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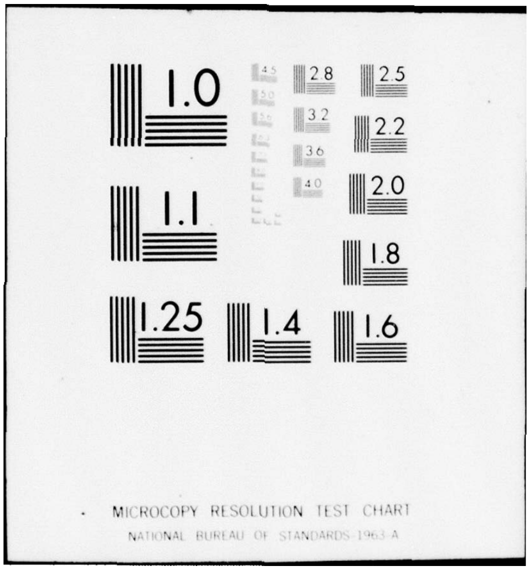

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Results have been obtained on the development of isometric fatigue in muscle after fatiguing and non-fatiguing bouts of isometric exercise in male human subjects. Change in maximum voluntary contraction (MVC) under these conditions showed that during isometric contraction at 5-10 percent of MVC and at 25 to 70 percent MVC, there was a linear fall in strength throughout the isometric effort. This was particularly surprising at 5-10 percent MVC since these levels are considered to be non-fatiguing. Endurance was reduced at 25 and 40 percent MVC →
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by performing exercises previously at any tension. When two contractions at 40 percent MVC were performed with an interval of 10 mins between them, the duration of the second contraction was always about 80 percent of that of the first. However, if a contraction of 10 percent MVC was maintained during the 10 min interval between the two fatiguing contractions at 40 percent MVC, the duration of the second contraction was reduced to 28 percent of the first. The findings suggest that the tension of the test contraction is important in permitting an accurate prediction of endurance from residual strength following sustained sub-maximal contraction.

INTRODUCTION

The endurance time for fatiguing submaximal isometric contractions has been well described in the literature (Lind 1959, Rohmert 1968, Funderburk et al 1974) as well as the associated blood pressure and heart rate (Lind et al 1964, Petrofsky and Lind 1975, Funderburk et al 1974), and electromyographic responses (Lloyd et al 1970, Eason 1960, Lind and Petrofsky 1976) during single and serial isometric contractions where the recovery interval was allowed to vary between 3 and 60 minutes.

The common denominator in all these experiments is that the subjects were required to maintain a given fraction of their isometric strength until their muscles fatigued. However, much of the isometric work that results in flying aircraft differs in that the isometric load is constantly varying. Therefore, the present investigation was conducted to obtain information on the capacity of muscles to perform when the muscle strength is changed and how this is related to endurance as well as the cardiovascular and electromyographic responses of muscle to isometric contractions where the tension exerted is varied.

The working hypothesis underlying our experimental procedures was that the endurance of sustained sub-maximal isometric contractions are directly related to the strength left to the muscles after preceding muscular activity.

METHODS

Subjects

Four male volunteers served as subjects in these experiments. All subjects were informed fully of all experimental procedures and the risks involved in these experiments and signed a statement of informed consent. They were physically examined, including a cardiovascular (ECG) stress test before taking part in the experiments.

Isometric Strength and Endurance

Isometric strength and endurance of the hand-grip were measured on a portable dynamometer similar to one described previously by Clark, Hellon and Lind (1958). To determine isometric strength the subject was first asked to exert two brief (3 sec) maximal efforts on each day; the highest tension was taken as the maximum voluntary contraction (MVC) of the subject. Endurance in any given experiment was determined either as the length of time of a sustained sub-maximum tension or as the time necessary for the subject's strength to be reduced from his MVC to 70% MVC while he continued to produce a sustained maximal effort. All contractions were done with the subject sitting with his elbow at an angle of 90°; only one experiment was done in a given 24 hour period.

EMG

The electromyographic activity of the active muscles of the forearm was recorded from 2 Ag-AgCl disc electrodes placed on the inner surface of the forearm approximately 8 cm apart. The EMG was amplified by a bio-isolation amplifier with an input impedance of 10^{10} ohms and a frequency response which is flat from DC to 2,000 Hertz. The amplified EMG was recorded on a Sangamo-Tanberg series 100 FM recorder and analyzed later on a LINC computer. Two types of analyses were performed. First, the EMG amplitude was analyzed over 1.5 sec intervals by digitalizing the raw EMG and then calculating the average positive amplitude over that interval. Second, the frequency of the surface EMG was analyzed over the same time intervals from a fundamental frequency of 4 Hz to a final frequency of 508 Hz; the average frequency was calculated from the resultant power spectrum. A complete description of this procedure is given elsewhere (Lind and Petrofsky 1976). The EMG was analyzed at the onset, middle, and end of the fatiguing contractions for each tension held.

Heart Rate

The heart rate was calculated over 15 sec intervals from a continuous recording of the ECG. Heart rates were counted at the onset and 20, 40, 60, 80 and 100% of the duration of each contraction.

Blood Pressure

The blood pressure was recorded by auscultation of the inactive arm as often as possible during the grip. These raw blood pressures were interpolated or extrapolated to obtain blood pressures at the onset and at 20, 40, 60, 80 and 100% of the duration of these contractions.

Statistical Analysis of Data

Means, standard deviations, correlations and t tests were calculated on a LINC computer. The level of significance was chosen at a value of 0.05 or less.

Training

All subjects were thoroughly trained to perform isometric contractions to fatigue as described previously (Petrofsky and Lind, 1975).

Four series of experiments were performed as described below: all experiments were performed on all subjects and in replicate.

Series One

The first series of experiments was intended to investigate the effect of non-fatiguing and fatiguing isometric contractions on maximum isometric strength. In four experiments, fatiguing isometric contractions were performed at 25, 40, 55 or 70% of each subject's strength. During these contractions, isometric strength was assessed from a brief maximal contraction interposed at about 25, 50, and 75% of the durations of the contractions. In two experiments, subjects held tensions of either 5 or 10% MVC for ten minutes. Interposed during this period at 1 min and 9 min, and at the end of the 10 min period, the subjects produced their brief maximal efforts.

Series Two

From the results of series one it was possible to predict the endurance of a contraction at, for example, 40% MVC immediately following a sustained contraction to fatigue, based on our working hypothesis that strength and endurance are directly related.

To test the hypothesis, the procedure in series two was as follows. 1) Following contractions held to fatigue at 40, 55, or 70% MVC the tension was dropped to 25% MVC and the endurance of that tension was measured and compared to the predicted values.

Similarly, after fatiguing contractions at 55 or 70% MVC the endurance of a contraction at 40% MVC was measured and compared to the predicted values.

2) In a similar fashion, the subjects exerted a hand grip contraction at 70% MVC to fatigue, following which the tension was dropped to 40% MVC; after fatigue at 40% MVC the tension was dropped again to 25% MVC and the contraction sustained to fatigue.

3) The subjects sustained a contraction for half the endurance time at 70% MVC and then, in separate experiments, allowed the tension to fall either to 25% MVC or 40% MVC, and the contractions were sustained to fatigue.

4) Finally, after sustaining a contraction at either 25% or 40% MVC for half of the control endurance time, the tension was elevated to 70% MVC and the contraction held to fatigue.

Series Three

Endurance after sustained maximal effort; in this series of experiments isometric endurance at either 25 or 40% MVC was measured immediately after a sustained maximal effort had resulted in a fall of tension from 100 to 70% MVC. In a second experiment, a sustained maximal effort was held until the tension fell to 70% MVC; the tension was dropped to 40% MVC and the contraction pursued to fatigue, at which time the tension was dropped again to 25% MVC and the contraction sustained to fatigue.

Series Four

In this final series of experiments, subjects performed a fatiguing isometric contraction at either 25, 40, or 70% MVC followed by a 10 min contraction at 10% MVC. A contraction at 40% MVC was then exerted to fatigue.

RESULTS

Series One

As in previous experiments, we found that the strength of the handgrip muscles fell linearly with time throughout sustained sub-maximum contractions at 25, 40, 55 and 70% MVC as shown in Fig 1. In addition, when the subjects held tensions of 5 or 10% MVC for 10 min, there was also a linear fall in the strength of the muscles, by 4% and 18% respectively; this finding was mainly the result of two of the subjects who showed a marked reduction in strength while the other two did not.

The data presented in Fig 1 provided the rationale for the later experiments. The working hypothesis was that the strength of the muscles is directly related to the endurance. Thereby, if a tension is held at 70% MVC to fatigue, the residual strength is 70% MVC which is also found exactly half-way through a sustained contraction at 40% MVC; as a result, after fatigue has been developed at 70% MVC, if the tension is then dropped to 40% MVC the remaining endurance should be half of the control value for endurance at that tension.

Series Two and Three

Strength and Endurance

The average endurance of a 40% MVC was 98 seconds (range 71 to 178 sec). At the end of a fatiguing contraction of 55% MVC the tension was dropped to 40% MVC and maintained to fatigue. The mean endurance of the 40% MVC was now 30 sec as seen in Fig 2; from Fig 1, the predicted endurance, or the basis of the loss of strength, was 25 sec. Following fatigue at 70% MVC the comparable value for endurance of the 40% MVC was 50 sec and the predicted endurance was 49 sec. Thereby, following sustained sub-maximal contractions, the endurance of a 40% MVC was well predicted on the basis of the residual strength of the muscles. But that was not the case when a sustained maximal effort resulted in a loss of strength to 70% MVC. The predicted endurance of a 40% MVC in this case was also 49 sec; the actual endurance averaged 81 sec.

When the test contraction was performed at 25% MVC following fatigue induced by a contraction at 40% MVC the actual endurance was 86 sec while the predicted value was only 59 sec. Following fatigue at 55% MVC the corresponding values were 125 and 100 sec respectively. Following fatigue at 70% MVC the actual and predicted values were the same, at 150 sec. Following a sustained maximal effort, the predicted value was also 150 sec, but the actual value was 180 sec.

After 10 min contractions at 5 and 10% MVC the endurance of the 40% MVC fell from the control value of 98 sec to 79 and 61 sec respectively. The corresponding values for the 25% MVC were 249 and 221 sec from the control endurance of 257 sec.

Heart Rates

In these experiments, the heart rate increased approximately linearly during the first contraction. At the end of those fatiguing sub-maximum contractions there was a pattern of increasing heart rate as the tension increased as shown in Fig 3. When the tension was dropped to 25% MVC and sustained to fatigue the heart rate declined steadily to a level that was constant at an average of 105 beats/min; the fall was statistically significant. At the end of a sustained maximal effort, the heart rate when the tension had fallen to 70% MVC was 115 beats/min (significantly lower than the value of 130 beats/min at the end of a contraction sustained to fatigue at 70% MVC) and by the end of the subsequent contraction at

25% MVC, it had fallen to 105 beats/min, a reduction that was not significantly different.

When the test contraction was 40% MVC, a similar pattern was seen but with an average heart rate of 115 beats/min at the end of the test contraction, the "reduction" of heart rate from the end of the preceding contraction was not significantly different.

Blood Pressures

The mean blood pressures at the point of fatigue at 25% and 40% MVC, as well as the preceding fatiguing contractions, were all similar, as shown in Fig 4. Within the first 15 sec of reducing the tension of the first contraction to that of the test tension there was a rapid fall of mean blood pressure by some 25 mm Hg and 10 mm Hg when the test tensions were 25% and 40% MVC respectively. The mean blood pressure thereafter increased in an approximately linear fashion during each of the test contractions.

EMG

The amplitudes of the EMG at the start of and the end of the test contractions at 25% and 40% MVC are shown in Fig 5. Included in the Fig are the values following not only the preceding contractions held to fatigue at higher tensions but also when the preceding contraction was a tension of 5 or 10% MVC for 10 min. A clear pattern emerged for both test tensions. The amplitude of the EMG at the start of the test contraction was inversely related to the tension of the preceding contraction at all tensions from 10% MVC and above. The amplitude increased during the test contraction by the same amount so that the inverse relationship with tension was again seen at the end of the test contraction. It is clear from Fig 5 that the amplitude at the start of the test contraction was higher than the control value when the preceding tension was low and was lower than the control value when the preceding tension was high. When the preceding tension was 5% MVC held for 10 min, the amplitude at the start of and at the end of the test contraction was not different from the control value.

The center frequency of the EMG (Fig 6) showed a different pattern from that described for the amplitude. The CF at the end of the test contraction was constant, at an average value of 116 Hz. At the start of the test contraction there was a constant tendency, which was not significantly different, for the CF to be higher (the average value was 120 Hz) when the preceding contraction had been exerted at a higher tension. The control value, with fresh muscles, showed the CF to start at 152 Hz and to fall to 115 Hz. Preceding contractions for 10 min at 5 and 10% MVC reduced the starting values by 3-10 Hz, values which were not significantly different from the control.

Table 1 shows the actual endurance at specified tensions after various maneuvers when the tension was either dropped or raised from preceding contractions, compared with the endurance predicted from Fig 1. Experiment 1. Following fatigue at 70% MVC, the tension was first dropped to 40% MVC, the duration of which compared favorably with the predicted value. The tension was then dropped to 25% but the actual endurance was now lower than the predicted value, a result that is reversed from the findings that actual endurance at 25% was longer than the predicted value when preceded by only a contraction to fatigue at 40% MVC (see Fig 2).

Experiment 2. A sustained maximal effort was held until the tension fell to 70% MVC. The tension was dropped to 40% MVC and held to fatigue; the actual endurance was much longer than the predicted value. The tension was then reduced to 25% MVC: the actual endurance was slightly greater than the predicted endurance.

In both experiments (1 and 2) the endurance of the 25% MVC following the sequence of fatiguing contractions of 70% and 40% MVC was significantly shorter than the endurance when the 25% MVC was preceded by a fatiguing contraction of either 70% or 40% MVC alone.

Experiment 3. After sustaining an isometric contraction for half the control endurance value at 70% MVC, a contraction was held to fatigue at either 40% or 25% MVC. The actual endurance time in either case was identical to the predicted endurance.

Experiment 4. After sustaining an isometric contraction for half the control endurance value for either 25% MVC or 40% MVC, the tension was increased to 70% MVC and sustained to fatigue. In both cases, the subjects were able to generate a tension and hold it for 6 to 7 sec, whereas the prediction was that there should be no endurance at that tension.

Series Four

When two successive contractions were held to fatigue at 40% MVC with an intervening 10 min interval, the duration of the second contraction was about 80% of that of the first. However, if a contraction of 10% MVC was maintained during the interval between the 2 contractions the duration of the second contraction was reduced to only 30% of the first.

DISCUSSION

Our results indicate that our working hypothesis that the strength of a group of muscles at any given moment can be used to predict the endurance of a sustained sub-maximum isometric tension appears to apply to some but not all the experimental circumstances examined.

When the test contraction was 40% MVC, the endurance of the muscles could be accurately predicted from the loss of strength by preceding fatiguing contractions up to 70% MVC, when the fatigue was induced by sub-maximum tensions. But when the strength of the muscles was reduced to 70% MVC by a preceding sustained maximal effort the endurance of the contraction at 40% MVC was much longer (35-40%) than the value predicted on the basis of residual strength.

When the test contraction was 25% MVC, the only circumstance in which the actual and predicted endurance times were close was when the preceding contraction was a sustained sub-maximal tension of 70% MVC. The predicted values were lower by about 30% and 15%, respectively, than the actual values when the preceding sustained sub-maximal tensions were 40% and 55% MVC. When the preceding contraction was a sustained maximal effort until the tension had fallen to 70% MVC, the predicted value was 15-20% lower than the actual value.

These findings suggest that the tension of the test contraction is important in permitting an accurate prediction of endurance from residual strength following sustained sub-maximal contraction. When the test contraction was 40% MVC, the predictions were reasonably good, whereas they were not when the test contraction was 25% MVC (except when the preceding contraction was at 70% MVC). At both test tensions the prediction of endurance was poor after a sustained maximal effort when the strength had been reduced to 70% MVC.

In considering the possible reasons for these changes in endurance, it is worth considering the causes of fatigue we have reported for sustained sub-maximum tensions (Lind and Petrofsky, 1976). That evidence showed that at 70% MVC, fatigue was solely in the contractile mechanisms whereas at 25% MVC, a substantial proportion of the fatigue was attributable to failure of neuromuscular transmission. Furthermore, both the CF and the amplitude of the EMG recovered rapidly following fatigue, at all tensions. In the present experiments our evidence shows that only following a sustained contraction at 70% MVC was the endurance of a 25% MVC predictable from the loss of strength. That would be in keeping with the fact that fatigue at 70% MVC was solely due to contractile events which are unlikely to recover rapidly. Moreover, the progressive, inverse disparity between actual and the predicted endurance, when previous evidence shows an inversely increasing failure in neuromuscular transmission would also be in keeping with the view that residual strength is a valid predictor of endurance capacity only if the fatigue from the earlier contractions is in the contractile elements. Finally, the major underestimate of endurance occurred following a sustained sub-maximal effort when the tension fell rapidly to 70% MVC. In these circumstances, the evidence from our experiments and that of others (Stephens and Taylor, 1972), suggests that the fatigue is wholly attributable to failure of neuromuscular transmission.

The results obtained with a test contraction fit the views given above. At tensions of 55 and 70% MVC there is little or no failure of neuromuscular transmission so that the prediction of endurance on the basis of residual tension would be expected to be good. By contrast, following the sustained maximal effort, when neuromuscular transmission provides the main (or whole) cause of fatigue, the prediction should be poor. The results shown in Fig 2 confirm that view.

These arguments make it clear that when the loss of strength is caused by failure of the contractile mechanisms, predictions of endurance capacity is good. But when the fatigue is due to failure of neuromuscular transmission, the endurance is longer than predictions based on residual strength. These findings presumably reflect the fact that failure of neuromuscular transmission is a less serious and more quickly reversible form of fatigue (given the right circumstances) than is failure of contractile mechanisms.

A surprising finding was that sustained contractions at low tensions that have been considered indefatiguable (Rohmert, 1968), resulted in a loss of strength for some subjects and in a reduction in the endurance of subsequent test contractions. These findings may well be related to different proportions of types of muscle fibers in our subjects. The results also imply that at low tensions there is little or no rotary function of different motor units but argue instead for specific and continued activation of the same population of motor units to generate any given tension.

In practice, it seems that muscular strength, at any given level, can be used to predict the endurance of sustained contractions at moderate levels. As the tension of the final contraction is lowered, the actual endurance is mostly higher than the value predicted by residual strength. Similarly, when the first exertion is maximal, the subsequent endurance is greater than that predicted by residual strength. Further experimental evidence will be required to clarify the interaction of muscle strength and isometric endurance when the muscles are presented with complex functions.

TABLE 1

Experiment	End_1 (sec)	End_2 (sec)	Pred. End_2 (sec)	End_3 (sec)	Pred. End_3
70-40-25	35.8 ± 11.5	45.1 ± 12.4	49.5 ± 6.3	68.3 ± 16.3	59.1 ± 7.1
MVC→70-40-25	28.3 ± 9.1	85.3 ± 13.1	49.5 ± 6.3	66.4 ± 14.7	59.1 ± 7.1
½ 70-40	18.1 ± 11.3	69.6 ± 16.3	73.5 ± 14.6	———	———
½ 70-25	18.7 ± 12.2	210.6 ± 28.3	207.0 ± 26.4	———	———
½ 40-70	47.5 ± 9.6	7.3 ± 6.1	0	———	———
½ 25-70	125.0 ± 24.3	6.2 ± 8.5	0	———	———

FIGURE LEGENDS

Figure 1: This figure shows the maximum strength determined when the subject was at rest (0) and after 25, 50, 75, and 100% of the duration of fatiguing isometric contractions of the handgrip muscles whose tension was set at either 25 (●), 40 (o), 55 (■), or 70 (□) % MVC. Each point illustrates the mean of two measurements on each of the 4 subjects ± the respective standard deviations.

Figure 2: This figure shows the endurance of a fatiguing isometric contraction whose tension was set at either 25 (●) or 40 (o) % MVC. Immediately before each contraction, a fatiguing contraction was exerted at tensions between 40 and 100% MVC. Each point illustrates the mean of 2 measurements on each of the 4 subjects ± the respective standard deviations.

Figure 3: Illustrated here is the average heart rate of each of the 4 subjects measured in 2 experiments ± the respective standard deviations recorded at the onset (open symbols) and end (closed symbols) of control contractions (0 previous tension) at 25 and 40% MVC and contractions at these tensions preceded by other fatiguing contractions whose tensions varied between 10 and 100% MVC.

Figure 4: Illustrated here is the average blood pressure of each of the 4 subjects measured in 2 experiments ± the respective standard deviations recorded at the onset (open symbols) and end (closed symbols) of control contractions (0 previous tension) at 25 and 40% MVC and contractions at these tensions preceded by other fatiguing contractions whose tensions varied between 10 and 100% MVC.

Figure 5: Illustrated here is the average EMG amplitude of each of the 4 subjects measured in 2 experiments ± the respective standard deviations recorded at the onset (open symbols) and end (closed symbols) of control contractions (0 previous tension) at 25 and 40% MVC and contractions at these tensions preceded by other fatiguing contractions whose tensions varied between 10 and 100% MVC.

Figure 6: Illustrated here is the average EMG frequency of each of the 4 subjects measured in 2 experiments ± the respective standard deviations recorded at the onset (open symbols) and end (closed symbols) of control contractions (0 previous tension) at 25 and 40% MVC and contractions at these tensions preceded by other fatiguing contractions whose tensions varied between 10 and 100% MVC.

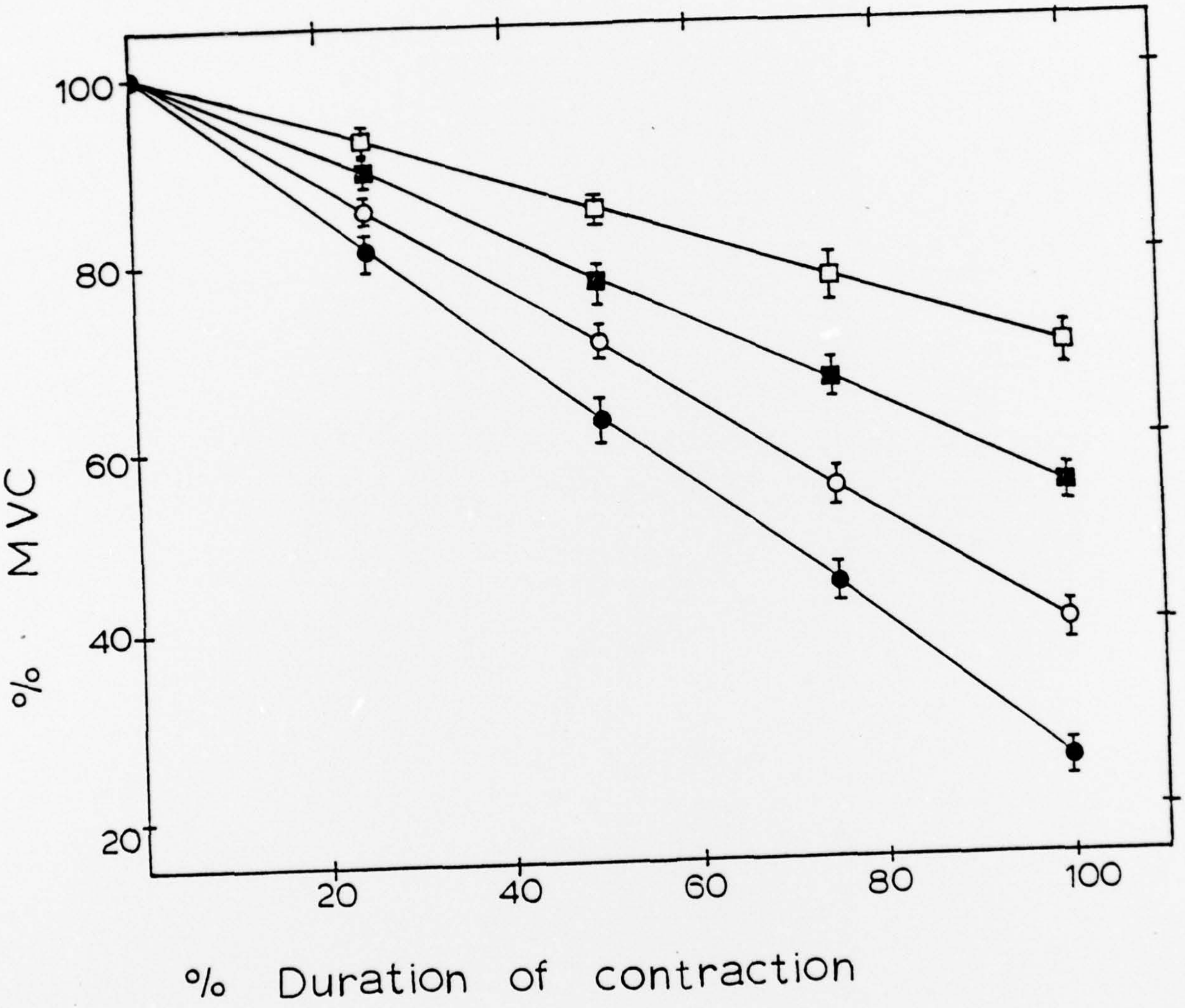
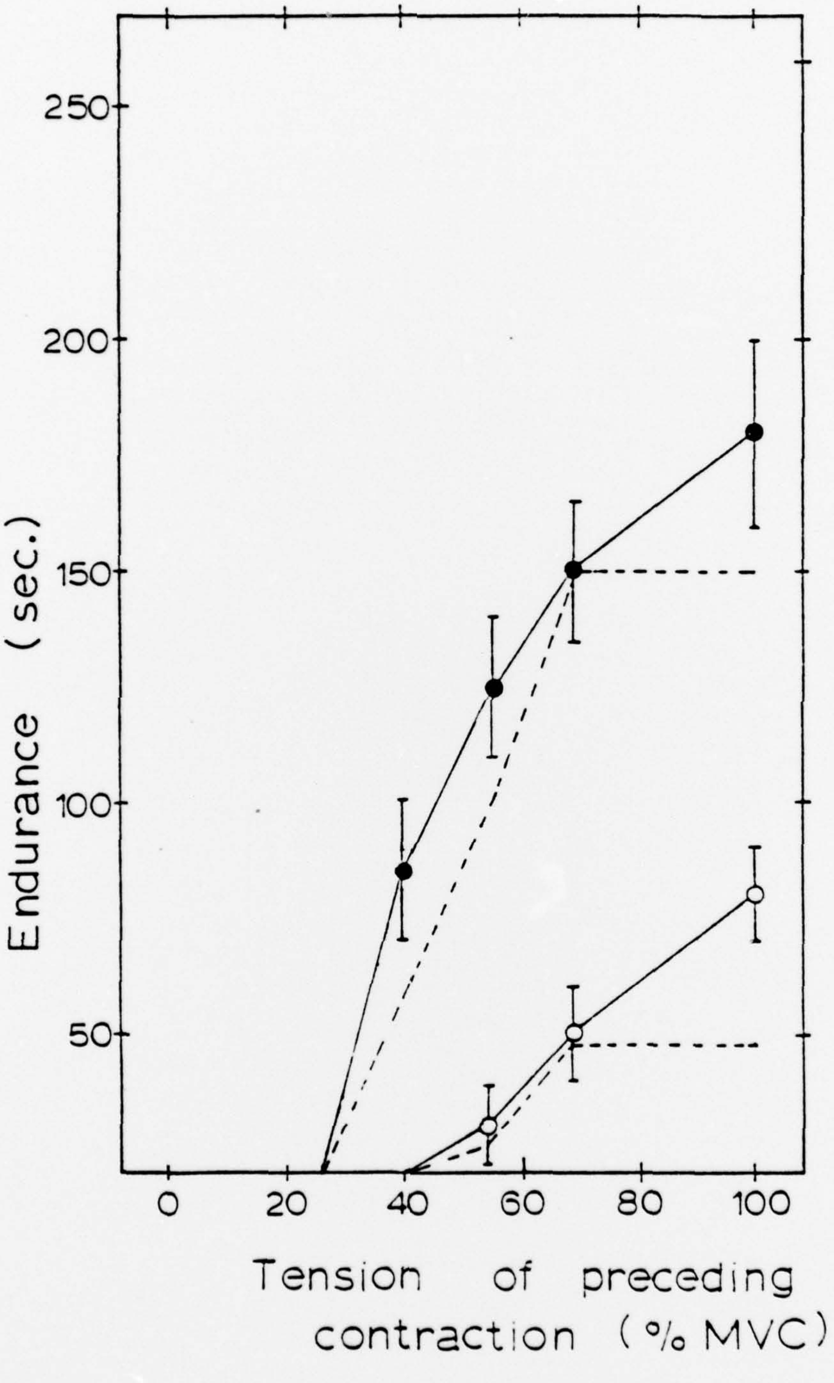


Figure 1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150
100
50
Endurance (sec.)
0
20
40
60
80
100
Tension of preceding contraction (% MVC)

Figure 2

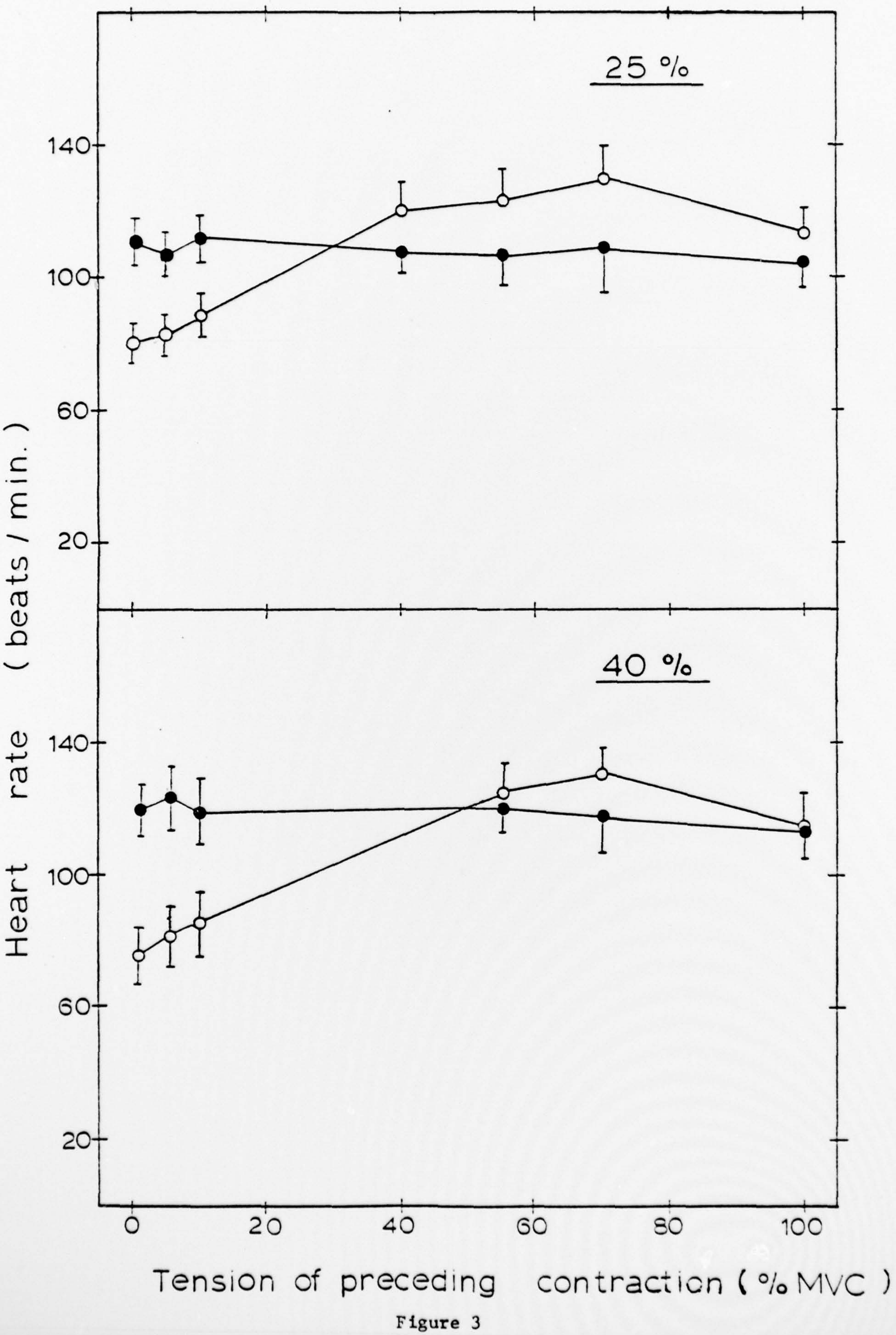
25 %
40 %
Heart rate (beats / min.)
140
100
60
20
0
20
40
60
80
100
Tension of preceding contraction (% MVC)

Figure 3

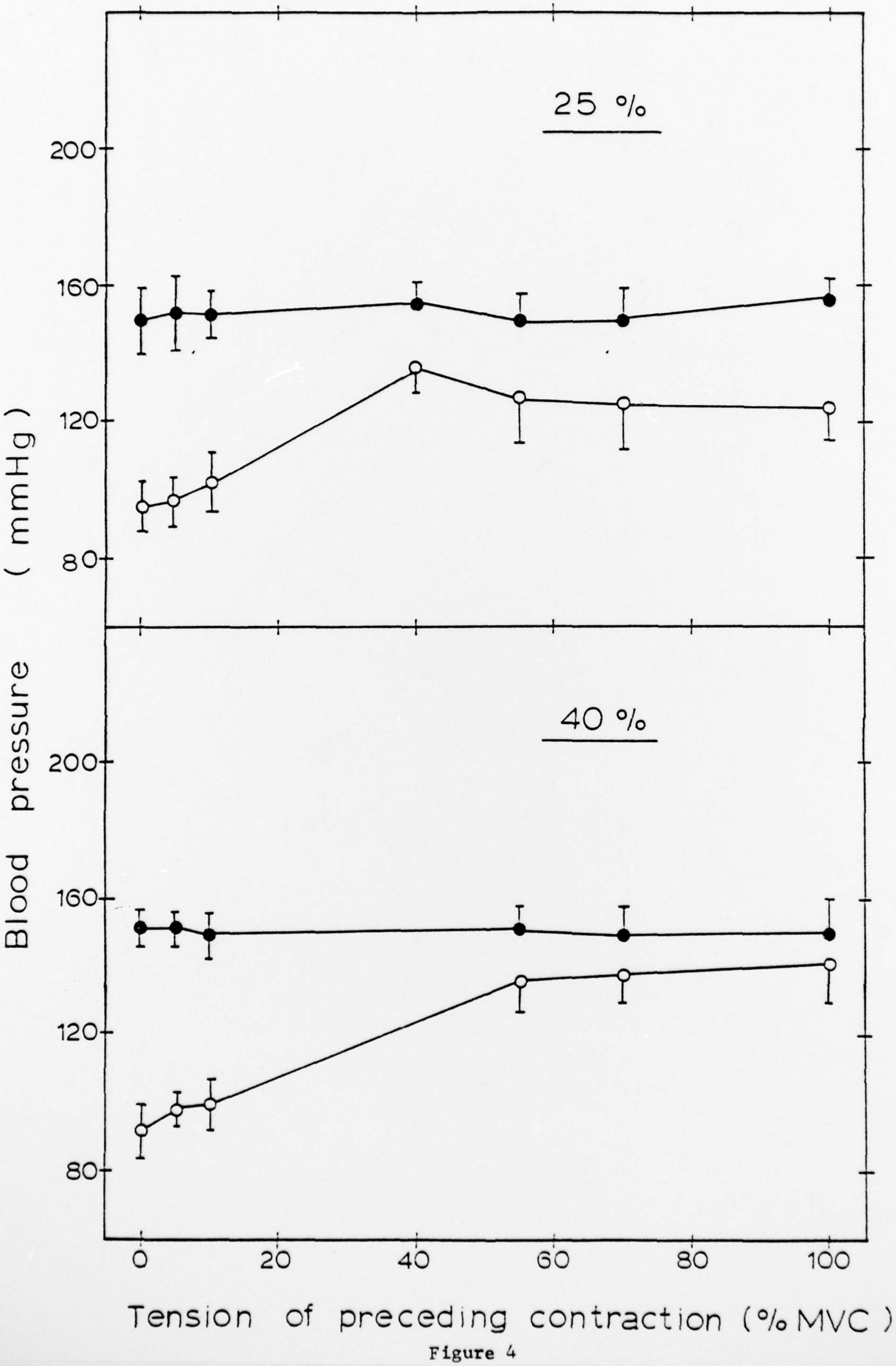
25 %
40 %
200
160
120
80
Blood pressure (mmHg)
0
20
40
60
80
100
Tension of preceding contraction (% MVC)

Figure 4

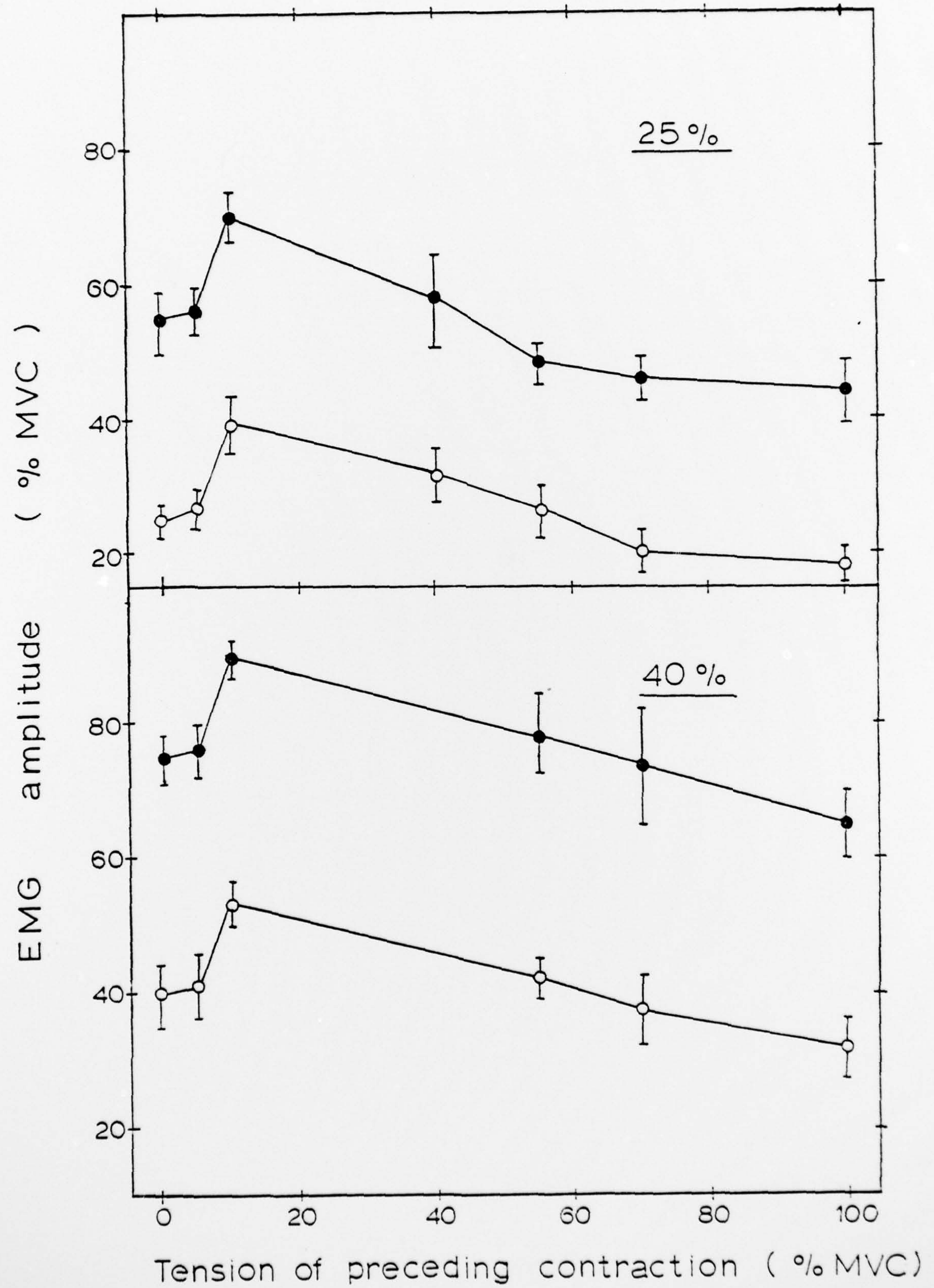
EMG amplitude (% MVC)
25 %
40 %
80
60
40
20
80
60
40
20
0
20
40
60
80
100
Tension of preceding contraction (% MVC)

Figure 5

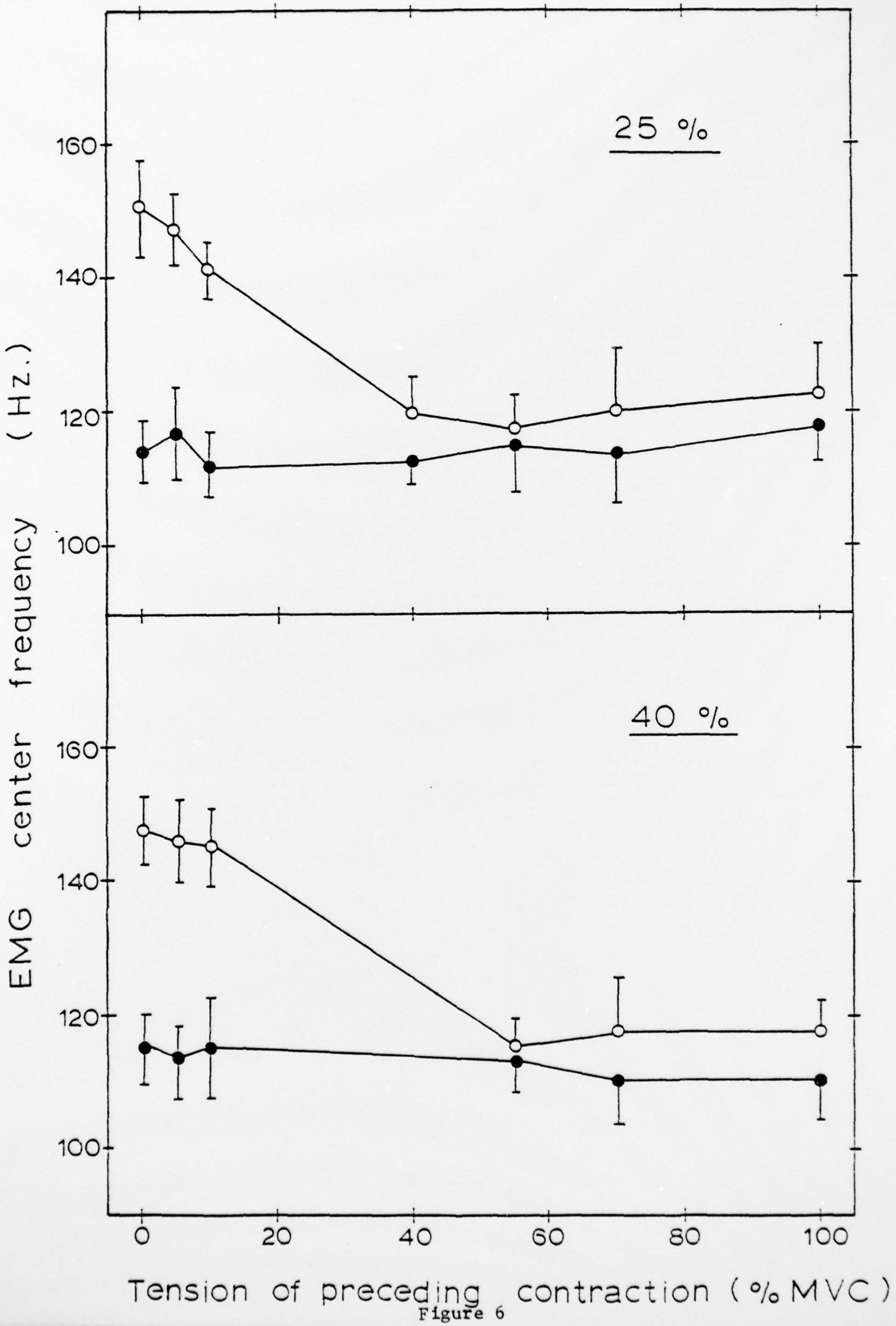
25 %
40 %
160
140
120
100
160
140
120
100
EMG center frequency (Hz.)
0
20
40
60
80
100
Tension of preceding contraction (% MVC)

Figure 6

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