

RADIATION OF PHASIC STRETCH REFLEX IN BICEPS BRACHII TO MUSCLES OF THE ARM IN MAN AND ITS RESTRICTION DURING DEVELOPMENT

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SUMMARY

1. The phasic stretch reflex in biceps brachii has been recorded in 372 normal subjects aged from 31 weeks gestation to 55 years. The stimulus used was a brief mechanical pulse delivered by a hand-held electromagnetic vibrator and the response was measured in the surface electromyogram.

2. The threshold for eliciting the reflex was low in the newborn and increased over the first 6 years to values corresponding to those of adults.

3. On the basis of timing it is concluded that the phasic stretch reflex has a monosynaptic component at all ages.

4. The surface electromyogram was also recorded in triceps brachii, pectoralis major, deltoid and hypothenar muscles. In some subjects evoking the phasic stretch reflex in biceps brachii resulted in short latency responses in these muscles, a phenomenon termed radiated response.

5. The probability of occurrence of radiated responses and their magnitudes were greatest at birth and decreased over 2–4 years.

6. Experiments were performed to determine how far mechanical transmission of the stimulus to biceps through the tissues of the arm might account for the radiated responses in the other muscles studied. It was concluded that the responses observed in triceps brachii, pectoralis major, deltoid and hypothenar muscles, following vibration of the biceps tendon, are primarily due to the radiation of the activity carried in biceps muscle afferents to the α -motoneurons of the respective muscles.

7. On the basis of timing it is concluded that in subjects below 2 years the radiated responses in the muscles studied have a monosynaptic component.

INTRODUCTION

Primary muscle spindle afferents predominantly excite α -motoneurons of the homonymous muscle, forming the basis of the phasic stretch reflex, and excite to a lesser degree motoneurons of synergistic muscles (cat: Eccles, Eccles & Lundberg, 1957*a, b*; baboon: Hongo, Lundberg, Phillips & Thompson, 1984). In the limbs activation of primary spindle afferents also evokes reciprocal inhibition of α -motoneurons of antagonistic muscles through group Ia inhibitory interneurons

(cat: Hultborn, 1972). Comparable reflex patterns of excitation and inhibition have been observed in adult human subjects between muscles of the limbs (Tanaka, 1974; Day, Marsden, Obeso & Rothwell, 1984; Plant & Miller, 1990).

In the newborn animal and the human neonate the patterns of stretch reflexes and reciprocal inhibition are less well defined and it is notable that the mature patterns are not yet established. Excitatory reflex actions from muscle afferents predominate (Skoglund, 1960; Saito, 1979; Myklebust, 1990). The kitten has been shown to have excitatory monosynaptic projections between primary afferents and α -motoneurons of non-homonymous and non-synergistic muscles, which become greatly reduced in comparison to the adult cat (Eccles, Shealy & Willis, 1963). Indeed, many excitatory intersegmental projections from primary afferents to motoneurons disappear during development (rat: Saito, 1979). In the human neonate Myklebust, Gottlieb & Agarwal (1986) and Myklebust (1990) observed that a tendon tap to triceps surae evoked excitatory reflex activity, not only in triceps surae, but also in its antagonist, tibialis anterior, and to more distant muscles of the lower limb, quadriceps femoris and the hamstring muscles. They termed the radiation of the reflex to tibialis anterior 'reciprocal excitation' and that to quadriceps and the hamstrings 'reflex irradiation'. Using indirect evidence Myklebust *et al.* (1986) concluded that the radiated responses resulted from monosynaptic or oligosynaptic excitatory projections from primary muscle afferents of triceps surae onto α -motoneurons of the other muscles, projections which later become masked or eliminated during normal development. Continuing these studies Myklebust (1990) has presented preliminary evidence in fifteen children that reflex radiation in the lower limb becomes restricted over the first 6 years of life. In children with spastic cerebral palsy the immature reflex pattern of reciprocal excitation is retained (Myklebust, Gottlieb, Penn & Agarwal, 1982). The actual transition from immature to mature patterns of myotatic reflexes is poorly understood, but it is likely to have particular relevance for the pathophysiology of spastic cerebral palsy.

The present aim was therefore to characterize in a large cross-sectional study of normal subjects the development of the phasic stretch reflex using biceps brachii as a model and to examine the degree of radiation of the reflex among muscles of the upper limb at different ages.

METHODS

Subjects. The study was performed on 372 subjects, 206 male and 166 female, ranging from pre-term babies of 31 weeks gestational age to adults of 55 years. The subjects were all healthy and had no past history or clinical signs of neurological disorder. Informed written consent was obtained from subjects aged more than 16 years and, where appropriate, from the subjects and/or their parents for those younger than 16 years. The study was approved by the University of Newcastle upon Tyne Ethical Committee.

Positioning of subjects. Subjects of less than 6 months were studied in a supine position. An evacuable plastic bag filled with polystyrene beads was used to stabilize the head in a mid-line anatomical position. Subjects of more than six months were seated either on a parent's knee or on a chair and the reflexes were studied with the head in the mid-line position. In all subjects the left elbow was positioned in approximately 45 deg of flexion from full extension; in those subjects where the responses to contralateral stimulation were recorded by applying the stimulus to the right biceps tendon, the right elbow was similarly positioned in approximately 45 deg of flexion from full extension.

State of arousal of subjects. Subjects under 1 month were studied while quietly awake or asleep and their state of sleep was determined either by observation ($n = 139$) or by polygraphic recording ($n = 10$) using the method of Anders, Emde & Parmelee (1971). Subjects over 1 month were studied while awake.

Phasic stretch reflex. The phasic stretch reflex was elicited in biceps brachii with a hand-held electromechanical vibrator, Ling Altec 200, delivering a single cycle of a 150 Hz sine wave over a peak-to-peak amplitude range of 0.2 to 3.1 mm (Plant & Miller, 1990). Each stimulus began from the zero crossing point of the sine wave giving an initial outward deflection. The stylus of the vibrator, a circular plastic disc of 1.0 cm diameter, was applied to the skin overlying the tendon of biceps brachii within the cubital fossa. The peak-to-peak amplitude of the stimulus was increased until a reflex response could be elicited in biceps brachii in 50% of the trials and this was defined as the threshold. The amplitude was then set to be 1.1 times the threshold so that a reflex response could be obtained in biceps brachii in all trials. In each subject an attempt was first made to elicit the reflex and define threshold in *relaxed* muscle. If no reflex response was obtained even at maximum peak-to-peak amplitude of the stimulus, the reflex was then elicited in the presence of background muscle activity in biceps brachii and the threshold defined in *contracting* muscle. In subjects older than 2 years this was achieved by giving the subject a 200 g weight to hold in the left hand; in subjects of 2 years and less, the reflexes were measured during periods of spontaneous EMG activity.

Electromyograms (EMG). EMGs were recorded using Ag-AgCl, skin-mounted, standard, EEG electrodes (5 mm in diameter with centres separated by 15 mm) from the following muscles of the left upper limb: biceps brachii, triceps brachii, deltoid, pectoralis major and those of the hypothenar eminence. In each case the recording electrodes were placed in the vertical anatomical plane over the belly of biceps brachii, the lateral head of triceps brachii and the hypothenar eminence, and in the horizontal plane over the clavicular fibres of pectoralis major and over the lateral aspect of deltoid. In twenty-eight subjects recordings were made simultaneously from all the muscles, in 148 subjects from biceps, triceps, deltoid and pectoralis major, in fifty-seven subjects from biceps and triceps, in twelve subjects from biceps and hypothenar muscles and in 127 subjects from biceps brachii alone. In addition to vibrating the tendon of the left biceps brachii, vibration was also applied in forty subjects to the right biceps brachii and recordings were made simultaneously in all the muscles listed on the left side. The EMGs were amplified using a Nicolet Physiological Amplifier (CA-1000) and filtered using a -3 dB bandpass of 5-1500 Hz. The impedance of the recording electrodes was measured and maintained between 1 and 5 k Ω .

Control for mechanical spread of stimulus. In each subject controls were carried out to determine if responses in muscles other than biceps brachii could be attributed to their direct response to mechanical spread of the stimulus through the tissues of the limb. The same stimulus magnitude used to evoke reflex responses (i.e. 1.1 times the threshold for evoking a reflex in biceps brachii) was also applied to the skin on either side of the biceps tendon in cubital fossa and to the medial and lateral epicondyles of the humerus. If these stimuli evoked a reflex response in any of the muscles, including biceps brachii, direct excitation of the muscles by mechanical spread was assumed and the data from the subject were excluded from further analysis.

As a further control the magnitude of the vibratory stimulus required to elicit reflex responses when applied to the epicondyles of the humerus was compared to that required when the stylus was applied to the tendon of biceps brachii. Twenty subjects representative of the total age range were studied. In these subjects the stimulus was applied to the epicondyles of the humerus and its intensity was increased until reflex responses were obtained in any of the muscles. The stimulus threshold for these responses was noted.

Electromagnetic stimulation of the cervical spine. The conduction delay in the motor nerve to biceps brachii was investigated in 175 subjects using electromagnetic stimulation (Barker, Freeston, Jalinous & Jarratt, 1987). The stimulating coil was placed initially in the coronal plane overlying the fifth to seventh cervical spines. The coil was then moved in small steps to the right to obtain the *longest* latency at threshold for a muscle action potential. Percutaneous electrical stimulation applied to the cervical spine at threshold is assumed to excite the motor nerves close to their exit through the intervertebral foramina (Plassman & Gandevia, 1989) and it is reasonable to assume that this is also the case with electromagnetic stimulation.

Data analysis. The EMGs were recorded on magnetic tape (Racal Store 4 tape-recorder) and analysed off-line for onset latency and presence of pre-stimulus background muscle activity. The

magnitudes of the responses were determined by measuring the area of the average of twenty responses from the onset of the averaged response to the point at which the trace returned to baseline.

RESULTS

Phasic stretch reflex in biceps brachii

In all 372 subjects tested a phasic stretch reflex in either relaxed or contracting biceps brachii was evoked by the vibratory stimulus applied to the skin overlying the

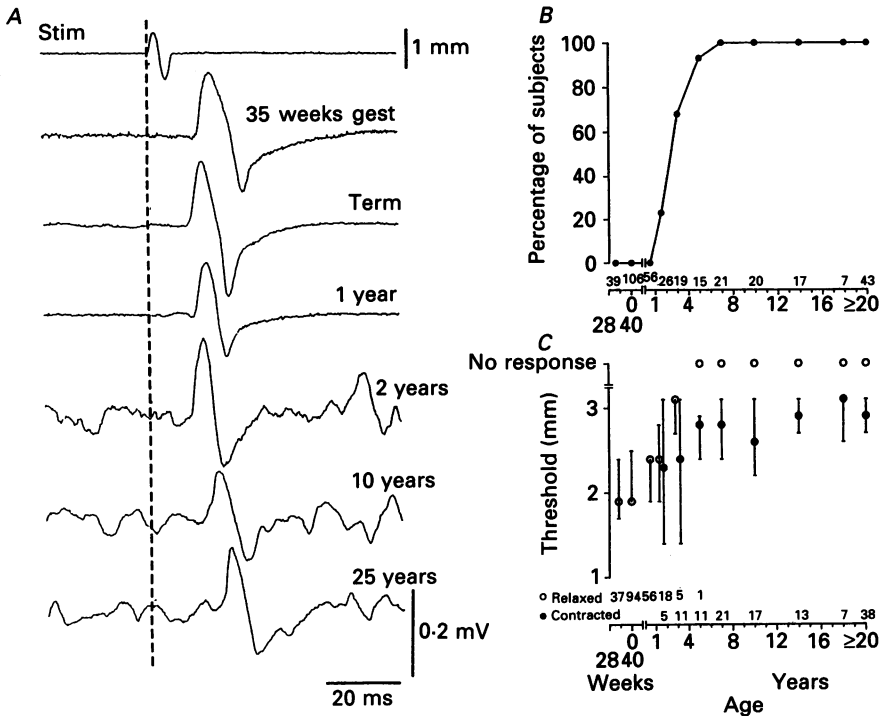


Fig. 1. *A*, phasic stretch reflexes in biceps brachii recorded in subjects of different ages: weeks gest, weeks of gestational age; Term, 40 weeks of gestational age. Dashed line indicates the onset of stimulation. *B*, percentage of subjects in which it was *not* possible to elicit the phasic stretch reflex in biceps brachii in relaxed muscle. Abscissa, age of subjects. The numbers above the abscissa indicate the number of subjects in each age group. *C*, threshold of the phasic stretch reflex in biceps brachii with age. The threshold is expressed in millimetres of the peak-to-peak amplitude of the vibratory stimulus. The output range of the stimulus was 0.2–3.1 mm. The symbols represent the median values for each age group and the bars the interquartile range. ●, observations obtained in contracting muscle; ○, observations obtained in relaxed muscle. The numbers above the abscissa indicate the number of subjects in each age group.

tendon. Figure 1*A* shows representative recordings of the biceps stretch reflex in subjects ranging in age from 31 weeks gestation to 25 years. It should be noted that in nearly all subjects under the age of 2 years the reflex could be elicited in relaxed muscle, whereas in the large majority of subjects older than 2 years background muscle activity in biceps brachii was required. Figure 1*B* shows the percentage of

subjects with age in whom it was not possible to elicit the phasic stretch reflex in relaxed biceps brachii and in whom facilitatory background muscle contraction was required. Three babies were excluded from this analysis because they were very active and insufficient periods of inactivity occurred for the stretch reflex to be tested in relaxed muscle.

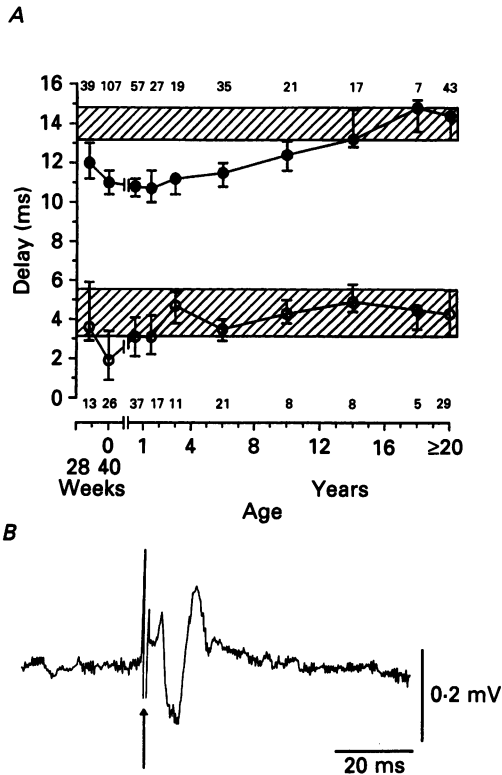


Fig. 2. *A*, onset latency of the phasic stretch reflex in biceps brachii (●) and the estimated central delay (○) as functions of age. The circles represent median values and the bars the interquartile range. The numbers above the abscissa indicate the subjects in each age group. The hatched area indicates the interquartile range in adult subjects. *B*, muscle action potential in biceps brachii following electromagnetic stimulation of the cervical motor roots in a subject aged 6 months. The arrow indicates the onset of stimulation.

The peak-to-peak amplitude of the vibratory stimulus at threshold for eliciting the reflex in relaxed and contracted muscle is shown in relation to the subjects' ages in Fig. 1*C*. The data in the three parts of Fig. 1 support the conclusion that up to the age of 6 years there is an increase in threshold for eliciting the phasic stretch reflex.

Onset latency of the phasic stretch reflex in biceps brachii

The shortest onset latency was determined from examination of at least twenty trials and is shown in relation to age in Fig. 2*A*. The latency initially falls over the first year after birth and then progressively increases to adult values, which are reached between 13 and 15 years of age.

To investigate whether the stretch reflex might have monosynaptic linkage during development, estimates of the central transmission delay were made in 175 subjects. The peripheral conduction delay in the motor nerve to biceps brachii was measured by electromagnetic stimulation applied over the cervical spines (Fig. 2*B*). At

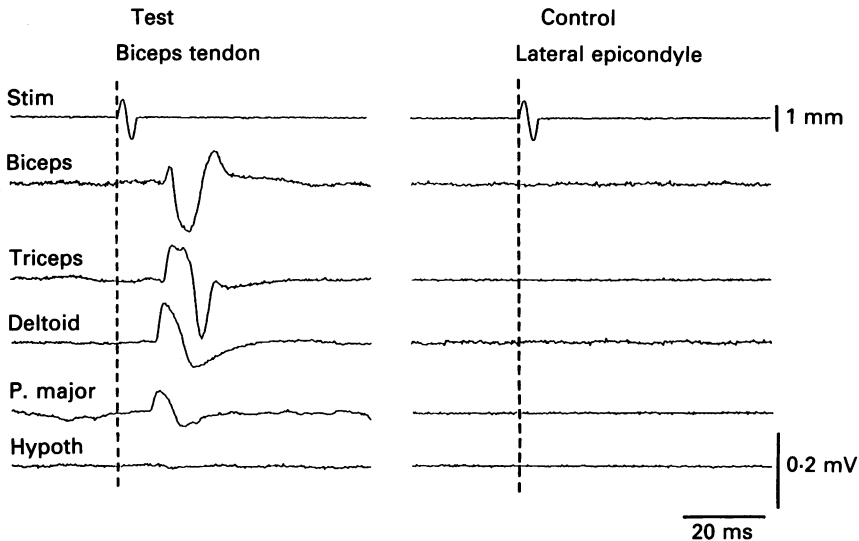


Fig. 3. Phasic stretch reflex in biceps brachii and radiated responses in other muscles in a neonate of 40 weeks gestational age, evoked with the vibrator placed on the tendon of ipsilateral biceps brachii (left-hand panel). No muscle responses occurred in these muscles in the control when the same stimulus was applied to the lateral epicondyle at the elbow (right-hand panel). Dashed line indicates the onset of stimulation. P. major, pectoralis major; Hypoth, hypothernar.

threshold this stimulus is thought to excite spinal motor nerves close to their emergence from the intervertebral foramina (see Methods). The delay in the afferent reflex arc to the intervertebral foramina was taken to be equal to the measured efferent delay, scaled according to the relative mean maximum conduction velocities for age in motor and sensory components of muscle nerves (Vecchierini-Blineau & Guiheneuc, 1984).

It should be noted that the measured efferent delay includes times for transmission within the muscle and at the neuromuscular junction, but they are likely to be small in comparison to the efferent conduction delay. They may therefore introduce only minor errors in the estimated afferent conduction delay. In addition, no separate account is taken of the receptor transduction delay in the afferent fibres, but this is again assumed to be small in comparison to the total conduction delay.

The central transmission delay was estimated by subtracting the sum of conduction delays in the efferent and afferent arcs, as defined above, from the minimum onset latency of the phasic stretch reflex. This delay will also include a period for conduction in motor and sensory roots within the vertebral canal, the synaptic delay and the period for the rising phase of the composite excitatory postsynaptic potential in the motoneurons. Figure 2*A* shows these estimated central transmission delays in relation to age. The delays at all ages are similar to,

or shorter than, those in adults, with the implication that the early component of the phasic stretch reflex is monosynaptic at all ages.

Radiation of the biceps stretch reflex to other muscles of the upper limbs

When a vibratory stimulus was applied to the tendon of biceps a stretch reflex was recorded, as described above. In some subjects excitatory responses were also

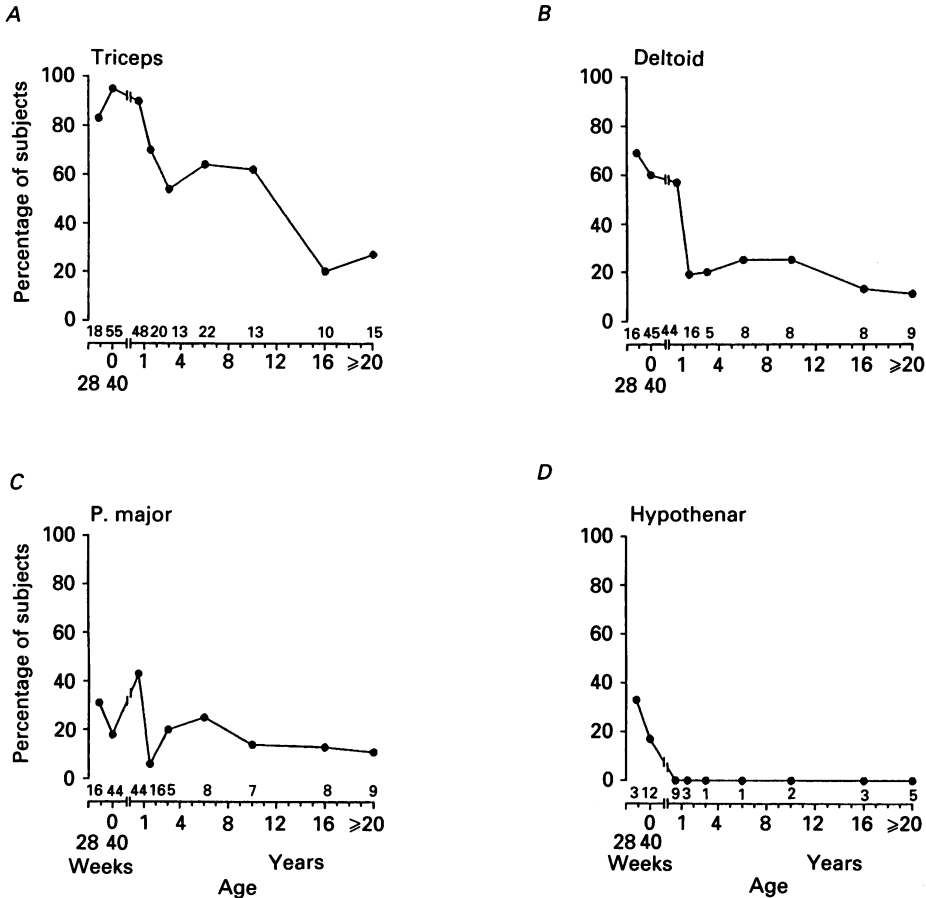


Fig. 4. Percentage of subjects showing radiated responses in relation to age. Radiated responses were considered to be present if the reflex ratio was equal to, or greater than, 0.1 since those of lesser magnitude were not significantly greater than background muscle activity. The numbers above the abscissa indicate the subjects in each age group. P. major, pectoralis major.

recorded in the EMGs of the ipsilateral triceps, deltoid, pectoralis major and hypothenar muscles and these are referred to as radiated responses (Fig. 3). The percentage of subjects studied in whom such radiated responses were observed is plotted for each muscle studied in Fig. 4. No contralateral radiated responses were observed in the muscles studied in the left limb when the same vibratory stimulus was applied to evoke a stretch reflex in the right biceps brachii.

The ipsilateral radiated responses might possibly have arisen from mechanical

spread of the stimulus through the arm to receptors in the muscles studied and the following controls were therefore performed (see Methods). The vibratory stimulus at 1.1 times the threshold for evoking a reflex in biceps brachii was applied in all subjects to the skin overlying soft tissue on either side of the tendon of biceps brachii

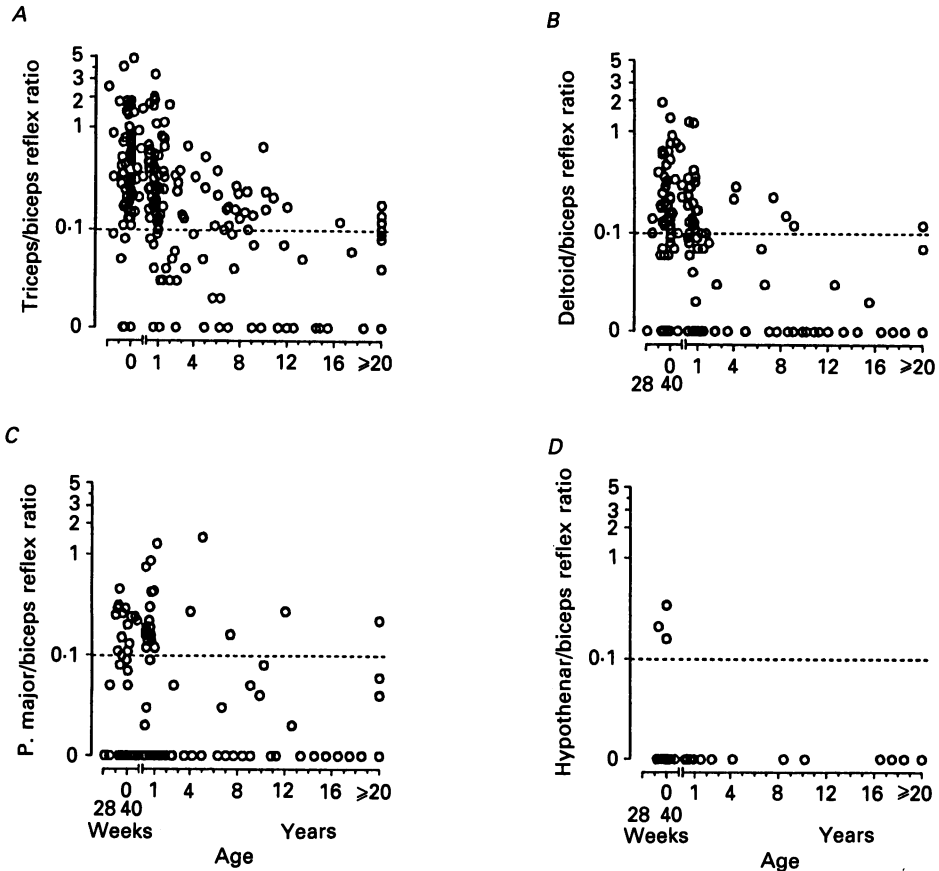


Fig. 5. Reflex ratios of radiated responses in different muscles in relation to the subjects' ages. The reflex ratio is given by the area of the average of twenty radiated responses divided by the area of the average of twenty phasic stretch reflexes in biceps brachii. *A*, ipsilateral triceps brachii ($n = 214$); *B*, deltoid ($n = 159$); *C*, pectoralis major ($n = 157$); *D*, hypothenar muscles ($n = 39$). The reflex ratio is plotted on a log scale. Reflex ratios of less than 0.1 indicate radiated responses not significantly greater than the background muscle activity. P. major, pectoralis major.

and to the medial and lateral epicondyles of the humerus (Fig. 3). In twenty-two of the 245 subjects tested this control stimulus evoked responses in biceps brachii and/or in one or more of the other muscles (biceps, 18; triceps, 12; deltoid, 9; pectoralis major, 4). The data from these subjects were excluded from further analysis. In twenty of the remaining 223 subjects, selected to cover the complete age range, the peak-to-peak amplitude of the vibratory stimulus required to elicit responses when applied to bone was compared to that required to elicit responses

when applied to the biceps tendon. The magnitude of the stimulus required when applied to bone or soft tissue was between 1.3 and 2.9 times the threshold for eliciting a reflex in biceps brachii when applied to the tendon of biceps brachii. No correlation was found between the relative magnitude of the stimulus and age.

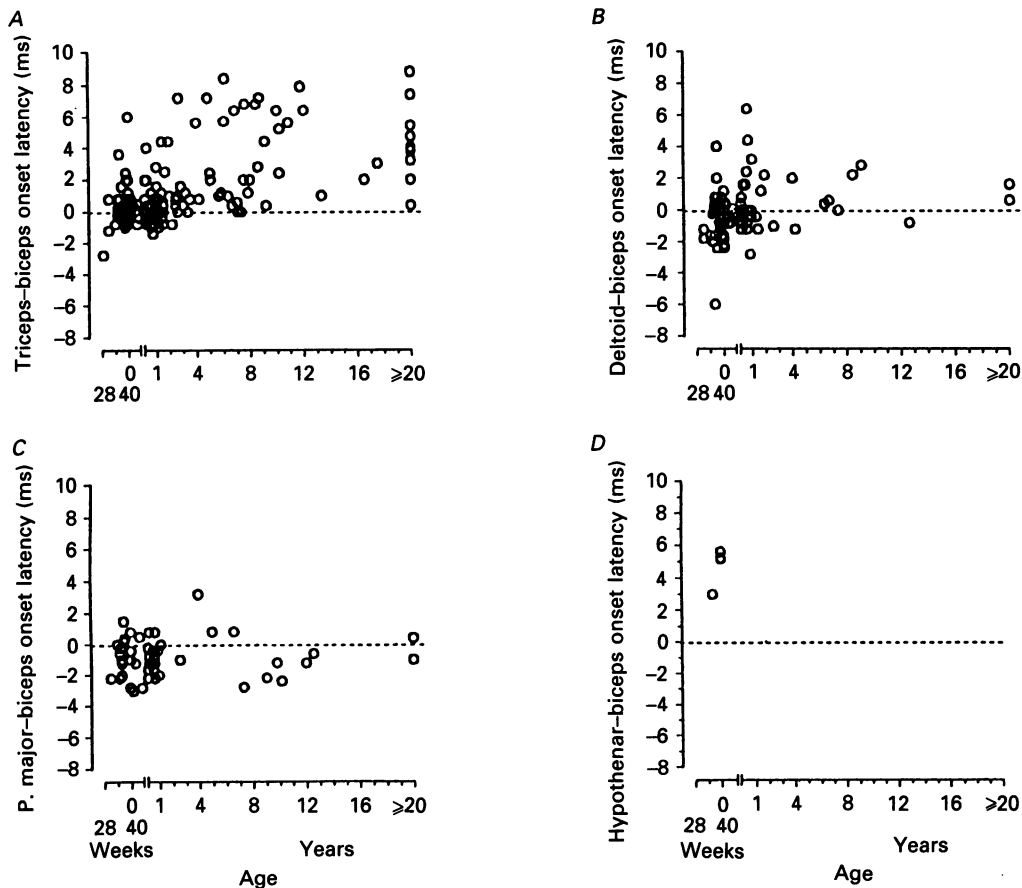


Fig. 6. Differences of onset latencies of radiated responses from those of biceps brachii. The onset latency of the phasic stretch reflex in biceps brachii in each subject has been subtracted from the onset latency of each radiated response. *A*, triceps brachii ($n = 214$); *B*, deltoid ($n = 159$); *C*, pectoralis major ($n = 157$); *D*, hypothenar muscles ($n = 39$).

In order to obtain estimates of the magnitudes of the ipsilateral radiated responses, the ratio was calculated of the area of the average of twenty radiated responses to the area of the average of twenty responses in biceps brachii, following the method used by Myklebust *et al.* (1986). The relative magnitudes of the radiated responses in the muscles studied in relation to age are shown in Fig. 5. Values of reflex ratio greater than 1 occurred in forty-one subjects, indicating radiated responses which were larger than the stretch reflex in the homonymous muscle, biceps brachii.

At all ages the probability and the magnitude of a radiated response was highest in triceps followed by deltoid and pectoralis major. In the hypothenar muscles a

small radiated response was recorded in only three subjects, all neonates. The probability and magnitude of a radiated response was greatest in the pre-term and term neonates and decreased with age. For all the muscles, restriction of radiated responses was most marked within the first 2 postnatal years. In adults a small radiated response was still observed in five subjects in triceps, in one subject in deltoid and in one subject in pectoralis major (Figs 4 and 5).

TABLE 1. The threshold, magnitude and latency of phasic stretch reflex in biceps brachii and its radiation to muscles of the upper limb in relation to sleep state in subjects aged less than 1 month

	Awake	Active sleep	Quiet sleep
Stretch reflex in biceps brachii			
Number of subjects	25	58	66
Threshold (mm)	2.0 ± 0.5	2.0 ± 0.4	2.0 ± 0.4
Latency (ms)	11.4 ± 1.0	11.3 ± 1.1	11.2 ± 1.0
Magnitude of response (arbitrary units)	434 ± 243	550 ± 285	590 ± 318
Radiated responses in other muscles			
Number of subjects	14	27	32
Percentage of subjects showing radiated responses in muscles indicated			
Triceps	93	93	91
Deltoid	27	75	66
P. major	16	22	21
Ratios of response magnitudes			
Triceps/biceps	0.54 ± 0.35	0.70 ± 0.91	0.56 ± 0.90
Deltoid/biceps	0.29 ± 0.36	0.21 ± 0.46	0.33 ± 0.29
P. major/biceps	0.14 ± 0.14	0.19 ± 0.09	0.16 ± 0.17

Comparison of onset latencies of radiated responses with those of biceps brachii

Where a radiated response occurred, the onset latency of the biceps stretch reflex was subtracted from the onset latency of the radiated response in each of the muscles. These differences are shown in relation to age in Fig. 6. Until the age of 2 years the differences for triceps brachii (Fig. 6A) have a median of 0 ms and an interquartile range of -0.4 to +0.5 ms, after which they increase to a median value of approximately 4 ms in adults. For deltoid (Fig. 6B) the differences in subjects up to 2 years have a median of -0.3 ms with an interquartile range of -1.2 to +0.4 ms. For pectoralis major (Fig. 6C) up to 2 years of age the median value is -1.0 ms with an interquartile range of -1.2 to -0.2 ms. For both deltoid and pectoralis major there is no evident change in the relative latencies with age. In the three subjects in whom radiated responses were obtained in hypothenar muscles (Fig. 6D) differences of 3.0, 5.1 and 5.7 ms were obtained.

Influence of state of arousal on the reflex responses in subjects aged less than 1 month

Of the 149 subjects aged less than 1 month, twenty-five were studied awake, fifty-eight in active sleep and sixty-six in quiet sleep. No significant differences were observed in the onset latency, amplitude and threshold of the biceps stretch reflex with the various states of arousal (*t* test on normalized values; Table 1). There was no significant difference (χ^2 test) in the probability of radiated responses with the exception of that in deltoid, which occurred less frequently in the awake state than

would be expected, nor were there significant differences (*t* test on normalized values) in the amplitudes of the radiated responses with the different states of arousal.

Comparisons between male and female subjects

No significant differences were found in the data obtained in male and female subjects.

DISCUSSION

This study has revealed three features of the development of the phasic stretch reflex in biceps brachii: an increase in the threshold for excitation with age, a high probability of radiation of excitation from biceps brachii afferents to the motoneurons of its antagonist, triceps brachii, and other muscles of the upper limb in early postnatal development, and the restriction of the radiation with age.

Increase in threshold of phasic stretch reflex with age

The present study provides the first systematic report of the changes in excitability of the phasic stretch reflex during development. In previous studies of stretch reflexes in neonates and children a tendon hammer has been used to elicit the reflex (Eisengart, 1970; Myklebust *et al.* 1986; Myklebust, 1990). Although such a stimulus can be used for determining the latency of response, it is suprathreshold for eliciting the stretch reflex in relaxed muscles and so cannot be used to differentiate changes in threshold with development. The vibratory stimulus employed in the present study is likely to excite predominantly primary spindle afferents (Burke, Hagbarth, Löfstedt & Wallin, 1976) and permits changes in the threshold of the phasic stretch reflex in biceps brachii to be determined by two criteria: (i) the magnitude of the stimulation required and (ii) the probability of eliciting the reflex in relaxed muscle. On the basis of both of these criteria an increase in threshold for the phasic stretch reflex in biceps brachii up to 6 years of age has been demonstrated (Fig. 1).

Developmental studies in children using H reflexes provide support for this observation. Thomas & Lambert (1960) and Mayer & Mosser (1969) have demonstrated H reflexes to small muscles of the hand and foot in the neonate which can no longer be evoked after the age of 12 months. Attempts to quantify the change of threshold during development using H:M ratios (Mayer & Mosser, 1969; Vecchierini-Blineau & Guiheneuc, 1981), however, have led to inconclusive results. The difficulties in these studies are likely to be due to the complex nature of the H reflex stimulus (Burke, Gandevia & McKeon, 1983) and to be compounded by the small numbers of subjects studied.

The development of cutaneous reflexes shows a similar pattern to that of the phasic stretch reflex, with an increasing threshold with age (Fitzgerald, Shaw & MacIntosh, 1988) and a decreasing magnitude of the early component of the response evoked by a standard stimulus over the first year (Issler & Stephens, 1983).

Factors underlying the change of threshold with age

Changes in the responsiveness of primary muscle afferents are unlikely to be responsible for the increase in threshold of the phasic stretch reflex. Muscle spindles in cat and man are innervated at an early stage of fetal development and rapidly

differentiate (Gregory & Proske, 1988). In the cat Skoglund (1960) demonstrated rapidly adapting responses to stretch at birth, and Gregory & Proske (1988) noted increased sensitivity and rate of firing of muscle spindle afferents to standard muscle stretch with increasing age, which would suggest the reverse of an increase of threshold. During development the excitability of α -motoneurons decreases in the cat (Kellerth, Mellström & Skoglund, 1971) and in the rat (Kudo & Yamada, 1987). These changes may result from increase in the membrane area of the soma (Conradi, 1976; Mellström & Skoglund, 1969) and of the dendrites (Conradi, 1976; Ramirez & Ulfhake, 1990), and increased negativity of the resting membrane potential (cat: Kellerth *et al.* 1971; rat: Ziskind-Conhaim, 1988). Furthermore, synapses are redistributed with greater density on the dendrites and less on the soma (monkey: Bodian, 1966; cat: Conradi, 1976) and spindle afferents are less effective synaptically with age (Eccles & Willis, 1965). The increase in threshold of the phasic stretch reflex in human development is therefore likely to reflect physiological changes within the spinal cord, which may, on the basis of the present results, continue in man up to the age of 6 years.

Radiation of phasic stretch reflex of biceps brachii to other muscles of upper limb

In the neonate the magnitude of the radiated responses often exceeded those of the phasic stretch reflex in biceps brachii (Fig. 5), which may indicate a powerful synaptic input to these non-homonymous and non-synergistic motoneurons early in development. Direct volume conduction of radiated responses is excluded in view of the earlier onset latencies of the radiated responses observed in deltoid and pectoralis major muscles. However, it is possible that the radiated responses could arise from mechanical transmission of the stimulus through the arm, presumably exciting the spindle afferents of other muscles, as Burke *et al.* (1983) discussed in a study of adult subjects. In twenty-two subjects application of the vibratory stimulus to surrounding bone or soft tissue at 1.1 times the threshold level for eliciting the reflex in biceps, when applied to its tendon, did evoke responses in biceps and occasionally in other muscles; the data from these subjects were excluded from analysis (see Methods and Results). In the remaining 223 subjects such bone and soft tissue stimulation failed to evoke radiated responses. In these subjects, if the mechanical spread of the stimulus induced activity in the primary afferents of the other muscles studied, the activity was subthreshold for motoneuronal discharge. It was therefore concluded that the responses observed in triceps, deltoid, pectoralis major and hypothenar muscles, following vibration of the biceps tendon, are primarily due to radiation of the activity carried in biceps muscle afferents to the α -motoneurons of the respective muscles. It cannot be excluded, however, that the radiated excitation from biceps muscle afferents sums with a subthreshold input from homonymous muscle afferents due to mechanical transmission of the stimulus through the arm.

There is direct evidence from studies in animals that the initial component of the phasic stretch reflex results from monosynaptic excitation of the α -motoneuron by primary muscle afferents (cat: Renshaw, 1940; Eccles *et al.* 1957*a*; primate: Clough, Kernell & Phillips, 1968). It has also been concluded on the basis of latency that the stretch reflex in the adult human subject has an initial monosynaptic component (Burke, Gandevia & McKeon, 1984). In the present study the estimated central delay for the stretch reflex at all ages was similar to, or shorter than, those in adults, with

the implication that the early component of the phasic stretch reflex is monosynaptic during development. This conclusion receives direct support from developmental studies in animals where the phasic stretch reflex has been shown to have a monosynaptic component in both fetus and newborn (rat: Saito, 1979; Kudo & Yamada 1987; cat: Wilson, 1962; Skoglund, 1960; Eccles & Willis, 1965).

On the evidence of timing in the present study it is likely that at least the initial components of the radiated responses in other muscles of the upper limb result from direct projections of muscle afferents from biceps brachii, which activate the relevant motoneurons monosynaptically. This conclusion is drawn from the observations that the radiated response in triceps brachii shares the same onset latency as biceps (Fig. 4A), where the efferent arc is of approximately the same length, and that the radiated responses in deltoid and pectoralis major both occur earlier than that of biceps, corresponding to the shorter efferent arcs to these muscles relative to that of biceps.

In fetal, newborn and adult animals a wide range of non-homonymous, monosynaptic muscle afferent projections have been reported. In the kitten Eccles *et al.* (1963) demonstrated monosynaptic connections between primary afferents and α -motoneurons of non-homonymous or non-synergistic muscles, a small proportion of which persisted in the adult cat (Eccles *et al.* 1957 *a, b*). In the fetal rat Saito (1979) demonstrated monosynaptic projections from afferents in L1 to L6 dorsal roots to motoneurons of L3 segment and in the fetal sheep Änggård, Bergström & Bernhard (1961) observed radiation of stretch reflexes from gastrocnemius to other muscles of the lower limb including direct antagonists. These observations would support the conclusion that the radiated responses observed in the present study arise from direct projections of biceps muscle afferents.

Restriction of radiation of biceps brachii phasic stretch reflex with age

Reduction of radiation of primary afferents to non-homonymous motoneurons has been observed in animal studies. The intersegmental radiation observed by Saito (1979) in the fetal rat (see above) became restricted so that at birth only the L3 dorsal root could evoke responses in L3 ventral root. Administration of strychnine restored the radiated responses in the postnatal period but failed to do so at later ages. Saito concluded that the early restriction of radiation arose in part from spinal inhibitory neuronal mechanisms, but that later the intersegmental projections providing the radiated responses had been eliminated. The suggestion of elimination of monosynaptic non-homonymous afferent projections during development receives support from the observations of J. C. Eccles *et al.* (1957 *a, b*) and R. M. Eccles *et al.* (1963) that fewer monosynaptic projections to motoneurons from non-homonymous muscles are present in the adult cat than in the kitten.

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