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Changes in stretch reflexes and muscle stiffness with age in prepubescent children

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Grosset J-F, Mora I, Lambertz D, Pérot C. Changes in stretch reflexes and muscle stiffness with age in prepubescent children. *J Appl Physiol* 102: 2352–2360, 2007. First published March 8, 2007; doi:10.1152/japplphysiol.01045.2006.—Musculo-articular stiffness of the triceps surae (TS) increases with age in prepubescent children, under both passive and active conditions. This study investigates whether these changes in muscle stiffness influence the amplitude of the reflex response to muscle stretch. TS stiffness and reflex activities were measured in 46 children (7–11 yr old) and in 9 adults. The TS Hoffmann reflex (H reflex) and T reflex (tendon jerk) in response to taping the Achilles tendon were evaluated at rest and normalized to the maximal motor response (M_{max}). Sinusoidal perturbations of passive or activated muscles were used to evoke stretch reflexes and to measure passive and active musculoarticular stiffness. The children's H_{max}-to-M_{max} ratio did not change with age and did not differ from adult values. The T-to-M_{max} ratio increased with age but remained significantly lower than in adults. Passive stiffness also increased with age and was correlated with the T-to-M_{max} ratio. Similarly, the children's stretch reflex and active musculoarticular stiffness were significantly correlated and increased with age. We conclude that prepubescent children have smaller T reflexes and stretch reflexes than adults, and the lower musculoarticular stiffness is mainly responsible for these smaller reflexes, as indicated by the parallel increases in reflex and stiffness.

prepubescent children; Hoffmann reflex; T reflex; stretch reflex; musculoarticular stiffness

THERE IS NO DOUBT THAT the human nervous system undergoes age-related changes that influence motor function so that activation capacity and contractile properties of prepubescent children improve with age (4, 17, 43).

Several studies have examined the maturation of neurones in newborns and during the first years of life by analyzing parameters extracted from electromyograms recorded in reflex conditions. These parameters are the Hoffmann reflex (H reflex), obtained by submaximal electrical stimulation of the motor nerve, and the tendon jerk (T reflex), obtained by tendon taps. These reflexes were usually characterized only by their latency to reveal changes in conduction velocity. The changes in latencies are due to both the end of myelinisation, as shown in masseter muscles (14, 20), and from increase in stature, as indicated for the leg muscles (10, 32, 34, 36, 37, 49).

The amplitudes of the H and T reflexes in children have rarely been analyzed. Only Vecchierini-Blineau and Guiheneuc (50) measured the H-reflex amplitude in awake children aged 0 to 4 yr; they reported a gradual reduction in this reflex during the first year of life. The H reflex increased slightly up to 4 yr of age but remained lower than adults' values. However, this study did not report data for children aged from 4 yr up to adulthood. To our knowledge, the stretch reflex induced by rapid joint displacements has been studied in prepubescent children only for masseter muscles, and authors reported an increase in the amplitude of the stretch reflex between the ages of 6 and 10 yr (14).

Although the H, T, and stretch reflexes are different notably in the way they can be evoked (in terms of their afferent volley or synaptic connections with motoneurons), nonetheless each of these reflexes predominantly involves the recruitment of the monosynaptic reflex pathway. In a recent review, Voerman et al. (51) detailed similarities and differences between the three types of reflexes. The amplitude of the reflexes is under the influence of both central and peripheral factors. Because H reflex bypasses muscle spindles, its amplitude mainly depends on central mechanisms, notably the motoneuronal excitability (although it does not give a direct measure of this excitability) and the synaptic efficacy (31, 51). The central mechanisms also influence T and stretch reflexes. Furthermore, when elicited from an external mechanical stimulus, these reflexes are also influenced by spindle sensitivity, gamma drive, and spindle recruitment through elastic structures of varying compliance (39, 40). This paper will focus particularly on this last factor of influence. Changes in the stiffness of the musculotendinous elements linked to the muscle spindles have been correlated with mechanically induced changes in the amplitude of reflexes in humans and rats (2, 3, 21). We have previously demonstrated an increase in musculotendinous stiffness with age in prepubescent children (23), and we now postulate a parallel increase in the amplitudes of the T and stretch reflexes.

This study, therefore, documents the relationship between a child's age and changes in the stretch reflex of the triceps surae (TS) muscle and ankle musculoarticular stiffness measured under active and passive conditions. The reflexes for the soleus (Sol) muscle and the whole TS were quantified to correlate the reflex excitability with the elastic properties of this muscle group.

METHODS

Subjects

A total of 46 prepubescent children (29 girls, 17 boys aged 7–11 yr) and their legal guardians were informed of the experimental procedures to be performed at the University Hospital Center in Amiens (Picardie, France). The pubertal status of each child was determined by the medical staff, and children were classified as prepubescent in

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terms of pubic hair, breast development, voice, and skin. Data on age, height, body mass, and left calf circumference were collected for each child. A reference group of adults included nine sedentary college students (21.0 ± 2.3 yr old). All subjects were free to withdraw from the experiment at any time. The experimental protocol was approved by the Consultative Committee of People Protection in Biomedical Research and by the local committee for hygiene, safety, and ethics of the University.

Ergometric Device and Apparatus

The ankle ergometer used in this study was a modified ankle ergometer initially designed for adults (46). It consisted of an electronic device including the power unit, the position and torque actuators, and a driving unit composed of a personal computer equipped with a 12-bit analog-to-digital converter, three timers, and a 16TTL output. The mechanical device consisted of an actuator (megatorque motor NSK RS 1010) and the transducers: a strain gauge torque (FGP CD 1050) and a 12-bit optical shaft encoder (Hengstler RA 585). Specific menu-driven software controlled all procedures and permitted the simultaneous recording of mechanical and electromyographic signals. A dual-beam oscilloscope gave the subject visual feedback on the procedure in progress.

The Achilles tendon was tapped with a custom-made electromagnetic reflex hammer made with a solenoid (Mecalectro). The reflex hammer was mounted on the foot support of the ankle ergometer. Electrical stimulations were applied using an isolated stimulator (Digitimer, DS7) with adjustable stimulation intensity. The cathode was a round-headed transcutaneous electrode, and the anode was a silver plate.

Experimental Protocol

Bipolar surface electrodes were placed over the belly of both gastrocnemius muscles [gastrocnemius lateralis (GL) and medialis (GM)] and 2 cm below the insertion of the gastrocnemii on the Achilles tendon for the Sol. The ground electrode (4 × 5-cm silver plate) was placed over the tibia. The standard Ag/AgCl surface electrodes (Beckman, 2-mm diameter) were spaced 15 mm center-to-center. After the skin was rubbed with an abrasive paste and cleaned with alcohol, the interelectrode impedance measured was under 5 kΩ. Electrode gel was used with all surface electrodes.

Subjects sat on a vertically and horizontally adjustable armchair. Dorsal support was provided during the rest periods, but not during voluntary contractions to prevent extraneous movements and to limit the contribution of other muscles such as the trunk extensor muscles. The left foot was firmly held in a sports shoe (identical model for all subjects) fixed to the footplate of the actuator. The ankle rotation axis (horizontal bimalleolar axis) was made to align with the rotation axis of the actuator. The knee was extended to 120°, and the ankle was placed at 90°, the suggested reference position for H-reflex studies (18).

The sequence of tests in an experimental session were *1*) Achilles tendon taps to elicit T reflexes of the TS at rest, *2*) electrical stimulation to record maximal H reflexes (H_{max}) and M waves at rest, *3*) maximum TS voluntary contractions under isometric conditions, *4*) sinusoid length perturbations under voluntary contractions [20%, 40%, and 60% maximal voluntary contraction (MVC)] and at rest (0% MVC) to *1*) record the TS stretch reflexes and *2*) determine the ankle musculoarticular stiffness. The total duration of the experimental protocol was ~90 min, including subject preparation.

T and H Reflexes

The H reflex was elicited by submaximal electrical stimulus (1 ms) of the posterior tibial nerve, with the cathode in the popliteal fossa (1-cm-diameter sphere) and the anode placed over the knee (3 × 3 cm silver plate covered with electrolyte gel), proximal to the patella. The intensity of the electrical stimulus was increased at 4-s intervals [to limit the postactivation refractory period (35, 52)] until there was a maximal Sol H reflex with no (or minimal) motor direct response (M wave). At that intensity, the H reflexes of GM and GL were near maximal. Although it would have been preferable to repeat H recordings to measure the precise maximal H responses of each muscle, experiment duration was so prolonged that this was not a practical option. Consequently, the H response of the TS muscle group was analyzed at the stimulus intensity giving the greatest reflex of the highly excitable Sol. The stimulus intensity was then increased until the direct maximal motor response (M_{max}) was obtained on each part of the TS. The M_{max} response was used to normalize all reflex responses.

The resting Achilles tendon was tapped using an electromagnetic hammer, placed in front of the maximal concavity of the Achilles tendon and 1 mm from the skin. The tap intensity was constant and was the heaviest deliverable by the apparatus. The recordings of M_{max}, H_{max}, or T responses were triggered by electrical pulses delivered by the stimulator and sampled at 2.5 kHz for 700 ms. During the H, T, and M response recordings, the experimenter checked using the control oscilloscope that there was no background activity (BGA) in any of the electromyograms (EMGs).

Data processing consisted of averaging the 10 highest (of 20) H responses and the 15 highest (of 30) T responses. The M_{max} response was obtained for each muscle by averaging five maximal M waves. The averaged EMG of Sol, GL, and GM were summed up to obtain TS M_{max}, TS H_{max}, and TS T responses. T, H_{max}, and M_{max} responses were quantified by their peak-to-peak amplitude. The mean amplitude (area/duration) of the averaged M_{max} response was also calculated because there were sometimes polyphasic tracings of the gastrocnemii muscles. This type of quantification has been justified and validated (8, 22). All EMGs studied in this paper were evaluated in mean amplitude to facilitate comparisons. T and H_{max} responses of TS were normalized to TS M_{max} (T/M_{max}, H_{max}/M_{max},) for test-to-test comparisons.

Sinusoidal Perturbations

Stretch reflexes. Stretch reflexes were elicited during sinusoidal length perturbations of the ankle superimposed on a voluntary contraction, as described by Rack et al. (40). The MVC was first determined in plantar flexion under isometric condition while the subject developed a maximal contraction against the actuator. Three maximal contractions of 3–4 s were recorded, with a 2-min rest after each attempt. MVC was defined as the greatest torque, maintained for at least 1 s, produced during the three attempts. The subject was instructed to maintain a torque (~5 s) at 20%, 40%, and 60% of MVC, despite the imposed sinusoidal perturbations. At least 30 s of rest were allowed after each trial. Thus this part of the experiment counted 44 trials (including the sinusoidal perturbations applied at rest, 0% MVC), lasting ~5 s each, thus representing a cumulative time of contraction of 3 min. Given the ≥30-s resting time after each trial, it can be assumed that these sinusoidal perturbations did not induce muscular fatigue. A low-pass filter (1 Hz) was applied to the torque signal shown by the feedback oscilloscope to help the subject maintain the target torque by masking the oscillations of the torque trace. After the isometric target torque had been maintained for 1 s, the experimenter imposed the sinusoidal length perturbations in the sagittal plane (displacement of 3° peak-to-peak around the reference position) at a given frequency ranging from 6 to 16 Hz at 1-Hz steps. The subject was instructed to relax as soon as the perturbation stopped.

Sol, GM, and GL EMGs were integrated over the 1 s of isometric contraction preceding the sinusoidal perturbations, and mean amplitudes (area/duration) were calculated. The BGA of TS was the sum of the mean amplitudes of the three muscles. BGA under submaximal condition is a percentage of maximal BGA calculated during MVC.

The stretch reflex data that were calculated after the first and last periods of sinusoidal perturbations were rejected to ensure that the target voluntary torque remained constant. Since the duration of these sinusoidal perturbations was maintained during 4 s regardless of frequency, the number of successive periods averaged to calculate the stretch reflex varied from 22 (at 6 Hz) to 62 (at 16 Hz). The EMG of Sol, GL, and GM were averaged over the selected periods, rectified, and summed up. From this data processing, the stretch reflex consisted essentially of its more time-locked short-latency component (22). The start and end of the stretch reflex burst were selected by the experimenter. Before this data processing, it was verified for each subject that the Sol exhibited the highest stretch reflex and that GM and GL presented comparable stretch reflexes. The stretch reflex of the TS (SR_{TS}) was quantified by its mean amplitude (area/duration) and related to BGA to give the $SR_{TS\text{-}BGA}$ values. The $SR_{TS\text{-}BGA}$ values were then related to the frequency of the sinusoidal perturbations. The area under this relationship, which represents the frequency distribution of the stretch reflex, gave an index of TS reflex excitability over the range of frequencies of the sinusoid perturbations (FD-$SR_{TS\text{-}BGA}$). The FD-$SR_{TS\text{-}BGA}$, calculated for each target torque (20%, 40%, and 60% MVC), has been validated and used to express changes in stretch reflex values (22).

Elastic characteristics. The experimental protocol and the data processing were previously reported by Lambertz et al. (24). The elastic properties of the musculoarticular system, including muscle-tendon and articular structures, were determined under passive (0% of MVC) and active conditions (20%, 40%, and 60% of MVC). Servo-controlled sinusoid length perturbations (3° peak-to-peak whatever the frequency of perturbations ranging from 6 to 16 Hz; see above) were used to establish frequency-response relationships (Bode-diagrams, in which the averaged displacement-to-torque ratios and the phase shifts between displacement and torque were plotted against the imposed frequency). A Bode diagram reflects the mixed mechanical contribution of inertia I, viscosity B, and elasticity K according to the formula: $Z(s) = I \cdot s + B + K/s$, where Z is the mechanical impedance and s is the Laplace operator.

K was calculated at 0%, 20%, 40%, and 60% MVC to construct the stiffness-torque relationship. Best fit for this stiffness-torque relationship was obtained by a linear model: $K = a\,T + b$, where T is the torque value and b the intercept point, representing the passive stiffness of the musculoarticular system. Because the youngest children exhibited an overactivation of the TS under submaximal condition (16), the musculoarticular stiffness was computed as the slope of the stiffness-EMG relationship (23) (as opposed to the use of the slope of the stiffness-torque relationship). The slope of this relationship gave the stiffness index of the musculoarticular system, based on TS activation ($SI_{MA\text{-}EMG}$).

Statistics

Values are reported as means ± SE. Linear regression analyses were used to analyse age-related changes in the various parameters. Bivariable linear regression analysis was performed to test both age and stiffness as predictors of stretch reflex to evaluate whether stiffness remains a significant predictor of stretch reflexes even once the regression coefficients are adjusted for the effect of age. Two-way repeated-measures ANOVAs were used to analyze the effects of age and gender and to compare data for children and adults. Significant interactions were followed by simple main effect designs, and, where relevant, a post hoc Fisher test was used to determine which means were significantly different. Regression lines were used to determine differences in FD-$SR_{TS\text{-}BGA}$-$SI_{MA\text{-}EMG}$ relationships. Differences were considered significant when the P value was <0.05 ($P < 0.05$).

RESULTS

We first verified that none of the measured parameters for a given age was influenced by the gender of the child. The data for girls and boys were pooled for each age group because there was no statistically significant gender dependence.

The mean anthropometric data for all children revealed that all the measured parameters (calf circumference, body height, and body mass) increased significantly with age ($P < 0.05$) (17). The anthropometric characteristics of the prepubescent children were always significantly lower than those of adults ($P < 0.05$). The mean calf circumference was 26.4 ± 0.6 cm for 7-yr-old children, 31.9 ± 2.5 cm for 11-yr-old children, and

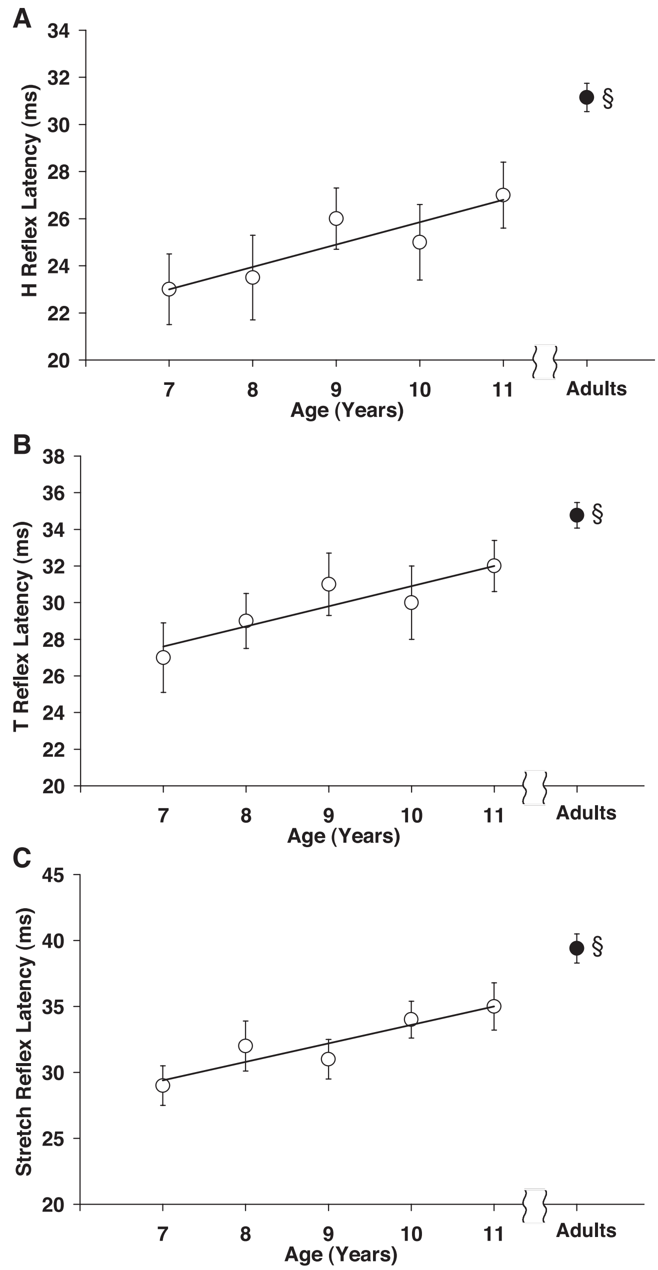

Fig. 1. Relationships between the latency of reflexes quantified for the triceps sural and the age of prepubescent children. The relationship concerns the H reflex (*A*), the T reflex (*B*) and the stretch reflex (*C*). H-, T-, and stretch reflex latencies were significantly correlated with the age of prepubescent children (○) (*A*: $r = 0.95$, $n = 5$; $P < 0.05$; *B*: $r = 0.97$, $n = 5$; $P < 0.05$; *C*: $r = 0.96$, $n = 5$; $P < 0.05$) and were lower than those for the adults (●). Data are means ± SE. §Significant differences between the adults and all prepubescent child groups from ANOVA ($P < 0.05$).

Table 1. *Peak-to-peak and mean amplitudes of the Sol and TS M waves*

	7-yr-old Group (n = 10)	8-yr-old Group (n = 9)	9-yr-old Group (n = 8)	10-yr-old Group (n = 11)	11-yr-old Group (n = 8)	Adult Group (n = 9)
			Peak-to-peak amplitude			
Sol M_{max}, mV	7.7±1.6	7.1±2.0	7.5±1.7	7.4±1.3	7.6±1.4	7.9±1.1
TS M_{max}, mV	18.3±1.3	17.8±1.8	18.6±1.5	18.8±1.3	18.4±1.2	19.6±0.8
			Mean amplitude (area/duration)			
Sol M_{max}, mV	1.3±0.2	1.1±0.4	1.2±0.3	1.3±0.2	1.2±0.3	1.3±0.3
TS M_{max}, mV	3.9±0.2	3.7±0.5	3.9±0.4	3.8±0.5	4.0±0.2	4.1±0.2

Values are means SE. Sol, soleus; TS, triceps surae; M_{max}, maximal M wave.

37.6 ± 1.5 cm for adults. The mean height was 126.6 ± 3.7 cm for 7-yr-old children, 150.9 ± 7.4 cm for 11-yr-old children, and 178.8 ± 6.4 cm for adults. Finally, the mean body mass was 26.2 ± 2.6 kg for 7-yr-old children, 41.7 ± 5.6 kg for 11-yr-old children, and 69.8 ± 5.8 kg for adults.

The latencies of H, T, and stretch reflexes were all correlated with age of the children ($P < 0.05$) (Fig. 1).

The peak-to-peak and mean amplitudes of the Sol and TS M waves were not affected by the age of the children and did not differ from adult values (see Table 1). The H_{max}-to-M_{max} and T-to-M_{max} ratios of all children and adults calculated from the peak-to-peak amplitude of the responses and from their mean amplitudes were similar ($P > 0.05$).

The H_{max}-to-M_{max} ratio did not change with age [59.2 ± 10.5% (Sol) and 48.6 ± 10.5% (TS) for 7-yr-old children and 60.7 ± 6.1% (Sol) and 49.4 ± 6.0% (TS) for 11-yr-old children] [Sol: $F(4,46) = 0.14$, $P = 0.97$; TS: $F(4,46) = 0.12$, $P = 0.96$], and they were similar to adult values (61.0 ± 5.5% for Sol and 49.0 ± 4.7% for TS) [Sol: $F(5,55) = 0.15$, $P = 0.98$; TS: $F(5,55) = 0.11$, $P = 0.97$] (Fig. 2).

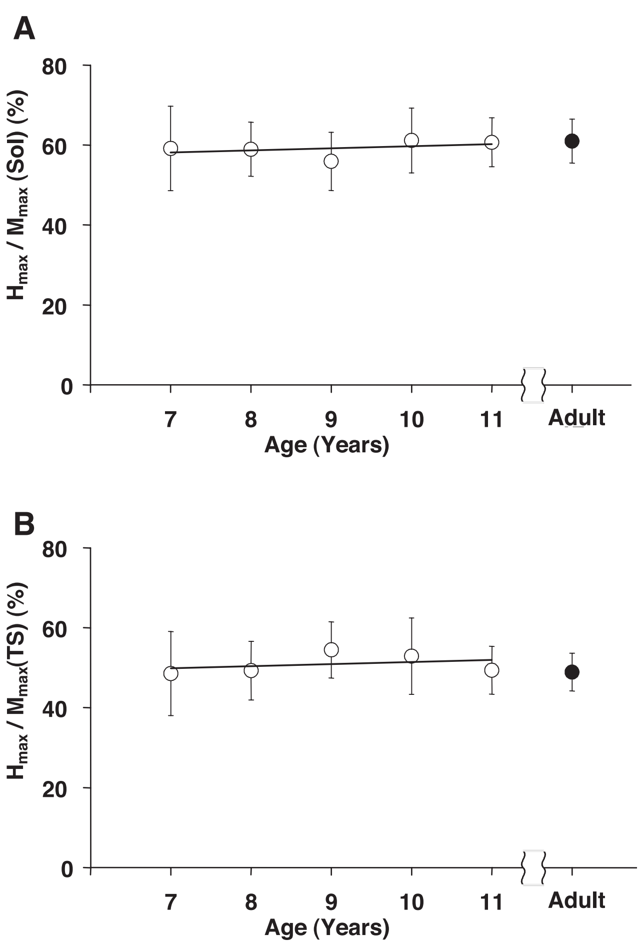

Fig. 2. Relationship between soleus (Sol; *A*) and triceps surae (TS; *B*) maximal H reflex-to-maximal M wave (H_{max}-to-M_{max}) ratio and the age of prepubescent children. None of the data for any of the muscles were correlated (*A*: $r = 0.40$; $n = 5$; $P > 0.05$; *B*: $r = 0.31$; $n = 5$; $P > 0.05$), and the mean values for prepubescent children (○) did not change significantly with age and were similar to adult values (●). Data are means ± SE.

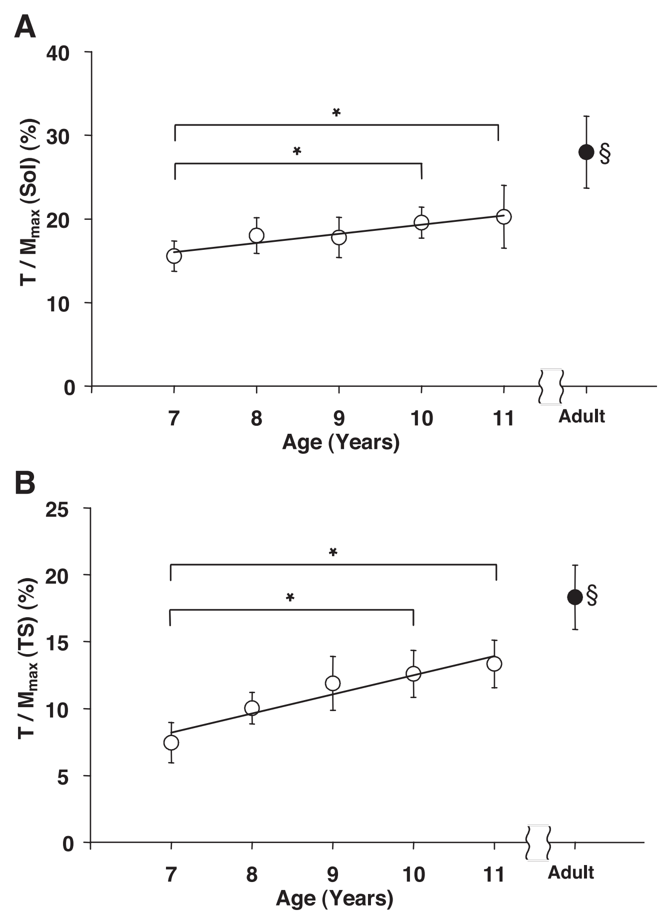

Fig. 3. Relationship between Sol (*A*) and TS (*B*) T-to-M_{max} ratios and the ages of prepubescent children. The T-to-M_{max} ratios were significantly correlated with the age of prepubescent children (○) (*A*: $r = 0.94$, $n = 5$; $P < 0.05$; *B*: $r = 0.96$, $n = 5$; $P < 0.05$). The T-to-M_{max} ratios for the Sol and TS muscles of all children were significantly lower than those for the adults (●). Data are means ± SE. *Significant differences between prepubescent children ($P < 0.05$). §Significant differences between the adults and all prepubescent child groups from ANOVA ($P < 0.05$).

The T-to-M_{max} ratios were notably affected by the age of the children. For the Sol, they increased from 15.6 ± 1.8% for the 7-yr-old children to 20.3 ± 3.7% for the 11-yr-old children, and for the TS muscle group from 7.5 ± 1.5% in 7-yr-olds to 13.4 ± 1.8% in 11-yr-old children [Sol: $F(4,46) = 5.2$, $P < 0.05$; TS: $F(4,46) = 18.1$, $P < 0.01$]. However, the children's values were still significantly lower than those of the adults (28.0 ± 4.3% for Sol and 18.3 ± 2.4% for TS) [Sol: $F(5,55) = 5.2$, $P < 0.05$; TS: $F(5,55) = 23.6$, $P < 0.01$]. The T-to-M_{max} ratios for Sol and TS muscles were significantly correlated with the age of the children (Fig. 3). The slope of this relationship was steeper for the TS muscle (1.43) than for the Sol muscle (1.09), but the difference was not significant.

Figure 4 illustrates the stretch reflexes recorded on each part of the TS during sinusoidal length perturbations imposed at 14 Hz and at 40% MVC for a 7-yr-old child, an 11-yr-old child, and an adult. The higher reflexes were exhibited by the Sol, with the GM and GL presenting a less but similar reflex amplitude. Whatever the muscle considered, the amplitude of the stretch reflex was lower in the youngest child. After it was verified that these results were confirmed at each frequency of sinusoidal perturbations, the Sol, GM, and GL were summed up to give the stretch reflex of the TS (SR_{TS}) and to calculate the frequency distribution of the stretch reflex over the range of frequencies of the sinusoid perturbations ($FD\text{-}SR_{TS\text{-}BGA}$). $FD\text{-}SR_{TS\text{-}BGA}$ decreased as activation increased. This decrease was smaller in 7-yr-old children than in 11-yr-old children, and it was more pronounced in adults (Fig. 5), as indicated by the slopes of the relationship between the stretch reflex index and the BGA. Figure 5 also illustrates the fact that the children overactivated their TS when maintaining the submaximal tasks. For example, the 7-yr-old children had a BGA-to-BGA_{max} ratio of ~0.8 at 60% MVC, when for the adults this ratio was ~50%. This overactivation phenomenon, presented in detail by Grosset et al. (16), contributed to the lower stretch reflex presented by the children.

The $FD\text{-}SR_{TS\text{-}BGA}$ was significantly correlated with the age of the children, regardless of the target torque required and the muscle considered (Fig. 6, *A* and *B*).

The musculoarticular stiffness under passive conditions (the intercept point of the stiffness-torque linear regression with the ordinate) increased significantly with age [$F(4,46) = 65.4$, $P < 0.01$] but was always significantly lower than that of the adults [$F(5,55) = 77.2$, $P < 0.01$] (Fig. 7*A*). Figure 7*B* shows the relationship between the age of the children and the musculoarticular stiffness index expressed according to the activation level ($SI_{MA\text{-}EMG}$). $SI_{MA\text{-}EMG}$ was significantly increased and correlated with the age of the prepubescent children [$F(4,46) = 25.3$, $P < 0.01$] ($r = 0.97$, $n = 5$, $P < 0.05$), but adult values were still significantly higher than that for any of the five age groups of children [$F(5,55) = 29.7$, $P < 0.05$]. The link between the changes in reflexes and stiffness at rest is indicated by the significant correlation ($r = 0.69$, $n = 30$, $P < 0.05$) between the TS T-to-M_{max} ratio and the passive stiffness (Fig. 8*A*). The same holds for active conditions. Thus $FD\text{-}SR_{TS\text{-}BGA}$ is significantly correlated with the musculoarticular stiffness index ($r = 0.55$, $n = 34$, $P < 0.05$) (Fig. 8*B*). Bivariable linear regression analyses showed that whatever the stretch reflex considered (TS T-to-M_{max} or $FD\text{-}SR_{TS\text{-}BGA}$), stiffness (passive stiffness or musculoarticular stiffness index, respectively) remains a significant sole predictor of stretch reflexes even once the regression coefficients are adjusted for the effect of age ($P < 0.01$ in both cases).

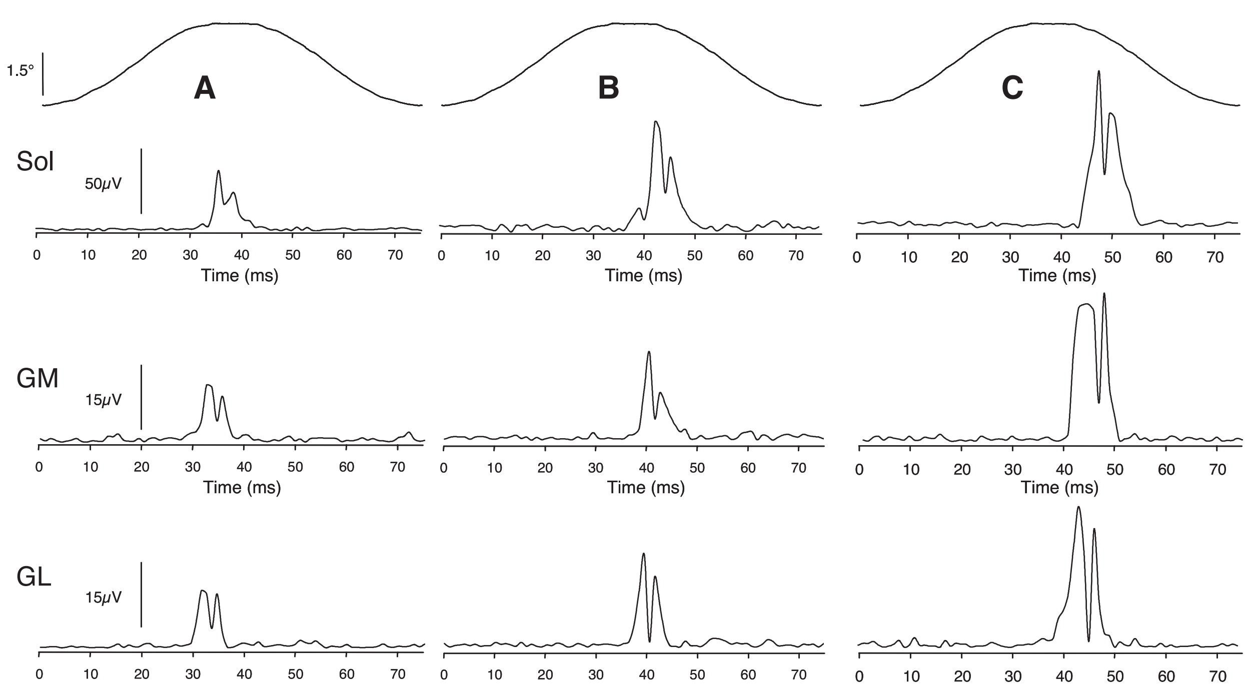

Fig. 4. Typical averaged tracings of angular displacement and rectified Sol, medial muscle (GM) and lateral gastrocnemius (GL) EMGs recorded under active conditions [40% maximal voluntary contraction (MVC)] during sinusoidal perturbations at 14 Hz. Data are from a 7-yr-old child (*A*), an 11-yr-old child (*B*), and an adult (*C*).

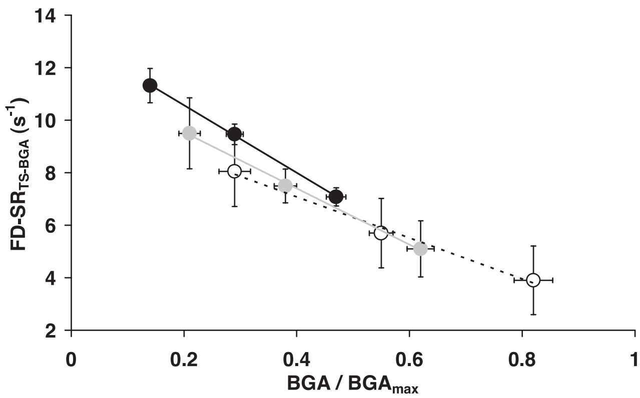

Fig. 5. Relationships between the stretch reflex index (FD-SR$_{TS\text{-}BGA}$) and the background activity related to the maximal EMG recorded in MVC (BGA/BGA$_{max}$) for the 7-yr-old children (open circles), the 11-yr-old group (shaded circles), and the adults (filled circles). The decrease in FD-SR$_{TS\text{-}BGA}$ was significantly correlated with the increase in the BGA-to-BGA$_{max}$ ratio (for the 7-yr-old, the 11-yr-old, and the adult groups: $r = 0.99$, $n = 3$, $P < 0.05$). The slope of the relationship was steeper for the adults (12.9 s^{-1}) than for the oldest children (10.7 s^{-1}) or the youngest ones (7.8 s^{-1}).

DISCUSSION

We have analyzed reflex excitability in prepubescent children of different ages so as to demonstrate that changes in musculoarticular stiffness (23) contribute to the enhancement of mechanically induced reflexes with age. Before discussing modification with age in the H, T, and stretch reflexes, a caveat should be brought to light. Indeed, the direct comparison between these reflexes is not entirely realistic because the three responses differ in some important aspects. For H reflex, the afferent volley is shorter in duration and better in terms of synchronization but involves more Ib afferents (31). Tendon tap to elicit T reflex mainly excites Ia afferents but also some afferents of group II (27). Oligosynaptic contributions are described for both the ankle jerk and the H reflex (7), whereas the short latency component of the stretch reflex can be considered as limited to monosynaptic connections (5, 45). The stretch reflex requires the active state of the muscle to be easily obtained; thus supraspinal controls are more effective on this stretch reflex than on the reflexes elicited at rest. Despite these differences, it is generally considered that the three responses are largely due to the activation of the monosynaptic reflex pathway; this validates their comparisons, provided the limitations of these comparisons are clearly enounced.

In the present study, the reflexes were evaluated for the whole TS muscle to relate the reflexes to the elastic properties of that muscle group. In addition to this, the reflex excitability of the Sol alone was quantified because most of the published data concerns said muscle.

The amplitudes of the Sol and TS M waves were identical in the children (whatever their age) and adults. An increase in M-wave amplitude was expected since it is known that *1*) muscle fiber diameter increases during growth [for review, see Christ and Brand-Saberi (9)] and *2*) muscle fibers of greater diameter produce higher action potentials [for review, see De Luca (12)]. However, we used the same area electrodes for all subjects, and they may have detected in their receptive field more muscle action potentials when placed on a small muscle, as in youngest children. The skin thickness may also differ with age, and this could influence the detection of EMGs [see Farina et al. (13) for review]. Thus the constant M wave in all groups may be due to a combination of factors: the number of muscle action potentials detected by the electrodes, the size of the muscle action potential unit, and the skin thickness (cutaneous and adipose tissues).

The reflex excitability of a muscle, or muscle group, depends on both central and peripheral mechanisms. The excitability of the spinal loop at rest is presently assessed by analyzing the H- and T reflexes. In children, the H-reflex is more often used to assess changes in conduction velocity along the reflex loop than to quantify the reflex excitability. Despite the difficulties and limitations to interpret H-reflex changes, it is commonly considered that changes in H-reflex amplitude in adults indicate changes in synaptic efficacy, neurotransmitter release, and/or motoneuron excitability, notably when the H reflex is evoked in quiescent muscle (28, 47, 52). With the lack of complementary experiments such as conditioning stimulations or vibrations needed to assess synaptic efficacy and presynaptic inhibition (19, 31), it is not possible to know which central mechanisms may affect an eventual modification of the H-reflex. However, the constancy of the Sol and TS H-reflex

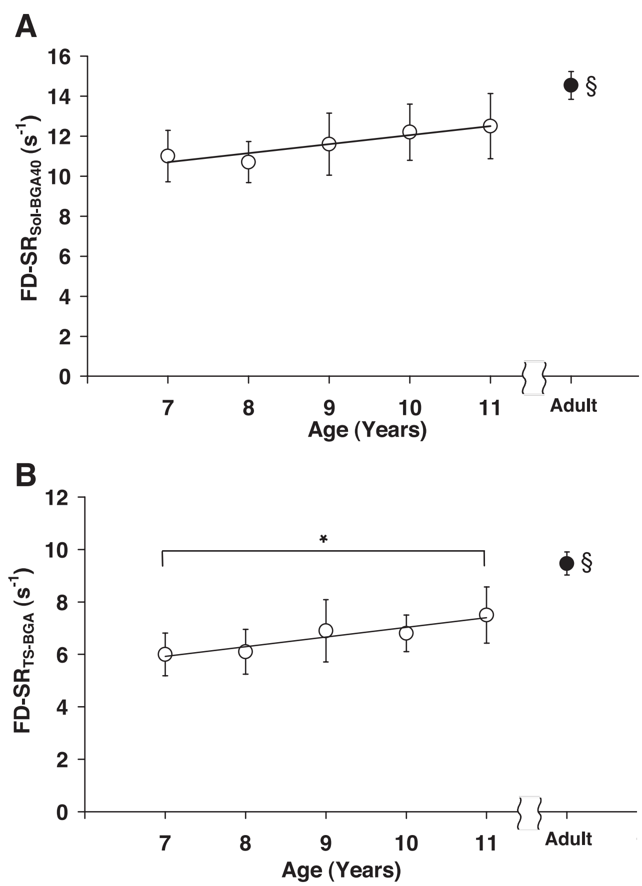

Fig. 6. Relationship between the stretch reflex index (FD-SR$_{TS\text{-}BGA}$) for the soleus (*A*) and triceps surae muscles (*B*), and the age of the prepubescent children for a target torque of 40% MVC. The FD-SR$_{BGA}$ values were significantly correlated with the age of the prepubescent children (○) (*A*: $r = 0.92$, $n = 5$, $P < 0.05$; *B*: $r = 0.94$, $n = 5$, $P < 0.05$) and were still higher for the adults (●). Data are means ± SE. *Significant differences between prepubescent children ($P < 0.05$). §Significant differences between the adults and all the prepubescent child groups from ANOVA ($P < 0.05$).

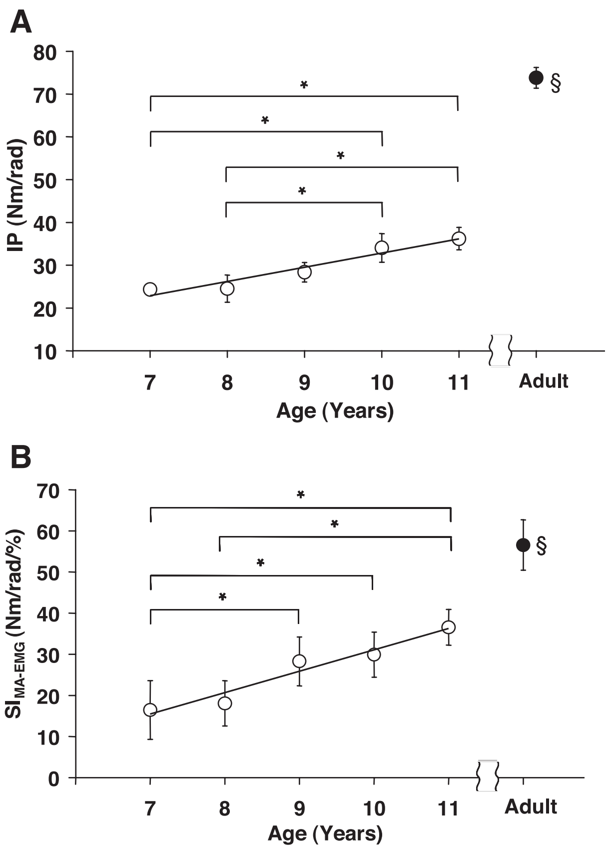

Fig. 7. *A*: correlation between passive stiffness of the musculoarticular system, defined as the intercept point (IP) of the linear musculoarticular stiffness-torque relationship, and the age of the prepubescent children (○) ($r = 0.96$, $n = 5$, $P < 0.05$). IP values were higher for adults (●). *B*: relationship between active stiffness of the musculoarticular system, defined as the slope of the musculoarticular stiffness-activation relationship (SI_{MA-EMG}) and the age of the prepubescent children (○) ($r = 0.97$, $n = 5$, $P < 0.05$). SI_{MA-EMG} was still higher for the adults (●). Data are means ± SE. *Significant differences between the prepubescent child groups ($P < 0.05$). §Significant differences between the adult subjects and all prepubescent child groups from ANOVA ($P < 0.05$).

amplitudes in the children indicates that these central mechanisms seem to be mature in children as young as 7 yr old.

The Sol H_{max}-to-M_{max} ratios calculated for the children and adults were comparable with published values (30, 33, 42, 50). The TS H_{max}-to-M_{max} ratios confirm that the H reflexes are lower in the gastrocmenius (48), also in children.

The T reflex, recorded when the child was relaxed, increased with age. This age-related increase in T reflex was less pronounced for the highly excitable Sol than for TS, but it was significant in both cases. The increases in the Sol and TS T reflexes with age may be due to an improvement in γ drive. However, the quiescent state of the muscle suggests that the γ activation was probably low so that it cannot account for the changes in the T reflex (35).

The increase in the T reflex could also be due to an increase in the sensitivity of the muscle spindles with age. The sensitivity of the spindle afferents changes with age in rats (29) and following a period of immobilization (15) or simulated microgravity (11, 41). Similarly, the patterns of spindle sensitivity in kittens and adult cats was also age dependent (44). It seems reasonable to consider that the intrafusal fibers mature with age in the prepubescent children examined in this study and that modifications of spindle sensitivity cannot be at the origin of the increase in the T reflex.

However, spindle recruitment can be influenced by the stiffness of the elastic elements linked to the muscle spindles. The increase in T-reflex amplitude with age may indicate that muscle stretch in response to tendon tap is transmitted to the muscle spindles via stiffer muscle-tendon structures. Part of the imposed movement of more compliant tendons is absorbed by the tendon itself so that less is transmitted to the muscle spindles, as shown by Rack et al. (40). Changes in the T reflexes of animals have been related to changes in musculo tendinous stiffness (1, 2). The recent study of Lambertz et al. (21) on the effects of spaceflight on humans found a significant correlation between the changes in the T reflex of the TS and passive musculoarticular stiffness, indicating that the passive elastic structures take part in the reflex adaptation.

The correlations established here between the amplitude of the T reflex and the passive musculoarticular stiffness supports the link between reflex amplitude and muscle stiffness. Such correlation suggests that adaptation of the elastic elements is the main cause of the increase in reflex excitability with age in prepubertal children.

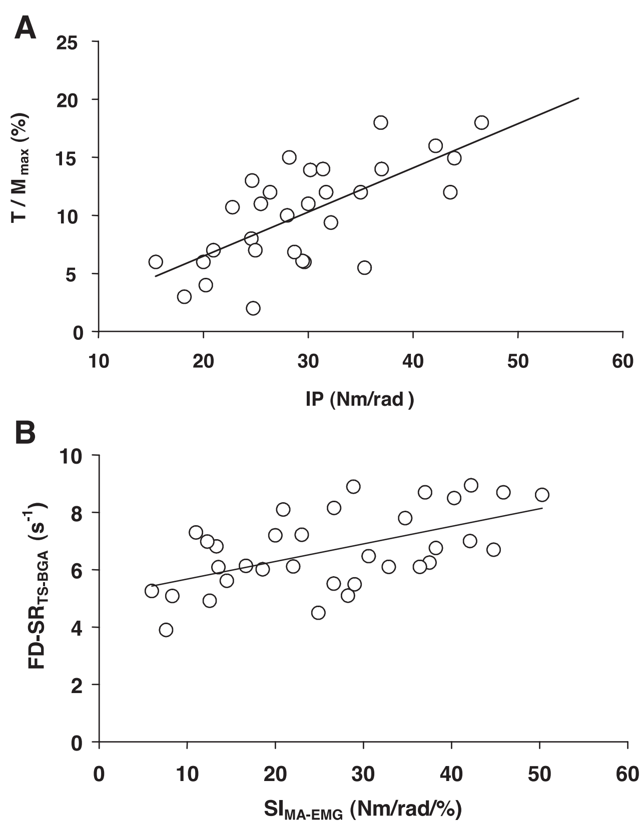

Fig. 8. Paired changes between reflex excitability and musculoarticular stiffness, under passive and active conditions, for prepubertal children. *A*: correlation between individual values of TS T-to-M_{max} ratio and musculoarticular stiffness calculated at rest (IP) for the whole population of prepubescent children ($r = 0.69$, $n = 30$, $P < 0.05$). *B*: correlation between individual values of stretch reflex index ($FD\text{-}SR_{TS\text{-}BGA}$) and musculoarticular stiffness calculated under active conditions (SI_{MA-EMG}) for the whole population of prepubescent children ($r = 0.55$, $n = 34$, $P < 0.05$). Data were obtained while the subjects maintained a torque of 40% MVC.

The increase in reflex with age is also observed when the reflexes are elicited under active condition by sinusoidal perturbation. The increase was shown by experimental monitoring (see Fig. 3) and supported by the values of the parameter, quantifying the stretch reflex over all the frequencies tested, in agreement with previous suggestions (22). Such an increase in stretch reflex amplitude with the age of prepubescent children has previously been described for the masseter muscles and attributed to a maturation of the sensorimotor pathways (14). Due to the active state of the TS, changes in γ drive may contribute to this reflex gain more so than when the reflex is evoked in quiescent muscles. However, once again, we suggest that changes in the elastic structures may account for the changes in reflex excitability. The correlation between the stretch reflex and the musculoarticular stiffness index evaluated under active conditions and the bivariable linear regression analysis indicates that the stiffness of the elastic structures contributes notably to the increase in stretch reflex amplitude with age. This correlation was established at a target torque of 40% MVC, well above the contraction needed for the tendon to act as a spring of constant stiffness [see Proske and Morgan (38) for review].

The analysis of the frequency distribution of the stretch reflex at different muscle activations is a new approach (22) to the "automatic gain principle." Marsden et al. (25) showed that the amplitude of the stretch reflex increases with the degree of agonist activation. This "automatic gain principle" was later developed by Matthews (26) in terms of frequency modulation and recruitment of motor units. Bloem et al. (6) proposed that this "automatic gain principle" could be evaluated by the relationship between the stretch reflex and the BGA (ratio method), leading to negative correlation between this relative stretch reflex and activation values. Lambertz et al. (22) used this ratio method to show that the slope of relationship between the frequency distribution of the relative stretch reflex and the muscle activation was steeper for a highly excitable muscle like the Sol. Similarly, the shallower slope for the $\text{FD-SR}_{\text{TS-BGA}}$-activation relationship indicated smaller changes in reflex excitability according to the level of TS activation in the youngest children. This result can be partly explained by the overactivation presented by the youngest children under submaximal conditions as shown in Fig. 5 and detailed in Grosset et al. (16).

We have thus used several methods to elicit stretch reflexes and obtain a better understanding of reflex excitability in prepubescent children. The constancy of the H reflex in the children of all ages indicates that the central mechanisms involved in this reflex pathway are mature. However, the mechanically induced reflex increases with the age of the child. Several mechanisms may be involved in this increase (improved spindle sensitivity and/or in γ drive), but the correlation between changes in reflex amplitude and muscle stiffness clearly indicates that the elastic properties contribute greatly to the increase in the stretch reflex with age.

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REFERENCES

1. **Almeida-Silveira MI, Lambertz D, Pérot C, Goubel F.** Changes in stiffness induced by hindlimb suspension in rat Achilles tendon. *Eur J Appl Physiol* 81: 252–257, 2000.
2. **Almeida-Silveira MI, Pérot C, Goubel F.** Neuromuscular adaptations in rats trained by muscle stretch-shortening. *Eur J Appl Physiol* 72: 261–266, 1996.
3. **Anderson J, Almeida-Silveira MI, Pérot C.** Reflex and muscular adaptations in rat soleus muscle after hindlimb suspension. *J Exp Biol* 202: 2701–2707, 1999.
4. **Belanger AY, McComas AJ.** Contractile properties of human skeletal muscle in childhood and adolescence. *Eur J Appl Physiol* 58: 563–567, 1989.
5. **Berardelli A, Hallett M, Kaufman C, Fine E, Berenberg W, Simon SR.** Stretch reflexes of triceps surae in normal man. *J Neurol Neurosurg Psychiatry* 45: 513–525, 1982.
6. **Bloem BR, van Dijk JG, Beckley DJ, Zwinderman AH, Remler MP, Roos RA.** Correction for the influence of background muscle activity on stretch reflex amplitudes. *J Neurosci Methods* 46: 167–174, 1993.
7. **Burke D, Gandevia SC, McKeon B.** Monosynaptic and oligosynaptic contributions to human ankle jerk and H-reflex. *J Neurophysiol* 52: 435–448, 1984.
8. **Castaingts V, Martin A, Van Hoecke J, Pérot C.** Neuromuscular efficiency of the triceps surae in induced and voluntary contractions: morning and evening evaluations. *Chronobiol Int* 21: 631–643, 2004.
9. **Christ B, Brand-Saberi B.** Limb muscle development. *Int J Dev Biol* 46: 905–914, 2002.
10. **Cruz Martinez A, Ferrer MT, Martin MJ.** Motor conduction velocity and H-reflex in prematures with very short gestational age. *Electromyogr Clin Neurophysiol* 23: 13–19, 1983.
11. **De-Doncker L, Picquet F, Petit J, Falempin M.** Characterization of spindle afferents in rat soleus muscle using ramp-and-hold and sinusoidal stretches. *J Neurophysiol* 89: 442–449, 2003.
12. **De Luca CJ.** The use of surface electromyography in biomechanics. *J Appl Biomech* 13: 135–163, 1997.
13. **Farina D, Merletti R, Enoka RM.** The extraction of neural strategies from the surface EMG. *J Appl Physiol* 96: 1486–1495, 2004.
14. **Finan DS, Smith A.** Jaw stretch reflexes in children. *Exp Brain Res* 164: 58–66, 2005.
15. **Gioux M, Petit J.** Effects of immobilizing the cat peroneus longus muscle on the activity of its own spindles. *J Appl Physiol* 75: 2629–2635, 1993.
16. **Grosset JF, Mora I, Lambertz D, Pérot C.** Voluntary activation of the triceps surae in prepubertal children. *J Electromyogr Kinesiol* doi:10.1016/j;jelekin.2006.11.002: 2006.
17. **Grosset JF, Mora I, Lambertz D, Pérot C.** Age-related changes in twitch properties of plantar flexor muscles in prepubertal children. *Pediatr Res* 58: 966–970, 2005.
18. **Hugon M.** Methodology of the Hoffman reflex in man. In: *New Development in Electromyography and Clinical Neurophysiology* (vol. III), edited by Desmedt JE. Basel: Karger, 1973, p. 277–293.
19. **Hultborn H, Meunier S, Morin C, Pierrot-Deseilligny E.** Assessing changes in presynaptic inhibition of I a fibres: a study in man and the cat. *J Physiol* 389: 729–756, 1987.
20. **Jaaskelainen SK.** The jaw reflex: maturation in the neonatal period and childhood. *Dev Med Child Neurol* 35: 708–714, 1993.
21. **Lambertz D, Goubel F, Kaspranski R, Pérot C.** Influence of long-term spaceflight on neuromechanical properties of muscles in humans. *J Appl Physiol* 94: 490–498, 2003.
22. **Lambertz D, Goubel F, Pérot C.** A method to evaluate reflex excitability of the human ankle plantarflexors despite changes in maximal activation capacities. *Exp Brain Res* 143: 89–99, 2002.
23. **Lambertz D, Mora I, Grosset JF, Pérot C.** Evaluation of musculotendinous stiffness in prepubertal children and adults, taking into account muscle activity. *J Appl Physiol* 95: 64–72, 2003.
24. **Lambertz D, Pérot C, Kaspranski R, Goubel F.** Effects of long-term spaceflight on mechanical properties of muscles in humans. *J Appl Physiol* 90: 179–188, 2001.
25. **Marsden CD, Merton PA, Morton HB.** Servo action in the human thumb. *J Physiol* 257: 1–44, 1976.

26. **Matthews PB.** Observations on the automatic compensation of reflex gain on varying the pre-existing level of motor discharge in man. *J Physiol* 374: 73–90, 1986.
27. **Milanov IG.** A comparison of methods to assess the excitability of lower motoneurones. *Can J Neurol Sci* 19: 64–68, 1992.
28. **Misiaszek JE.** The H-reflex as a tool in neurophysiology: its limitations and uses in understanding nervous system function. *Muscle Nerve* 28: 144–160, 2003.
29. **Miwa T, Miwa Y, Kanda K.** Dynamic and static sensitivities of muscle spindle primary endings in aged rats to ramp stretch. *Neurosci Lett* 201: 179–182, 1995.
30. **Morelli M, Sullivan SJ, Seaborne DE.** Comparison of human triceps surae H-reflexes obtained from mid and distal recording sites. *Electromyogr Clin Neurophysiol* 30: 181–186, 1990.
31. **Morita H, Petersen N, Christensen LO, Sinkjaer T, Nielsen J.** Sensitivity of H-reflexes and stretch reflexes to presynaptic inhibition in humans. *J Neurophysiol* 80: 610–620, 1998.
32. **Myklebust BM, Gottlieb GL, Agarwal GC.** Stretch reflexes of the normal infant. *Dev Med Child Neurol* 28: 440–449, 1986.
33. **Nordlund MM, Thorstensson A, Cresswell AG.** Variations in the soleus H-reflex as a function of activation during controlled lengthening and shortening actions. *Brain Res* 952: 301–307, 2002.
34. **Pereon Y, Nguyen Tich S, Fournier E, Genet R, Guiheneuc P.** The electrophysiological recording of deep tendon reflexes: normative data in children and in adults. *Neurophysiol Clin* 34: 131–139, 2004.
35. **Pierrot-Deseilligny E, Mazevet D.** The monosynaptic reflex: a tool to investigate motor control in humans. Interest and limits. *Neurophysiol Clin* 30: 67–80, 2000.
36. **Prakash U, Bhatia BD.** H-reflex latency: a maturity criterion for newborn babies. *Electromyogr Clin Neurophysiol* 37: 435–437, 1997.
37. **Prakash U, Bhatia BD, Kumar M, Singh OP.** Electrophysiological studies (MNCV and H-RL) in twin babies. *Electromyogr Clin Neurophysiol* 34: 351–354, 1994.
38. **Proske U, Morgan DL.** Tendon stiffness: methods of measurement and significance for the control of movement. A review. *J Biomech* 20: 75–82, 1987.
39. **Rack PM.** Stretch reflexes in man: the significance of tendon compliance. In: *Feedback and Motor Control in Invertebrates and Vertebrates*, edited by Barnes WJP and Gladden MH. London: Croom Helm, 1985, p. 217–229.
40. **Rack PM, Ross HF, Thilmann AF, Walters DK.** Reflex responses at the human ankle: the importance of tendon compliance. *J Physiol* 344: 503–524, 1983.
41. **Rosant C, Nagel MD, Pérot C.** Adaptation of rat soleus muscle spindles after 21 days of hindlimb unloading. *Exp Neurol* 200: 191–199, 2006.
42. **Scaglioni G, Ferri A, Minetti AE, Martin A, Van_Hoecke J, Capodaglio P, Sartorio A, Narici MV.** Plantar flexor activation capacity and H reflex in older adults: adaptations to strength training. *J Appl Physiol* 92: 2292–2302, 2002.
43. **Seger JY, Thorstensson A.** Muscle strength and electromyogram in boys and girls followed through puberty. *Eur J Appl Physiol* 81: 54–61, 2000.
44. **Skoglund S.** Activity of muscle receptors in the kitten. *Nature* 186: 478–479, 1960.
45. **Toft E, Sinkjaer T, Espersen GT.** Quantitation of the stretch reflex. Technical procedures and clinical applications. *Acta Neurol Scand* 79: 384–390, 1989.
46. **Tognella F, Mainar A, Vanhoutte C, Goubel F.** A mechanical device for studying mechanical properties of human muscles in vivo. *J Biomech* 30: 1077–1080, 1997.
47. **Tucker KJ, Tuncer M, Turker KS.** A review of the H-reflex and M-wave in the human triceps surae. *Hum Mov Sci* 24: 667–688, 2005.
48. **Tucker KJ, Turker KS.** Muscle spindle feedback differs between the soleus and gastrocnemius in humans. *Somatosens Mot Res* 21: 189–197, 2004.
49. **Vecchierini Blineau MF, Guiheneuc P.** Electrophysiological study of the peripheral nervous system in children. Changes in proximal and distal conduction velocities from birth to age 5 years. *J Neurol Neurosurg Psychiatry* 42: 753–759, 1979.
50. **Vecchierini Blineau MF, Guiheneuc P.** Excitability of the monosynaptic reflex pathway in the child from birth to four years of age. *J Neurol Neurosurg Psychiatry* 44: 309–314, 1981.
51. **Voerman GE, Gregoric M, Hermens HJ.** Neurophysiological methods for the assessment of spasticity: the Hoffmann reflex, the tendon reflex, and the stretch reflex. *Disabil Rehabil* 27: 33–68, 2005.
52. **Zehr PE.** Considerations for use of the Hoffmann reflex in exercise studies. *Eur J Appl Physiol* 86: 455–468, 2002.