THE FUNCTION OF M. DEPRESSOR CAUDAE AND M. CAUDOFEMORALIS IN PIGEONS

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THE usual method of determining the function of a muscle is by gross dissection and study of attachments. Results of such observations are frequently inconclusive and inaccurate because of differential action of the muscle and synergistic actions of other muscles.

This study was concerned primarily with M. caudofemoralis (Figure 1), which is a particularly difficult muscle to which to assign a function in birds. It is attached at each end to a freely movable part of the skeleton—the caudal vertebrae at one end and the femur at the other.

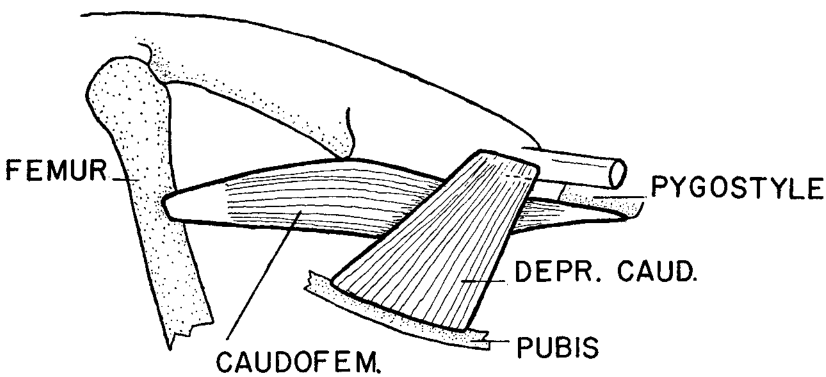

FIGURE 1. Lateral view of M. caudofemoralis and M. depressor caudae in the Domestic Pigeon.

Morphologically, the vertebral attachment is the origin and the femoral end the insertion. However, because of the small size of the muscle and the relative massiveness of the hind limb as compared to the tail, the caudal connection may be the functional insertion, as suggested by Fisher (1946: 666). Contraction of M. caudofemoralis may result in depression of the tail, if bilateral activity of the muscles is involved, or in side-to-side movement of the tail if the muscles act unilaterally.

M. depressor caudae would appear to have two possible actions—depression of the entire tail, especially the lateral rectrices, if the muscles on the two sides contract simultaneously, and tilting of the tail if the muscles act individually. Some spreading of the rectrices may be possible.

Both muscles, because they are attached to the tail, could have an effect on the pattern and force of landing. Depression of the tail to form an air brake to reduce speed and increase lift, spreading of the rectrices to form a wider surface, and lateral, rudderlike motions are possible results of action by these two muscles.

The Experiments

Valuable information on muscle function may be obtained through complete incapacitation of a muscle. Disability of a muscle can be accomplished by local administration of anesthetic drugs such as procaine, by resection of nerves leading to the muscle, or by resection of the entire muscle.

All three methods were used on Domestic Pigeons (*Columba livia*). Local anesthesia proved impracticable on the small muscles because of varying rates of diffusion and the danger of disabling muscles other than the desired ones. Cutting of nerves proved feasible, but there was always the possibility of incomplete enervation; sites of innervation were individually variable, and multiple innervation was sometimes found. Consequently, most reliance and emphasis in these experiments were on complete removal of the muscle.

M. depressor caudae was removed under general anesthesia and without damage to other muscles, through an incision 0.5 inches long. Five-millimeter pieces of M. caudofemoralis were removed through half-inch incisions; one piece was taken near the caudal attachment and another near the femoral attachment of each muscle.

Two pigeons (one for each muscle) were used in each set of experiments, and the experiments were repeated three times over a period of two years. Thus, four pigeons were used for the study of the function of each muscle. Each pigeon acted as its own control.

The pigeon was first flown through the flight procedure described by Fisher (1956a) and landed on the force-recording platform (Fisher, 1956b). One hundred such control flights were made for four successive weeks to give an average picture of the pattern of landing and the forces exerted by each bird. After the last series of control flights, the designated muscle was disabled and the bird permitted to fly in a 6- by 10-foot cage.

After six weeks the birds were fully recovered from these minor operations, and 100 experimental flights were made in each of three successive weeks to indicate the postoperative patterns and forces.

Results

Depressor caudae.—Pigeons No. 1, 2, 3, and 4 were used in this work. In Table 1 only the data for pigeons 1 and 2 are presented; data for pigeons No. 3 and 4 approximated those for No. 1 in all regards, and No. 1 is therefore to be considered more typical than No. 2.

Bird No. 1 exhibited learning in its control flights as well as in its experimental flights, as demonstrated by decreased landing force during each day's trials. However, progressive learning from week to week was indicated only in forward forces (called "back" forces in previous papers) where there was a significant decrease between the first and last days in the control and the experimental series.

Bilateral removal of M. depressor caudae in birds No. 1, 3, and 4 resulted in a statistically significant increase of 40 to 60 per cent in forward force of landing between the last control and the first experimental series (Table 1). Futhermore, this increased force was a constant feature of the postoperative series of flights (Figure 2). Conversion of the data in millimeters to data in grams is possible by use of the calibration curve given by Fisher (1956b: 338).

TABLE 1

AVERAGE FORCES (IN MM.) OF 100 LANDINGS BY DOMESTIC PIGEONS

Pigeon number	*Control, trial days* 1	2	3	4	*Experimental, trial days* 1	2	3
				forward			
1	9.6	10.4	8.9	8.2	12.5	8.3	11.1
2	8.5	7.6	9.1	8.8	10.5	8.6	9.7
5	9.2	9.4	7.1	7.5	9.0	7.4	9.2
6	12.9	12.5	11.2	11.3	11.9	10.9	11.4
				downward			
1	8.9	10.7	8.9	9.4	8.1	10.2	8.9
2	7.7	7.5	7.9	8.2	6.9	7.8	8.4
5	12.2	9.1	8.5	8.7	8.8	7.7	8.6
6	13.7	11.2	10.8	10.8	11.3	11.3	10.0
				total			
1	27.3	31.8	26.0	27.3	28.7	26.8	29.0
2	23.9	22.6	24.8	25.3	22.7	24.3	26.6
5	33.5	27.6	24.2	24.8	26.5	23.9	26.4
6	40.3	34.8	32.7	32.8	34.5	33.5	31.3

Downward forces in these same birds were not significantly changed by the operations. In Figure 2 the apparent postoperative decrease early in the experimental flights is not significant.

Total forces were nearly identical in the control and experimental series, despite the increased forward forces. This is possible because downward force usually constitutes a major portion (approximately two thirds) of the total force.

Bird No. 2 exhibited patterns of behavior and landing forces not found in any other bird of the total of 26 used in these and similar experiments. The pattern of its approach to the landing platform

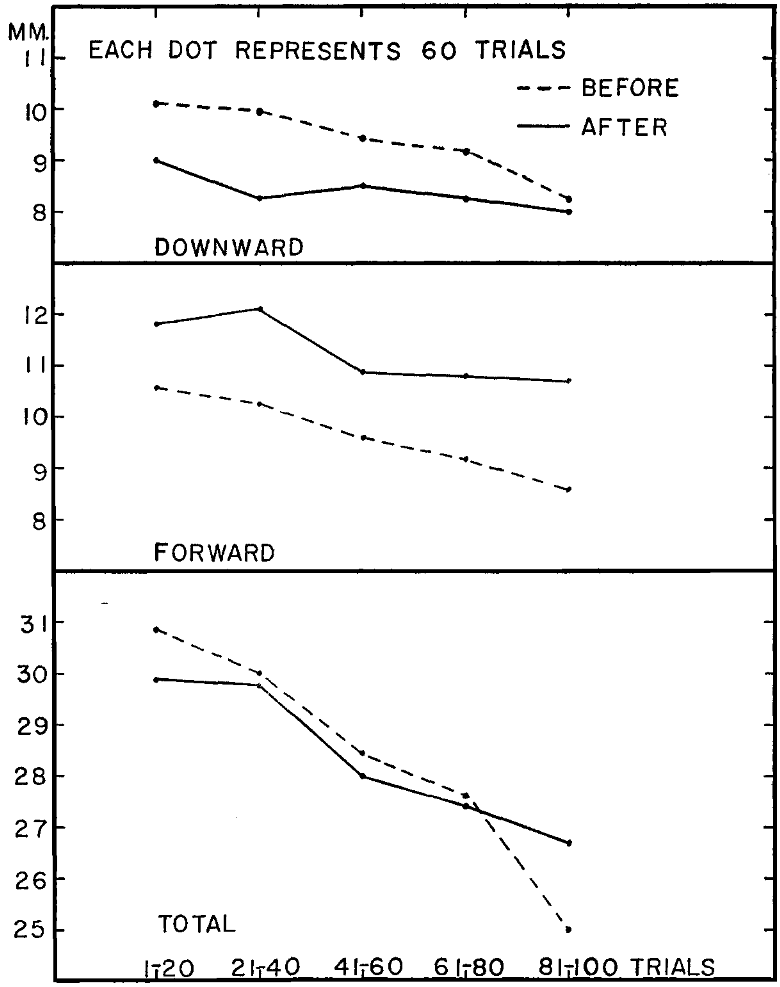

FIGURE 2. Forces of landing (mm.) before and after removal of both Mm. depressor caudae in Domestic Pigeons.

was inconstant from day to day. Although the forces of landing decreased somewhat during each day's trials, the bird showed no decrease from day to day in either the control or the experimental series. Pre- and postoperative forces were the same except for forward force, which was somewhat increased ($P = 0.05$) by the removal of the M. depressor caudae.

Autopsy of these four birds one week after the last experimental landings showed identical and complete extirpation of the designated muscles, with no adhesions.

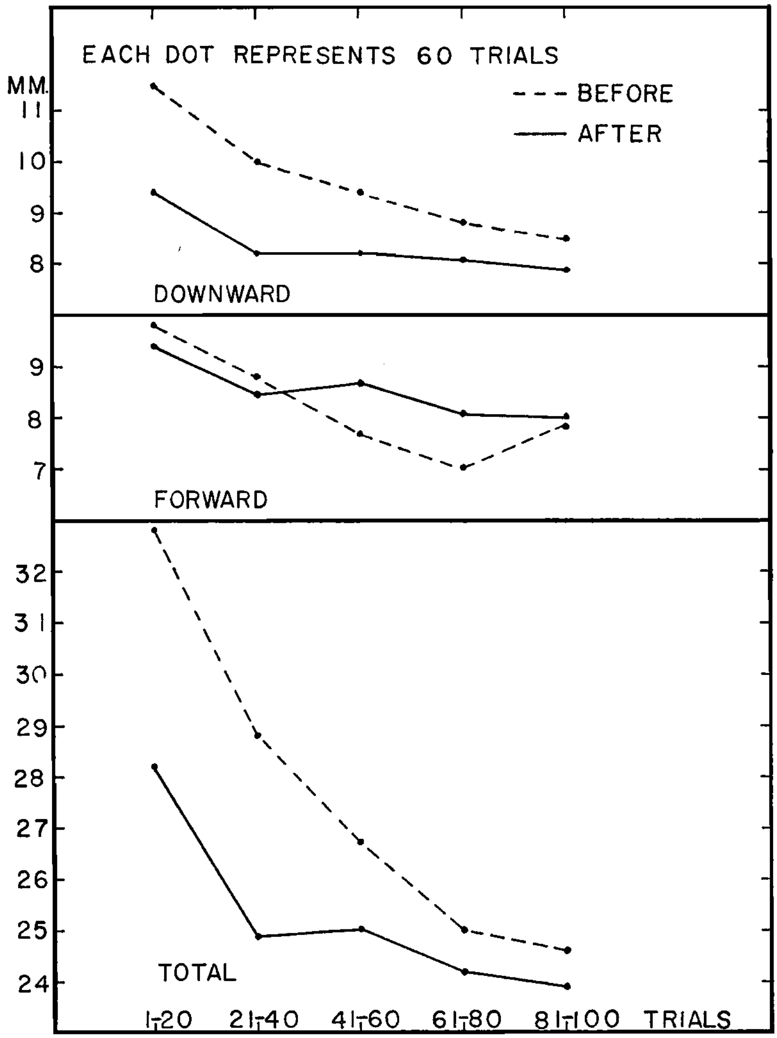

FIGURE 3. Forces of landing (mm.) before and after both Mm. caudofemoralis were disabled in Domestic Pigeons.

Caudofemoralis.—Pigeons 5, 6, 7, and 8 were used in this part of the study. Data for bird No. 5 are presented in Table 1 as indicating the typical forces in this series of experiments. All these birds showed decreased forces during the flights made each day in the control and the experimental series; the forces of No. 6 exhibited the least decrease.

All four birds displayed decreases from day to day during the control series of landings (Table 1), but none of them gave any indication of such day-to-day decreases in the postoperative series.

Birds No. 5, 7, and 8 exhibited slight but variable and insignificant increases in forward forces after removal of the M. caudofemoralis. Other forces did not increase after the expected decrease during the first or second week of the control landings. There was no significant change in any force used by No. 6, after the second week of the control series.

Figure 3 presents the typical trends of forces of birds No. 5, 7, and 8, as exhibited by pigeon No. 5. Average downward force in the first 40 trials of each postoperative series was actually significantly less than during comparable control landings; this is further reflected and magnified in the curves for total force. Average forward forces exhibited no changes between comparable parts of the control and experimental series of landings. It is important to note in Figure 3 that the average forces used during the last 20 trials on each day of the control and of the experimental landings are nearly identical.

Birds 5 to 8 were autopsied within a week after the postoperative flights. Mm. caudofemoralis were almost completely atrophied in Nos. 5 and 7; in Nos. 6 and 8 the attachments of the muscles were atrophied, but the bellies of the muscles were only slightly smaller than usual. In these two birds it was evident that the blood and nerve supply had not been badly disturbed.

Discussion and Summary

Increased landing forces, postoperative, would indicate a loss of function, and they could be presumed to result from the operation. The increased forces might indicate the part that a muscle plays in accomplishing a certain movement of the body. However, because it is apparent that several muscles contract to depress the tail and because it is likely that none of these contract to their fullest extent in normal landings, loss of one muscle's contribution may be partly or completely compensated for by other muscles. Increased forces, therefore, can be interpreted only as indicating that the disabled muscle was a part of the mechanism for depression of the tail or abduction of the rectrices to widen the tail surface. Absence of any change in forces after disablement might indicate no function in the movement tested for, or complete compensation.

Removal of Mm. depressor caudae in four birds caused a significant increase (40 to 60 per cent) in forward or braking forces as the birds landed on the platform. This probably resulted from decreased ability to depress the tail to form a more effective airbrake. Further, the position of M. depressor caudae indicates that it could have an abducting effect on the rectrices. Close observation of experimental birds indicated that the tail was not as broadly fanned out as before removal of the muscles, although there was no way to measure separately this loss of function.

Depression of the tail to form air flaps would be expected to increase lift, as well as to slow forward motion. The absence of any increase in downward forces, after removal of these muscles, seems to indicate that in pigeons, at least, normal depression of the tail primarily affects forward motion. This is not unexpected, for it is well known that when the angle of incidence of a surface of a moving object is greater than about 60 degrees, lift decreases sharply or disappears, leaving only a slowing or braking effect. In the control landings the tail of the pigeon was usually held downward more than 60 degrees from the line of flight. Postoperatively, the tail was not depressed to such an extent. Thus, it seems that decreased depression of the tail in the pigeon may actually decrease the downward force of landing, by increasing the lift vector, as was insignificantly indicated after removal of Mm. depressor caudae but was demonstrated at a statistically significant level after the Mm. caudofemoralis were incapacitated.

Disabling of Mm. caudofemoralis by removing five-millimeter sections at each end of the muscle resulted in no significant increases in the forces of landing. Further, other than slightly less depression of the tail, no changes in manner of landing were observed. One indication that these muscles function in landing was that the birds showed no day-to-day decrease in forces after the operation although they showed (as did all other birds used in similar experiments) expected decreases in preoperative control flights. The absence of any day-to-day decrease in forces after the muscular action was disturbed would seem to indicate a disruption of the normal pattern. The postoperative decrease in downward forces has already been discussed. It further seems apparent that any function the caudofemoralis muscles have in moving the tail, when a bird lands, is relatively so minor that it is easily and largely compensated for by other muscles.

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