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NEURAL FACTORS VERSUS HYPERTROPHY IN THE TIME COURSE OF MUSCLE STRENGTH GAIN[1]

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INTRODUCTION

It is a common observation that repeated testing of the strength of skeletal muscles results in increasing test scores in the absence of measurable hypertrophy (1, 2, 4, 5). Such increasing test scores are typically seen in daily or even weekly retesting at the inception of a muscle strength training regimen. In one case in our laboratory, seven weeks of intensive weight training of the elbow flexors resulted in a seventeen percent improvement in strength without a measurable change in girth (4). It has also been shown that when only one limb is trained, the paired untrained limb improves significantly in subsequent retests of strength but without evidence of hypertrophy (2, 5, 7).

Rasch and Morehouse (13) demonstrated strength gains from a six week training program in tests when muscles were employed in a familiar way, but little or no gain in strength was observed when unfamiliar test procedures were employed. They suggested that their findings indicate that the higher scores in strength tests resulting from the exercise programs reflected largely the acquisition of skill.

All of the above findings support the importance of "neural factors", which although not yet well defined, certainly contribute to the display of maximal muscle force which we call strength. On the other hand, a strong relationship has been demonstrated both between absolute strength and the cross-sectional area of the muscle (14) and between strength gain and increase in muscle girth or cross-sectional area (3, 6).

A reasonable hypothesis for describing the time course of strength gain with respect to its two major determinants is that suggested by De Lorme and Watkins (3) who postulated that: "The initial increase in strength on progressive resistance exercise occurs at a rate far greater than can be accounted for by morphological changes within the muscle. These initial rapid increments in strength noted in normal and disuse-atrophied muscles are, no doubt, due to motor learning.... It is impossible to say how much of the strength increase is due to morphological changes within the muscle or to motor learning."

We now have available EMG instrumentation and methodology which make it possible to separate muscle activation level (motor learning) from hypertrophic effects (morphologic changes) as described by deVries (4) and Moritani

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and deVries (11). This paper is directed to the elucidation of the time course of strength gain with respect to the contribution of neural factors and hypertrophy. It is hypothesized that early changes are largely due to neural factors with a gradually increasing contribution of the hypertrophic factor as the training continues.

METHODS AND PROCEDURES

Theoretical basis

It has been known for some time that the ratio of muscle activation (as measured by IEMG) to the force produced reflects the level of hypertrophy in skeletal muscles (4). Furthermore the level of IEMG attained during maximal voluntary contraction (MVC) is a measure of the maximal activation of the muscle under voluntary contraction. The activation level is necessarily the result of the interaction of both facilitatory and inhibitory phenomena which may act at various levels of the nervous system. Since these factors are complex and not yet clearly defined, we refer to them collectively as "neural factors".

We have recently shown that, under certain experimental conditions, the IEMG-force relationship for the elbow flexors is linear throughout the entire range of forces up to and including maximal voluntary contraction (11). Thus we have at hand the method for separation of the proportional contributions of neural factors and hypertrophy throughout the time course of a muscle training regimen. Figure 1 illustrates the application of this method. If strength gain is brought about by "neural factors" such as "learning to disinhibit" as has been suggested by earlier studies (8, 9), then we should expect to see increases in maximal activation without any change in force per fiber or motor units (M.U.s) innervated as shown in figure 1A. On the other hand, if strength gain were entirely attributable to muscular hypertrophy, then we should expect the results shown in figure 1B. Here the force per fiber (or per unit activation) is increased by virtue of the hypertrophy but there is no change in maximal IEMG. Figure 1C shows our method for evaluation of the percentual contributions of the two components when both factors may be operative in the course of strength training.

Subjects and testing procedures

The subjects who volunteered for this investigation were seven young healthy males (18–26, mean 22.0 years) and eight females (17–20, mean 18.2 years).

Both right and left elbow flexor muscle groups were tested isometrically at a joint angle of 90 degrees with the hand in a position midway between pronation and supination. The subject was instructed regarding the nature of the method and instrumentation and was positioned on a table inside a Faraday cage according to the methods described in a previous communication (11).

After several trials at submaximal levels of contraction for familiarization, a 2-min rest period was provided and then maximal strength was measured by

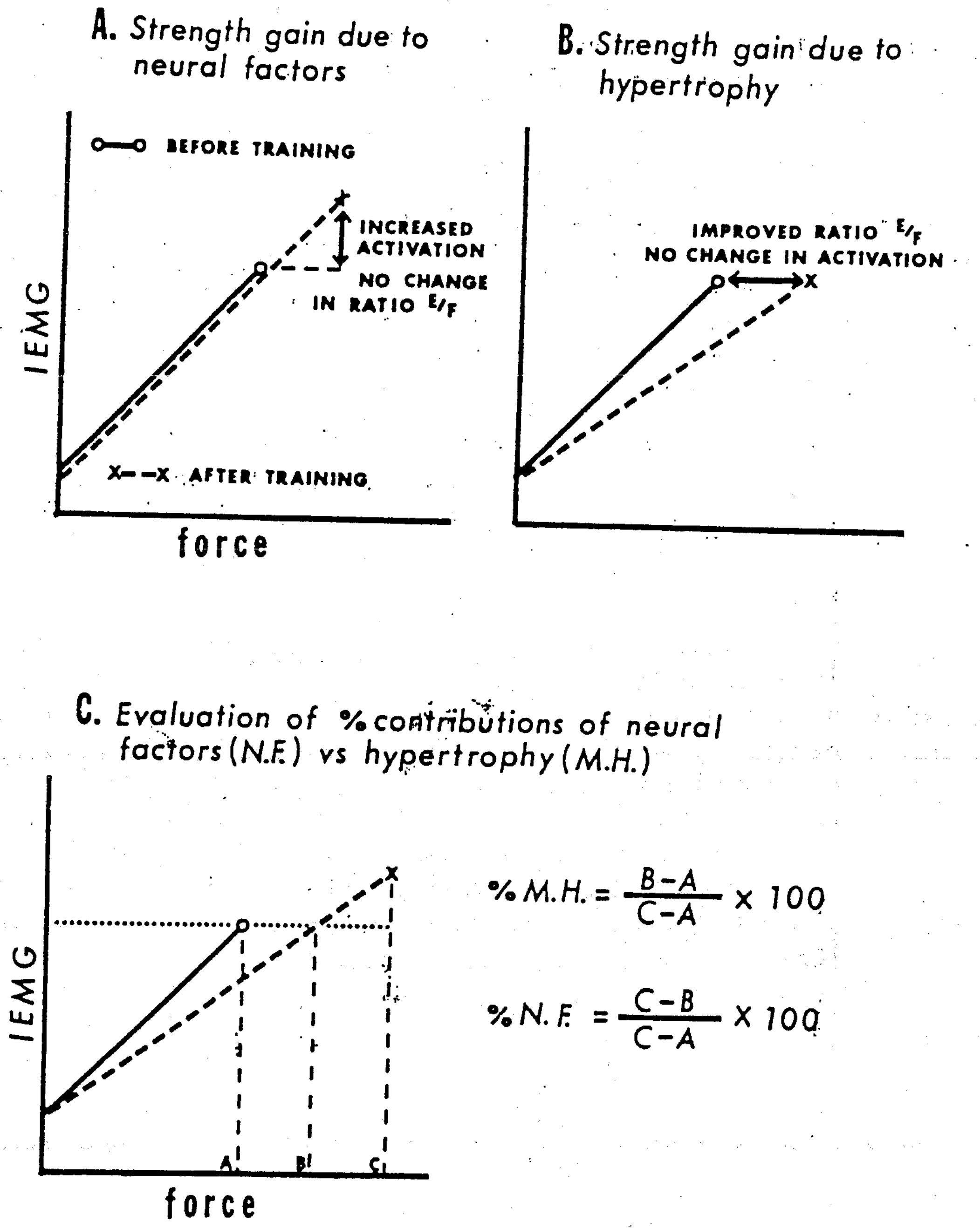


FIG. 1. Schema for evaluation of percentual contributions of neural factors and hypertrophy to the gain of strength through progressive resistance exercise, based upon EEA concept (4).

three trials of which the best of the three was recorded as maximal voluntary contraction (MVC). The subject was then asked to exert consecutive submaximal isometric tensions induced by contractions against given weights up to the 10 lb (5 lb for female) increment nearest his maximal strength. (e.g., 80 lb if his maximal strength was between 81 and 90 lb). This test provided a force-EMG relationship throughout the entire domain of force levels for both right and left elbow flexor muscle groups. In all cases, a period of 2 min of rest was allowed between contractions and 5 min between the tests for the elbow flexors.

EMG instrumentation

Our EMG instrumentation and procedures as well as the dynamometry used were identical to those described in a recent communication (11). Reproducibility of the method was evaluated by testing and retesting from 2 to 7 days apart six subjects at identical force values which ranged from minimum to near maximum. Figure 2 shows these reproducibility data. The test-retest correlation was $r = 0.988$, $p < 0.001$.

Estimation of changes in cross-sectional area of muscle

Since girth of a limb segment may be unduly affected by the thickness of skin and subcutaneous fat, the cross-sectional area of the elbow flexor groups

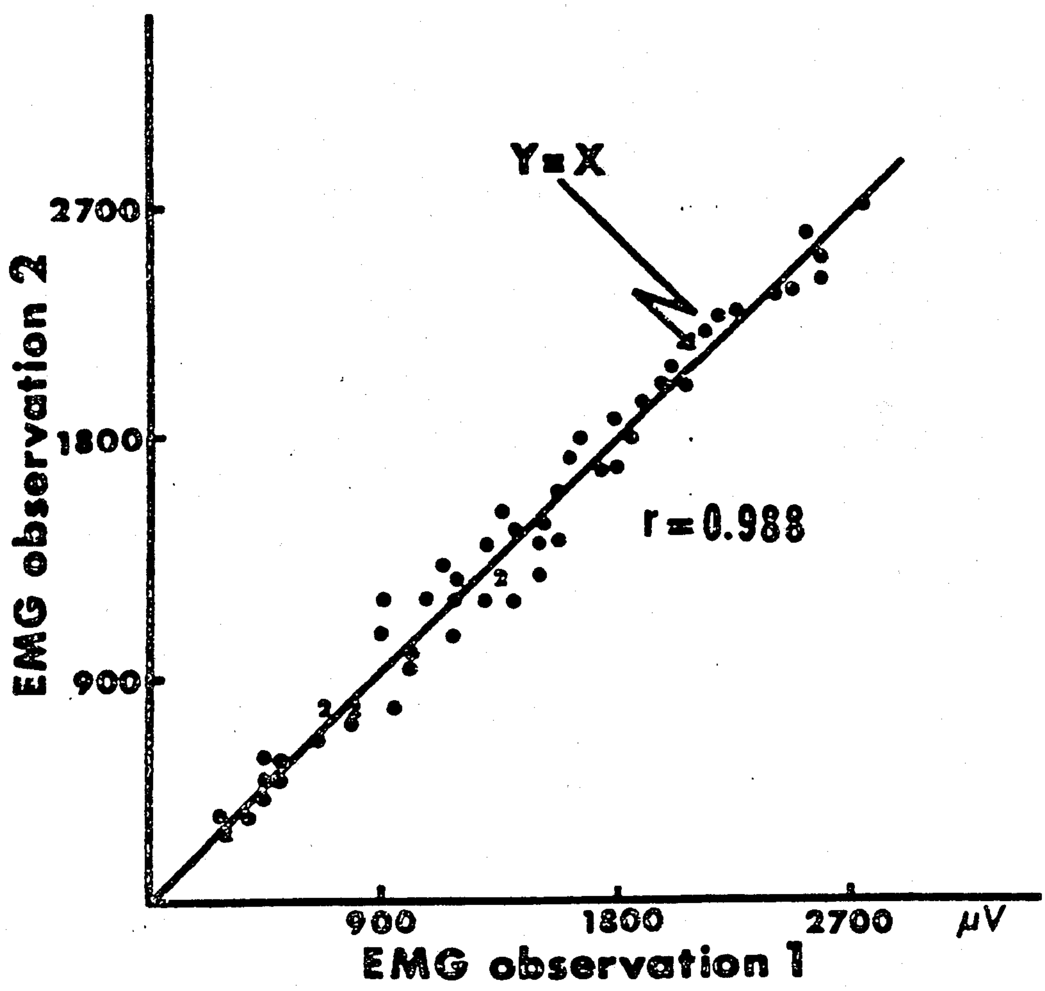
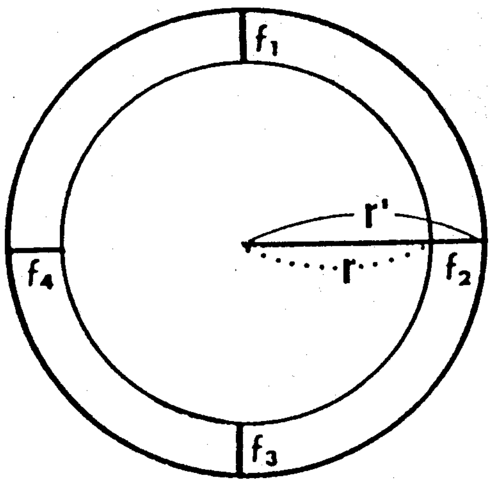


FIG. 2. Reproducibility of EMG values with placement-replacement of electrodes on different days (2–7 days apart). Each data point represents the two different EMG values found for the same force produced on the dynamometer.



f_1, f_2, f_3, f_4 represent skinfold measurements to allow correction for skin and subcutaneous fat dimensions.

$$C = 2\pi r' \quad \therefore \; r' = \frac{C}{2\pi} \quad \cdots\cdots (1)$$

$$r = r' - \frac{\sum_{i=1}^{4} f_i}{4} \quad \cdots\cdots (2)$$

Substituting

$$r = \frac{C}{2\pi} - \frac{\sum_{i=1}^{4} f_i}{4} \quad \cdots\cdots (3)$$

Since area of circle (A) is given by the following equation

$$A = \pi r^2, \text{ substituting } (3)$$

$$A = \pi \left[\frac{C}{2\pi} - \frac{\sum_{i=1}^{4} f_i}{4} \right]^2$$

FIG. 3. Method for estimation of changes in the cross sectional area of muscle.

was estimated after correction for these factors by four skinfold measurements as shown in figure 3. This method rests on three simplifying assumptions: 1) the arm segment is circular in cross-section, 2) bone dimensions are not appreciably changed by this short period of muscle training, and 3) unexercised muscles do not contribute to change in measured girth. While these assumptions could create large errors in the *absolute* magnitude of cross-sectional area measured, they are unlikely to do so for the *changes* brought about by training which are our concern here.

Muscle training regimen

The strength training program consisted of progressive resistance dumbell exercise consisting of 10 repetitions of ⅔ maximum for the elbow flexors twice a day three times per week for a period of 8 weeks. Subject's maximal strength was tested at two week intervals and the training work load was adjusted to maintain the ⅔ maximal load.

RESULTS

Time course of changes in the trained arm

Highly significant training effects were observed in the trained elbow flexor muscle groups in all parameters tested. It is clear that the significant strength increase (mean gain of 21.2 lb, $p < 0.001$) after the training was brought about by both "neural factors" and "hypertrophy" as demonstrated by the significant changes in the muscle activation level (mean increase of 223 μv, $p < 0.002$) and the EMG slope coefficient (mean decrease of −6.36, $p < 0.007$) respectively (table 1).

Our earlier work has shown that when maximal strength was increased significantly, the EMG slope coefficient (expressed in μv per pound of force) decreased (improved) significantly (4). The correlation analysis in the present study revealed that the increase in the cross-sectional area was highly correlated with the decrease in the EMG slope coefficient ($r = -0.789$, $p < 0.001$) (fig. 4). This finding provides further strong support for the concept of "Efficiency of Electrical Activity (EEA)" that the ratio of a given muscle activation level to the force produced (E/F ratio) reflects not only a genotypic factor,

TABLE 1
Changes in the trained muscle over the experimental period (N = 5)

Variable	Mean	SE	Difference	t	p
Cross section (post)	47.60 Cm^2	4.14	2.91	5.93	0.004
Cross section (pre)	44.69 Cm^2	3.76			
Max. strength (post)	79.40 lb	7.80	21.20	9.17	0.001
Max. strength (pre)	58.20 lb	7.01			
Activation level (post)	2111.40 μv	148.00	223.20	7.45	0.002
Activation level (pre)	1888.20 μv	146.92			
E.E.A. (post)	26.59 μv/lb	2.66	−6.36	−5.13	0.007
E.E.A. (pre)	32.95 μv/lb	3.76			

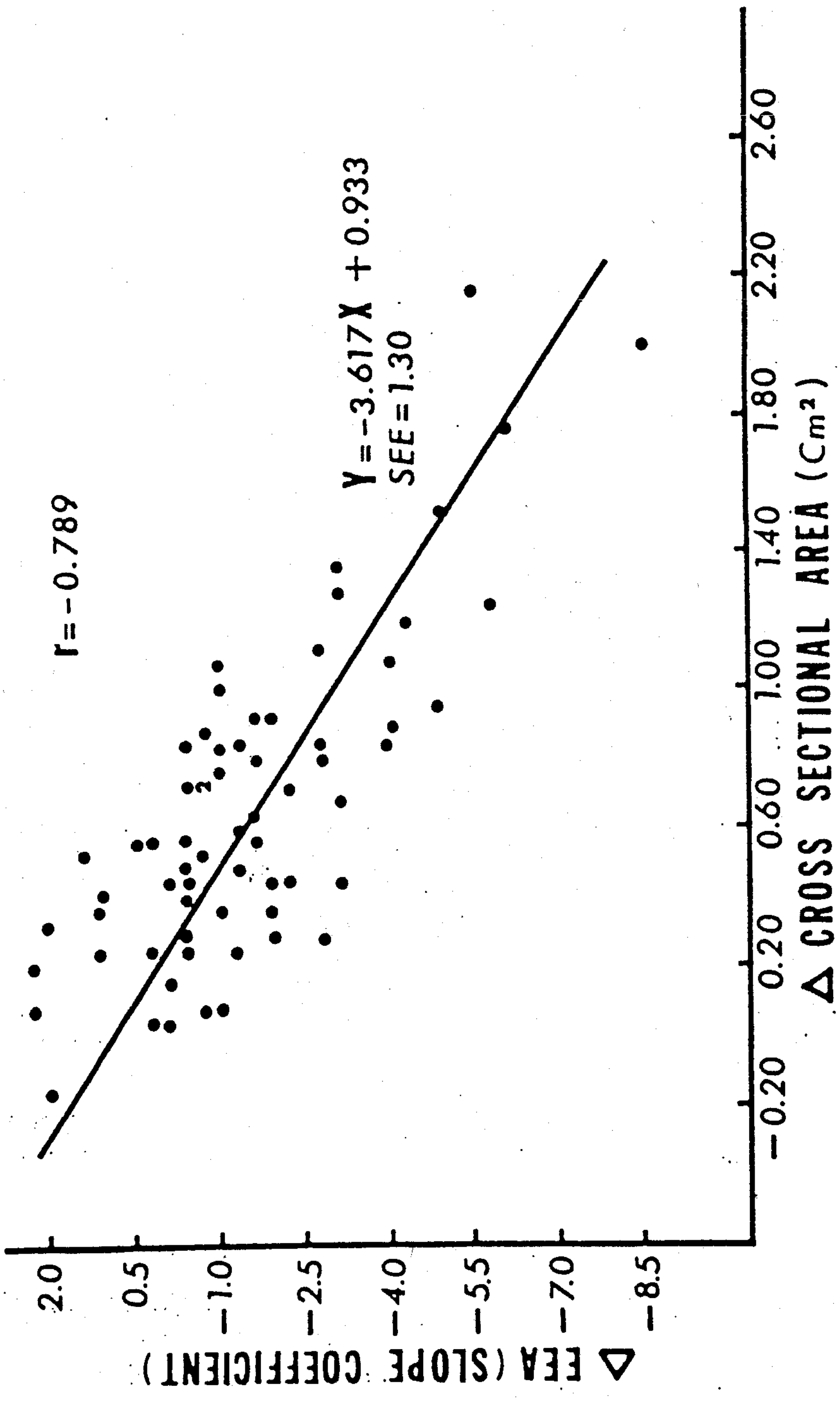
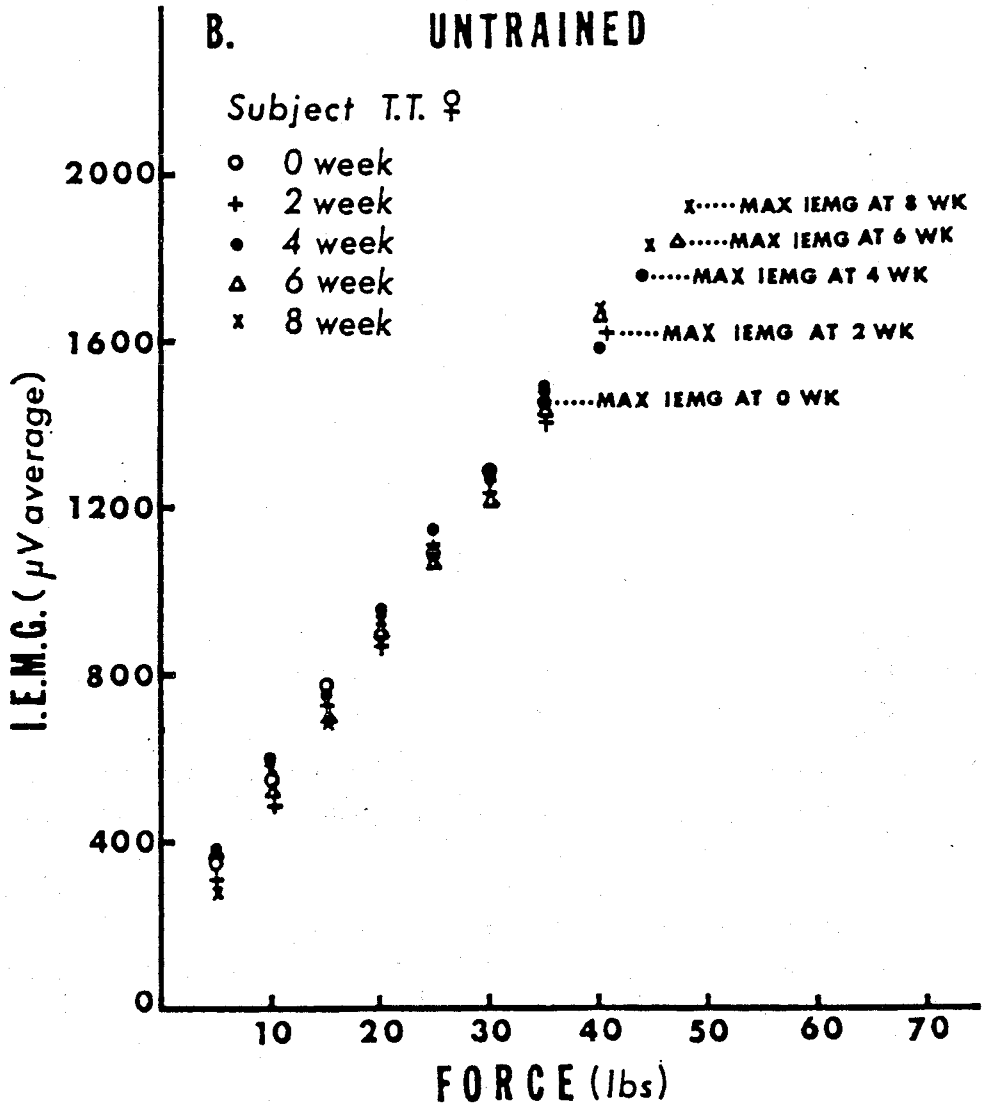


FIG. 4. Relationship between changes in EEA (Δ EEA) and changes in muscle cross sectional area (Δ cross sectional area) over two week periods.



changes in the E/F ratio (hypertrophy).

"neural factors" in which the maximal muscle activation level would be expected to increase without any changes in the E/F ratio (EEA). This was in fact the case in our study as confirmed by the finding of a significant increase in the muscle activation level (mean gain of 383 μv, $p < 0.001$).

Figure 5 presents the data plotted so as to show the typical changes in the trained arm as compared to the untrained arm with respect to the time course. Note that both arms gained in strength but only the trained arm showed significant hypertrophy changes as manifested in the E/F ratio.

Findings in later period of the training regimen

It is interesting to note that even in the trained arm the EMG slope coefficient after 2 weeks of training remained almost identical to that of the

TABLE 2

Changes in the untrained muscle over the experimental period ($N = 5$)

Variable	Mean	SE	Difference	t	p
Cross section (post)	45.25 Cm^2	4.22	0.09	0.47	0.662
Cross section (pre)	45.16 Cm^2	4.26			
Max. strength (post)	67.60 lb	4.94	13.40	8.37	0.001
Max. strength (pre)	54.20 lb	4.76			
Activation level (post)	2170.00 μv	102.76	383.40	8.01	0.001
Activation level (pre)	1786.60 μv	99.71			
E.E.A. (post)	33.35 μv/lb	3.51	−0.02	−0.03	0.980
E.E.A. (pre)	33.37 μv/lb	3.32			

pre-training value, although the regression line rose to higher maximal IEMG values. This of course represents an increase in the muscle activation which was responsible for almost the entire strength gain observed at this early stage of the training. However, as the training proceeded, the EMG slope started decreasing, indicating that some degree of muscular hypertrophy gradually became important in the picture of strength display. On the other hand, the rapid increase in the muscle activation level was no longer maintained, but now increased at a considerably diminished rate. These findings seem to support our hypothesis that early changes in strength may be largely due to neural factors followed by a gradually increasing contribution of the hypertrophic factor as the training continues.

As to the changes in the untrained arm flexors, no apparent changes in the EMG slope were observed throughout the entire time course, although there was a significant strength gain. This result provides further support for the concept of a cross education effect on the contralateral untrained limb (2, 5, 7) and sheds some light on the physiology involved. Our data suggest that this cross education effect on strength may solely rest on the neural factors (increased facilitation or disinhibition) acting at various levels of the nervous system which could result in the higher muscle activation level.

Neural factors and hypertrophy

Figures 6 and 7 illustrate the time course of strength gain with respect to the calculated percentual contributions of neural factors and hypertrophy by using the method described earlier in this paper. The results clearly demonstrate that the neural factors played a major role in strength development at early stages of strength gain and then the hypertrophic factor gradually dominated over the neural factors in the contribution to the strength gain. The results presented in figures 6 and 7 seem to suggest that both male and female showed a similar response pattern in the percentual contribution of neural factors and hypertrophy. However, the absolute increase in the cross-sectional area for the females was found to be about 53% that of the male subjects after the completion of the training (the mean increase for females was 2.24 ± 0.19 and for males was 4.23 ± 0.45, respectively).

Dominant vs. nondominant arm

Figure 8 shows the percentual contributions of both factors to the strength gain among the subjects (N = 3, males) who trained both dominant and nondominant arm flexors. Although our data suggest that the hypertrophic factor seemed to follow with a considerable time delay in the nondominant arm, the result should be interpreted with caution due to the small number of subjects and considerable individual variation.

DISCUSSION

In the light of the data presented in this paper it would seem reasonable to suggest that early changes in strength may largely be accounted for by the neural factors with a gradually increasing contribution of the hypertrophic factor as the training proceeds. The early work of Ikai and Fukunaga (7), using ultrasonic measurement, reported a 92% increase in strength with only a 23% increase in cross-sectional area of arm flexors after 100 days of ten second isometric contractions. They also found that the significant gain in strength observed at the early stage of the training was not accompanied by any significant increase in the cross-sectional area. Our data corroborate their findings and further suggest that the initial increase in strength occurring at a rate far greater than can be accounted for by hypertrophy may be explained by this major role of the neural factors in the early course of strength development. This may also explain common findings that repeated strength testing results in increasing test scores without evidence of measurable muscular hypertrophy (1, 2, 4, 5).

Interestingly, there has been some evidence suggesting that strength development can be achieved by involuntary contractions initiated by electrical stimulation (10, 12). However, both experiments resulted in a considerably smaller strength gain than the values found in normal voluntary training. Since the motor pathways are probably minimally involved in electrical training, it seems likely that a training stimulus resides in the muscle tissue itself and hence the hypertrophic factor is the principal constituent for strength development. The fact that the training effect was considerably less than that of voluntary contraction seems to suggest that some degree of the training effect may reside in the facilitatory and inhibitory synaptic pathways acting at various levels of the nervous system. Our data suggest that this improvement of the neural factors can be achieved by ipsilateral progressive resistance exercise and may be even cross-transferred to the untrained contralateral arm flexors. It is reasonable to believe that the increase in the maximal muscle activation level brought about by changes in the neural factors may be the mechanism whereby the muscle is able to increase strength without hypertrophy as typically seen in the contralateral untrained limb (2, 5, 7), or by the use of unusual sensory stimuli, such as a sound of gun shot, shout, hypnosis (1, 8).

The hypertrophic factor, on the other hand, undoubtedly played a dominant role in the course of strength development, especially after the onset of the

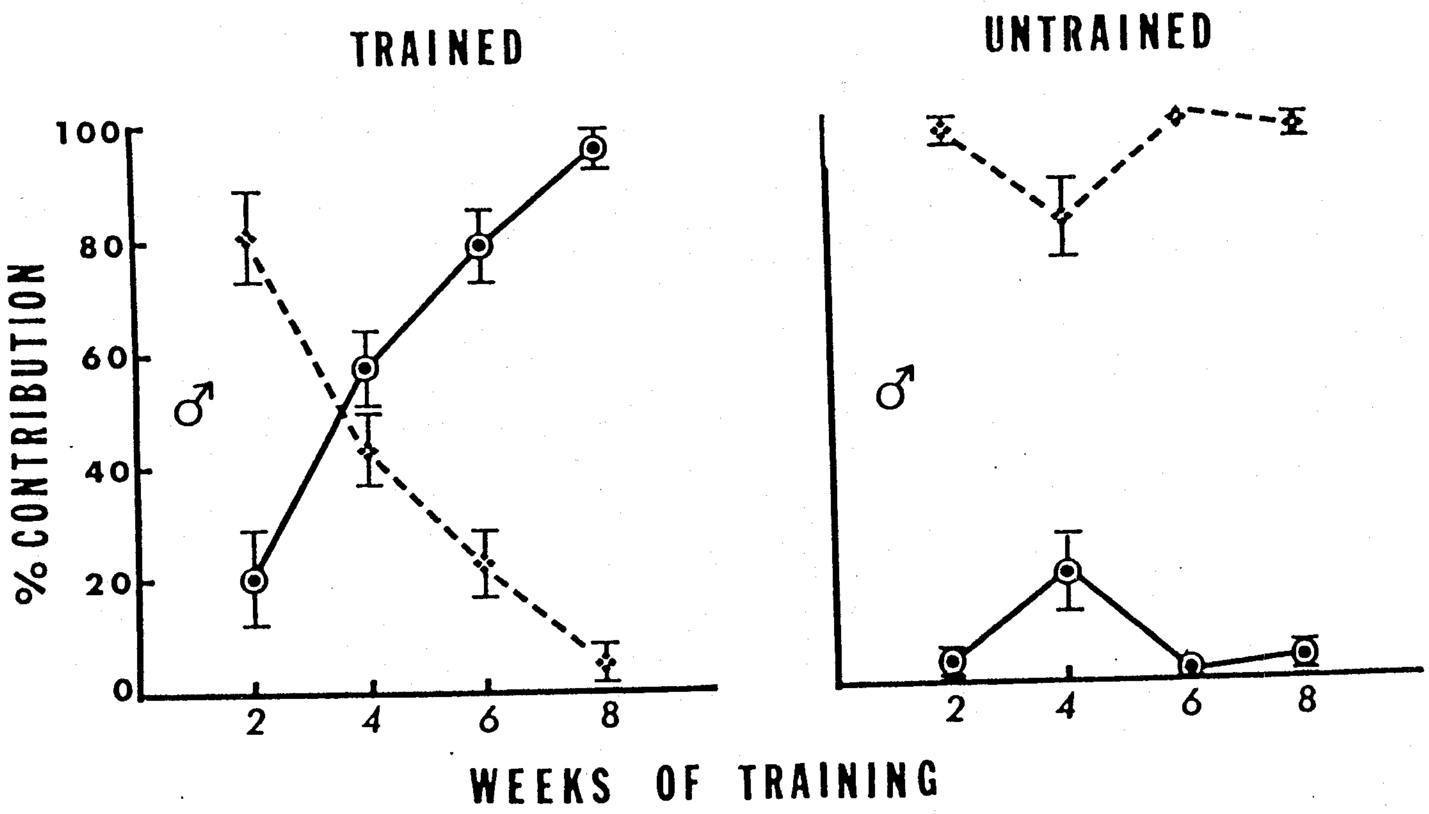


FIG. 6. The time course of strength gain showing the percentual contributions of neural factors (squares and broken lines) and hypertrophy (circled dots and solid lines) in the trained and untrained arms of two male subjects.

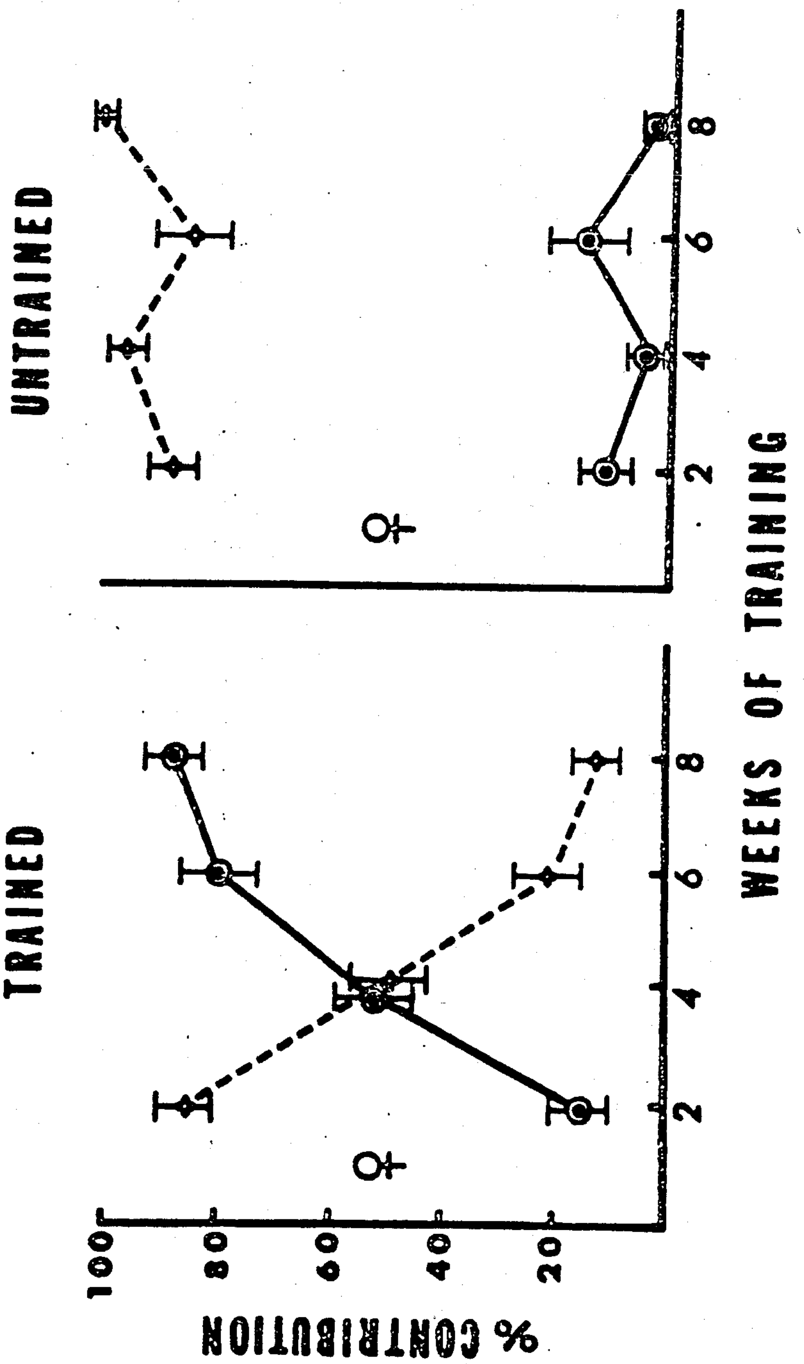


FIG. 7. The time course of strength gain showing the percentual contributions of neural factors (squares and broken lines) and hypertrophy (circled dots and solid lines) in the trained and untrained arms of three female subjects.

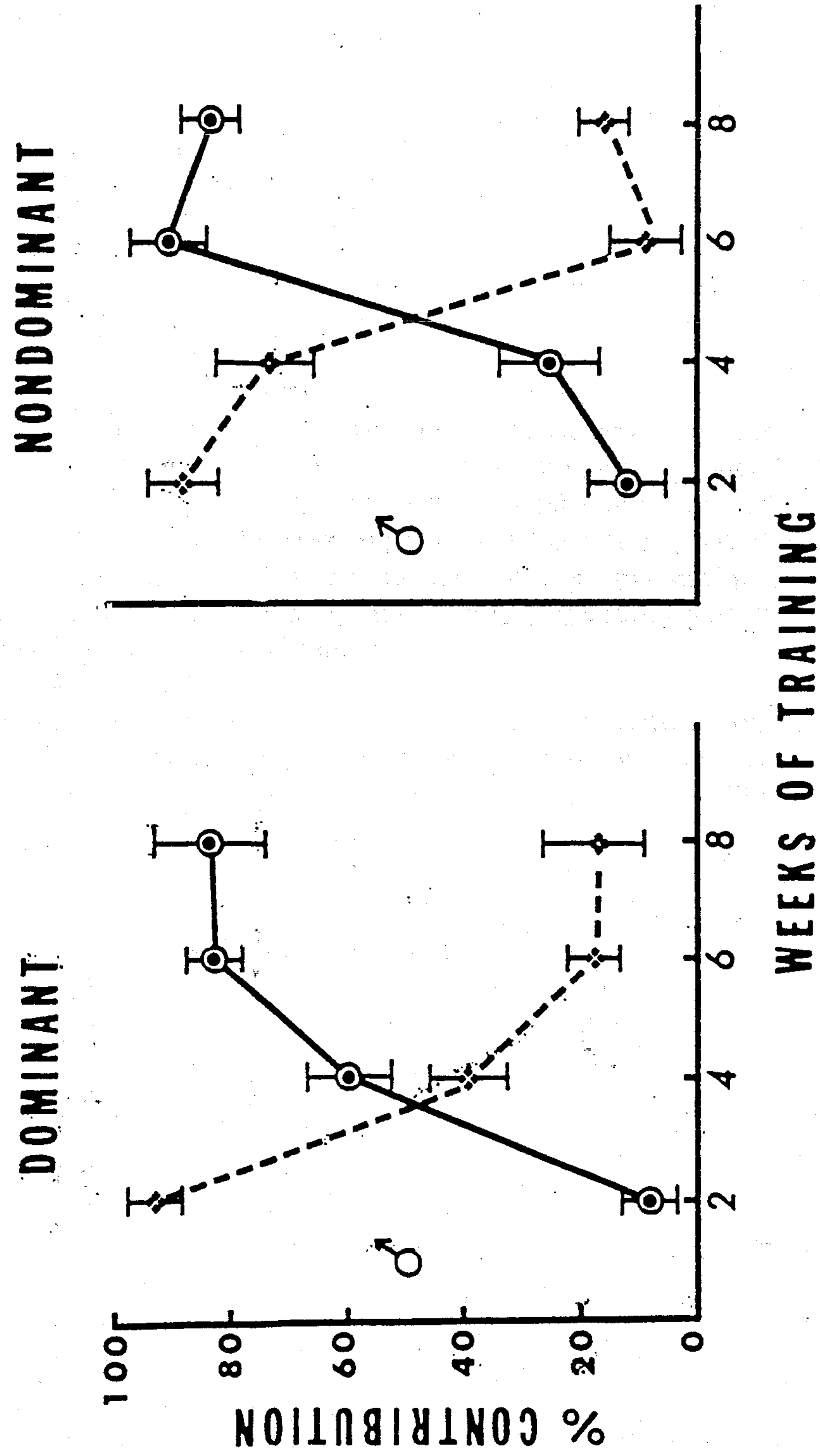


FIG. 8. The effects of hand dominance upon the time course of strength gain (Neural factors, squares and broken lines; hypertrophy, circled dots and solid lines).

neural factors which largely contributed to the strength gain only at the initial stage of the training. We have observed that the hypertrophic factor displayed a significantly greater contribution than the neural factors after some 4 to 6 weeks of training.

On the basis of the work reported here, together with that of earlier workers, it appears that two factors primarily contribute to the development of muscle strength by voluntary effort; one is the increase in the maximal muscle activation level brought about by changes in the neural factors, the other is a morphological change in the contractile tissue itself (hypertrophic factor) brought about by tension induced through training. The former may be considered as responsible for the finding of strength gain in the absence of measurable hypertrophy.

SUMMARY

The time course of strength gain with respect to the contributions of neural factors and hypertrophy was studied in seven young males and eight females during the course of an 8 week regimen of isotonic strength training. The results indicated that neural factors accounted for the larger proportion of the initial strength increment and thereafter both neural factors and hypertrophy took part in the further increase in strength, with hypertrophy becoming the dominant factor after the first 3 to 5 weeks.

Our data regarding the untrained contralateral arm flexors provide further support for the concept of cross education. It was suggested that the nature of this cross education effect may entirely rest on the neural factors presumably acting at various levels of the nervous system which could result in increasing the maximal level of muscle activation.

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