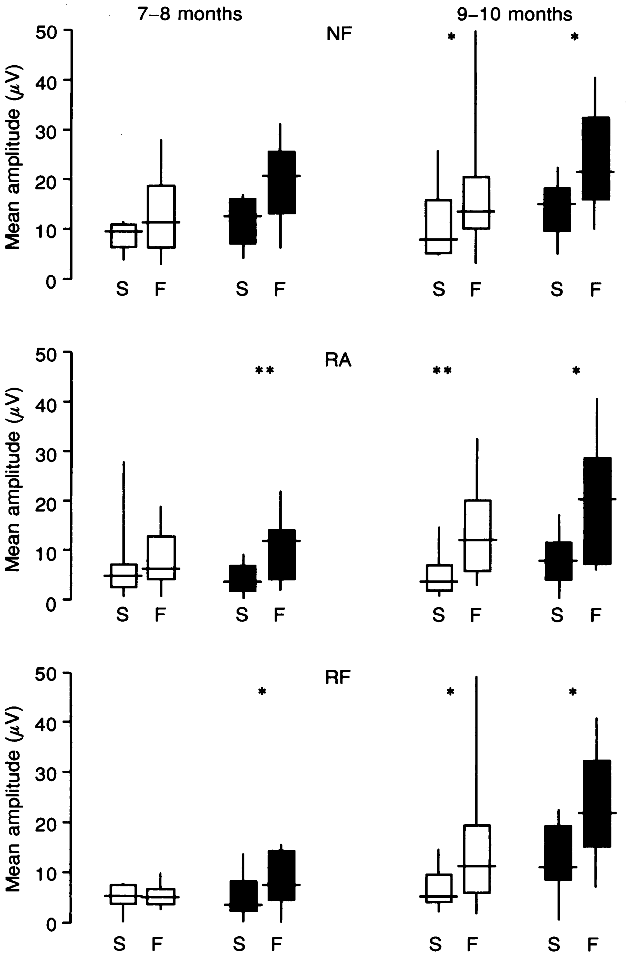

Figure 5. Velocity effect on mean flexor amplitude during Fw translations

Group data on mean flexor EMG amplitudes, calculated during the first 400 ms of the response during slow and fast Fw translations at 7–8 and 9–10 months. The data are presented as ranges (vertical bars), interquartile ranges (boxes) and median values (horizontal bars) of the individual means of the flexor amplitude values. □, non-trained group; ■, trained group. Asterisks indicate statistically significant differences between slow (S) and fast (F) perturbations: * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$.

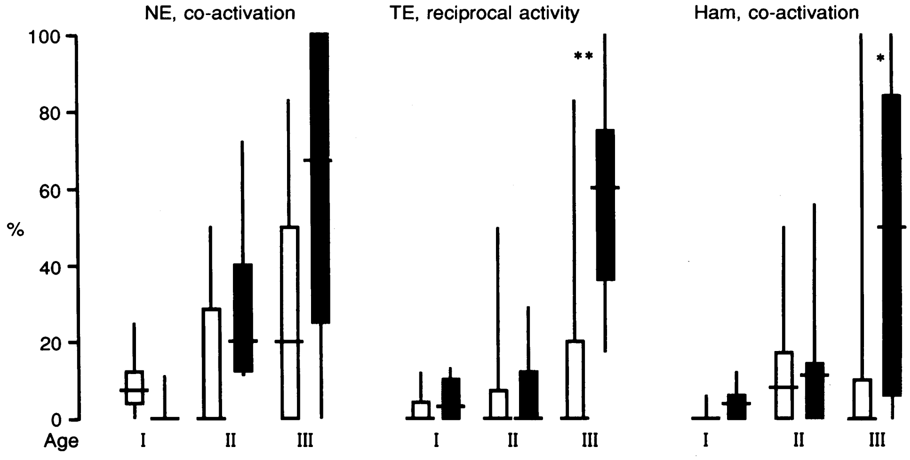

Figure 6. Antagonist activity during slow Fw translations

Group data on rates of NE co-activation, reciprocal activity in TE, and Ham co-activation during slow Fw translations. The specific response rate of a muscle was calculated for each infant by dividing the number of trials during which a response was found by the total number of trials. The data are presented as ranges (vertical bars), interquartile ranges (boxes) and median values (horizontal bars). □, non-trained infants; ■, trained infants. Asterisks indicate statistically significant differences between the two groups: * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$. I, 5–6 months; II, 7–8 months; III, 9–10 months.

The order in which the muscles were activated showed a large variation, both during Fw and Bw translations. At 5–6 months, the responses often started in the neck muscles and only rarely in the leg muscles. At 9–10 months, the frequency of responses, in which the leg muscle started, increased to about 30% of the trials in the non-trained infants and to about 50% of the trials in the trained infants. This held true for slow and fast perturbations in both directions.

Displacement of body parts

At the youngest ages, the angular displacement of head, pelvis and body sway showed a large variation. This variation decreased with increasing age, most clearly so for pelvis rotation. At the oldest age, trained infants showed significantly less pelvis displacement than the non-trained infants during slow Fw translations (MANOVA: $F = 12{\cdot}3$, $P < 0{\cdot}01$; Fig. 7). Moreover, in the trained group, the angular displacement of the pelvis during slow Fw

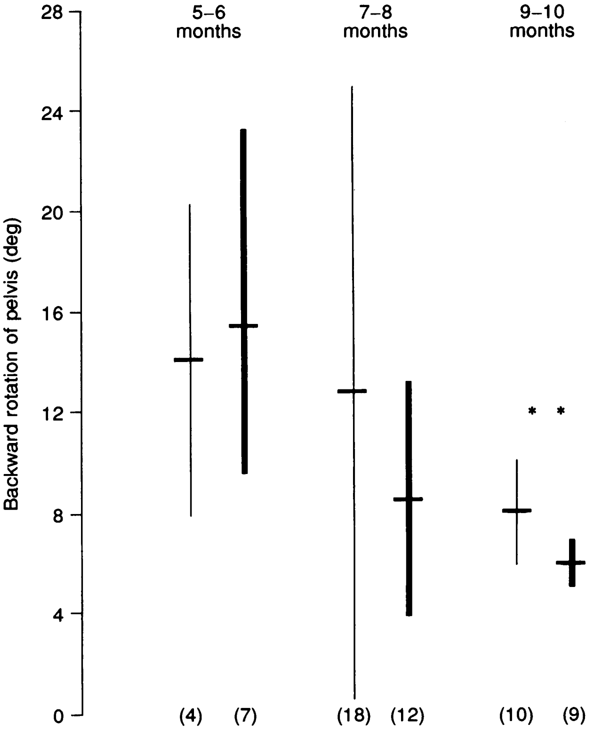

Figure 7. Amount of backward rotation of the pelvis during slow Fw translations

Development of the amount of backward rotation of the pelvis elicited during slow Fw translations in two infants of the trained (thick lines) and non-trained (thin lines) group. The data are presented by means (horizontal bars) and S.D. (vertical bars). The numbers in parentheses indicate the number of trials. The asterisks indicate a significant training effect as revealed by MANOVA with subject and response pattern as co-variates ($F = 12{\cdot}3$, $P < 0{\cdot}01$).

perturbations showed a significant negative correlation with RA_{400} ($r = -0{\cdot}74$, $P < 0{\cdot}02$). No significant training effect was found for pelvis displacement in the other testing conditions, nor for angular displacement of the head and body.

DISCUSSION

The present study provided neurophysiological evidence, that daily balance training can accelerate the development of postural control. The effect occurred at both levels of the postulated postural CPG model, i.e. training facilitated selection of the most complete, direction-specific response pattern and it accelerated the development of response modulation.

Training method

Our training method differed from our testing method. Training consisted of balancing during self-generated perturbations of equilibrium, i.e. during reaching to objects presented sidewards and semi-backwards in the border zone of reaching-without-falling, whereas testing occurred through external perturbations produced by a platform. The parents reported that a training session consisted in general of ten balancing movements, implying that a whole training period consisted of 2500–3000 exercise trials. Quite rightly we assumed that the strong positive effect of a large number of training movements (Wolpaw, 1985), would overpower the effect of an imperfect match between training and testing movements (Gottlieb, Corcos, Jaric & Agarwal, 1988).

Training and the postural CPG model

Training promoted a decrease in response variation during Fw and Bw translations. This resulted in a predominance of the most complete responses at the oldest testing age, a finding which is in line with Woollacott's recent data on the effect of training on the development of postural responses during standing (Woollacott, 1994). We argued before (Hadders-Algra *et al.* 1996) that a developmental decrease in response variation could be explained by two complementary mechanisms: (1) selection from a repertoire of primary response patterns and (2) a maturation-induced increase of synaptic efficiency within the circuitry of the complete response patterns (cf. Berger, Altenmüller & Dietz, 1984). The present data point to a significant role of response selection, which is, according to Edelman's 'neuronal group selection' theory, driven by experience (Edelman, 1989, 1993; Sporns & Edelman, 1993). The facilitation of response selection and response strengthening implies that training affects the development of the basic circuitry at the first level of the postural CPG.

Training also enhanced the development of the circuitry at the second level of the CPG model, an effect which was mainly observed during Fw translations. First, training accelerated the development of the ability to modulate EMG amplitude in relation to platform velocity and initial pelvis angle. The effect of training on the development of modulation with respect to platform velocity was stronger than that on the ability to adapt response amplitude to the more subtly varying initial sitting position. Second, training affected the use of antagonist muscles during Fw translations. Before the age of 9–10 months such antagonist activity was virtually absent, but at this age trained children displayed co-ordinated antagonist activity in more than half the trials. In the non-trained infants the prevalence of antagonist activity remained low. No data exist on the normal age of onset of antagonist activity during Fw translations, but similar antagonist activity has been observed in non-trained children of 1·5 years (M. Hadders-Algra, unpublished observations). Antagonist activity in the neck and leg occurred in a pattern of co-activation. Co-activation of the upper leg muscles has also been observed in 7- to 11-year-old children (Brogren, Hadders-Algra & Forssberg, 1996) and in adults (Forssberg & Hirschfeld, 1994), whereas the neck muscles in these age groups were activated in a reciprocal way during Fw translations. Co-activation results in increased joint stabilization, and may be used to secure balance (Hogan, 1984). In this respect it is interesting to note that adults do co-activate their neck muscles during perturbations inducing a Bw sway of the body, when the perturbations are elicited by a legs-up rotation (Forssberg & Hirschfeld, 1994). Third, training tended to affect the temporal ordering of the responses. Postural adjustments in sitting and standing school-age children and adults start in the most distal muscles (Nashner, 1977; Forssberg & Nashner, 1982; Forssberg & Hirschfeld, 1994; Brogren *et al.* 1996). Before the age of 9–10 months, responses starting with the leg muscle were rare. But from 9–10 months onwards a distal response onset became apparent, especially so in the trained infants. The tendency of the trained infants to start the responses more often with the leg muscle than the non-trained infants is probably related to the more consistent latency to leg muscle onset in the trained group.

An improvement of response regulation after 3–3·5 months of training was also reflected in more stable kinematic patterns during Fw translations. This was especially true for the angular displacement of the pelvis, which showed a negative correlation with RA amplitude.

The effect of training on the development of postural adjustments was more obvious in responses during Fw translations than those during Bw translations. Three explanations for this difference can be offered. In the first place, training focused on movements eliciting a (nearly) Bw fall of the body, which corresponds to the movement induced by Fw translations. Secondly, the dissimilarity in balancing difficulty between Fw translations causing an unusual and dangerous backward sway of the body, and Bw translations resulting in a familiar forward movement of the body, could have contributed to the directional difference in training effect. Thirdly, in analogy to the fact that the flexor muscles during Fw translations can be modulated more easily than the extensor muscles during Bw translations (Hadders-Algra *et al.* 1996), it could be surmised that the muscles used during Fw translations are more sensitive to experience than the ones used during Bw translations.

Little is known about the neurobiological mechanisms underlying experience-induced developmental changes. During many years Hebb's hypothesis was favourite (Hebb, 1949; Changeux & Danchin, 1976; Rauschecker & Singer, 1981). It stated that those synapses are strengthened which show a high degree of coincidence of electrical activity in pre- and postsynaptic neurons, whereas synapses with asynchronous activity in pre- and postsynaptic elements are weakened or eliminated. However, recently it has been demonstrated that not all activity-dependent synapse elimination follows Hebb's time-coincident rules, but rather results from topological convergence and postsynaptic activity (Nelson, Fields, Yu & Liu, 1993). Moreover, the idea is gaining ground that activity-dependent developmental plasticity in the cerebral cortex not only involves synapse elimination but also growth of neuropil and synapse formation (Liu, Field, Fitzgerald, Festoff & Nelson, 1993; Purves, 1994). Possibly, the training effects found in the present study could be explained by both regressive and progressive synaptic events. Selection of the most complete responses might be mediated mainly by synapse weakening of circuits involved in triggering of incomplete responses, whereas the (accelerated) maturation of response modulation might be attributed chiefly to selective synaptogenesis and synapse strengthening.

'Nature' and 'nurture' in the development of postural adjustments

Complex direction-specific postural adjustments are present before infants can sit without help (Hirschfeld & Forssberg, 1994; Hadders-Algra *et al.* 1996). This points to the innate origin of such complex motor patterns, which is in line with the view of the 'maturationalists' (e.g. Gesell, 1940; McGraw, 1943). It also corresponds to the findings of Taub, who studied motor development in monkeys whose forelimbs were deafferented before or shortly after birth. Notwithstanding the severe and early deficit in afferent input, the monkeys developed a normal repertoire of arm movements, all be it with some delay and inaccuracy (Taub, 1976).

Starting with a genetically predetermined large repertoire of direction-specific responses, development progresses through an experientially guided selection and strengthening of the most appropriate responses. With respect to the development of response modulation, the relative roles of 'nature' and 'nurture' have not been elucidated yet. Experience plays an obvious role and probably helps to find the best connections among the myriad options provided by genetic information. Like Thelen and co-workers (Thelen, 1988; Ulrich, 1989), we conclude that learning-by-doing plays an important role in the development of automatic motor behaviour, but in contrast to the Thelen group we underscore the significance of epigenetic processes directing neurological development.

The training in the present study was applied at an 'opportune time', i.e. during a phase with large developmental changes in sitting behaviour (McGraw, 1985). We demonstrated that training carried out by parents at this 'opportune time' can affect the development of postural control to a large extent. This could have important implications for the treatment of children with cerebral palsy, in whom dysfunctional postural control is a key symptom.

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