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THE POSTURAL SUPPORT OF MOVEMENT IN CAT AND DOG

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Abstract. The postural adjustment which accompanies single limb movement in the standing cat and dog was analyzed. Four trays equipped with strain gauges were used for measuring the vertical forces exerted by each limb before and during movement performance. Three types of movements were analyzed: flexion movements elicited by motor cortex stimulation, placing movements, conditioned movements of either forelimb or hindlimb (lift-off in cat, flexion with maintained final position in dog).

In both cats and dogs the postural adjustment during movement consists of a bipedal stance on two diagonally opposite limbs. Large quantitative differences were observed depending on the type of movement. Cortical stimulation elicited an adjustment where changes of forces exerted by the forelimb a hindlimb were nearly equal. During conditioned fore- and hindlimb lift-off in the cat there was a tendency to use only forelimbs for the postural adjustment associated with forelimb movement and hindlimbs for the adjustments associated with hindlimb movement. For placing in the cat and conditioned movement in the dog, the adjustment was intermediate, that is a predominant contribution of forelimb support with forelimb movements but nevertheless an associated contribution from hindlimbs. The general significance of the results with respect to the mechanism of postural adjustment associated with movement is analyzed.

INTRODUCTION

It is well established that different kinds of movements of animals and humans are accompanied by appropriate changes in posture (1, 2, 10–12, 17).

During either forelimb or hindlimb movement the standing quadruped uses a diagonal support pattern: one forelimb and the opposite hindlimb are loaded, whereas the limb diagonally opposite to the moving limb is unloaded. These results have been obtained in the dog (3, 11) during conditioned fore- and hindlimb movements, and in the cat during movement elicited by cortical stimulation (7), during placing movements (6) and during conditioned lift-off movement of the limb (13). If the general pattern of the postural support for movement is the same, one may question whether there are quantitative differences in the way that the postural support is organized both for different species, such as cat and dog, and for different types of movement.

The aim of this paper was to compare the results obtained separately in two laboratories on the cat and the dog, with different types of movement. Common criteria for the reanalysis of the results were defined. No basic differences were found between the postural adjustment in cat and dog, but there are large quantitative differences in the postural adjustment according to the type of movement.

METHODS

These results were collected from 3 dogs weighing from 12 to 25 kg and 7 cats weighing from 2.5 to 3.5 kg.

FORCE RECORDING

The animals stood on four platforms equipped with strain gauges for measuring the vertical force exerted by each limb.

DC force recordings were made with inkwriting EEG. Traces from cats were digitized and stored on disk using a digital computer.

EXPERIMENTAL PROCEDURE

Dogs. Two types of conditioned reflexes were elaborated. In the first type, the dog was trained to lift one limb and keep it above a certain level (about 10 cm) to avoid electrical stimulation (15 Hz, 1 ms pulse duration, 0.6–3.0 mA) of the skin of the same limb (5). The second one involved a more precise motor reaction: to avoid electrical shock (US) the dog had to lift the limb into a "safety zone" 4 cm wide located at about 10 cm above the platform and to hold it there (4). A tone 200 Hz served as conditioned stimulus (CS). The CS–US interval was 0.6 s in the first case and 5 s in the second one, and the combined presentation of both stimuli lasted for 4.5 s and 10 s respectively. In this paper the data reported concern hindlimb movement for the first kind of conditioned reflex (latency between onset of conditioned stimulus and lift-off: 0.6–0.65 s) and forelimb movement for the second one (latency between onset of conditioned stimulus and lift-off: 0.45–0.7 s).

Cats. Several types of movement and associated postural adjustments were compared.

1. *Movements elicited by cortical stimulation.* Electrodes (10 to 20 nickelchrome needles, insulated except at the tip) were permanently implanted in the fore- and hindlimb motor areas bilaterally, to a depth of 1.5 to 2 mm. Monopolar stimulation was used to elicit movement, the intracortical electrode being the cathode, the large silver indifferent electrode at the level of the frontal sinus, the anode. Ten to twenty stimuli were delivered to a given cortical site during each session. The on-line calculation by the computer of the projection of the center of gravity allowed for stimulation only when desired conditions were maintained for a period of one second, i.e. $25\% \pm 10\%$ of the animal's total weight supported by each leg and speed of displacement of the center of gravity less than 20 mm/s. Two experimental series were performed, one with intensity of cortical stimulation adjusted to produce a displacement of the limb of 4 to 5 cm above the supporting tray, the other being subthreshold for lift-off. The time between the onset of cortical stimulation and the lift-off was between 0.07 and 0.09 s for forelimb movements and between 0.08 and 0.11 s for hindlimb movements.

2. The *placing reaction* was elicited in the standing cat by contact of a forelimb with a moving tray. This tray was mobilized when certain conditions of weight distribution (as described for cortical stimulation) were held for 0.5 to 1 s. The stimulated limb was pushed backwards and the animal then performed a placing movement onto the moving tray. This moving tray was 35 mm above the level of the supporting tray. The time from the contact of the moving tray with the corresponding forelimb to the lift-off was between 0.18 and 0.35 s.

3. *Conditioned lift-off movements* were elicited by a discontinuous tone serving as conditioned stimulus and a milk reward was given as soon as the appropriate limb was lifted off, that is when the weight supported by that limb dropped to zero. The cat raised the limb only

a few mm to a few cm above the supporting tray. The time allowed from the beginning of the conditioned stimulus until the lift-off was 2 s. Prior to the conditioned stimulus, a continuous tone of 0.5 to 0.8 s duration was used as a preparatory signal during which the cat had to have an appropriate distribution of weight on the four legs, as explained for cortical stimulation.

During the training procedure, the cat was first required to keep a quiet posture during 0.5 to 0.8 s. A continuous sound was delivered if the quiet posture was adequate. Thereafter, a discontinuous sound (conditioned stimulus) was added during which the lift-off movement of the appropriate limb had to take place. The first movements were obtained by manually pushing the limb backwards.

Only movement of a given leg were elicited during a session. Training was then repeated for many sessions before the movement of another limb was tested. Data were obtained from both forelimbs in two cats (latency between CS and lift-off 0.5–0.6 s), from right forelimb only in a third, and from left hindlimb (mean latency of lift-off 0.7 s) only in the fourth.

DATA ANALYSIS

The purpose of this paper was to compare the data obtained from cats and dogs under several experimental conditions. For each animal and for each type of movement, the data were collected from one or two representative sessions, each having from 10 to 30 trials. The choice of the session was made after having verified from the previous data analysis that very little variation in the results took place from one session to another. The following parameters were systematically measured:

1. *Instantaneous indices.* Antero-posterior weight distribution (AP)

$$AP = \frac{W1 + W2 - W3 - W4}{W1 + W2 + W3 + W4} .$$

Lateral weight distribution (L)

$$L = \frac{W2 + W4 - W1 - W3}{W1 + W2 + W3 + W4} .$$

Torsion (T)

$$T = \frac{W1 + W4 - W2 - W3}{W1 + W2 + W3 + W4} .$$

W1, W2, W3 and W4 are the forces measured for the left forelimb, right forelimb, left hindlimb and right hindlimb respectively (see Fig. 1).

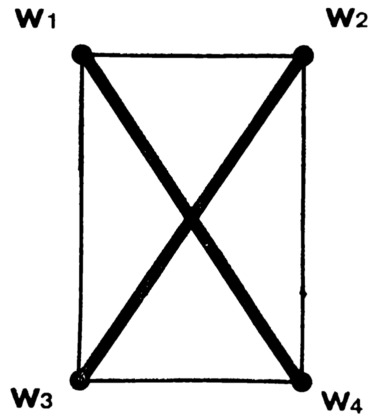

Fig. 1. The four corners of the rectangle represent the four platforms supporting the limbs. W1, W2 are the forces measured for the left and right forelimbs while W3, W4 are for the left and right hindlimbs. The difference in the force (weight) distribution along the two diagonal lines joining one forelimb and the opposite hindlimb is used for the measure of torsion.

Each of these indices was measured twice, an *initial value* calculated at the onset of cortical stimulation, contact of the moving tray with the corresponding forepaw, or onset of the conditioned stimulus and a *final value* at the time of lift-off. In the case of cortical stimulation subthreshold for lift-off, measurement of the final value was made at the time of minimum force of the "moving limb". In addition, a third measure was obtained from dogs during maintained position of the lifted limb.

2. *Differential indices.* Two differential indices were used for the analysis of the data. The reason for their choice will be explained in the result section.

Diagonal index (D)

$$D = 1 - \frac{|\Delta W1 - \Delta W4| + |\Delta W2 - \Delta W3|}{|\Delta W1| + |\Delta W2| + |\Delta W3| + |\Delta W4|}.$$

ΔW is the difference in weight between the final and the initial values.

Antero-posterior differential index (A-P)

$$\text{A-P} = \frac{|\Delta W1| + |\Delta W2| - |\Delta W3| - |\Delta W4|}{|\Delta W1| + |\Delta W2| + |\Delta W3| + |\Delta W4|}.$$

RESULTS

RIGID OBJECT

For a better understanding of the biomechanical events taking place during movement of one limb in the standing quadruped, it is interesting to examine first the behavior of a rigid, four-legged object when one of the four supporting trays is dropped. Let us consider a first case in which the weight is equally distributed on the four legs (Fig. 2). Before dropping one supporting tray, initial values of the Antero-Posterior, Lateral and Torsion indices are equal to zero. After dropping one support, the values of A-P and L are still zero, because the center of gravity remains in a central position. However torsion increases to the maximum absolute value of 1, the rigid object being supported by only one pair of diagonally opposite legs.

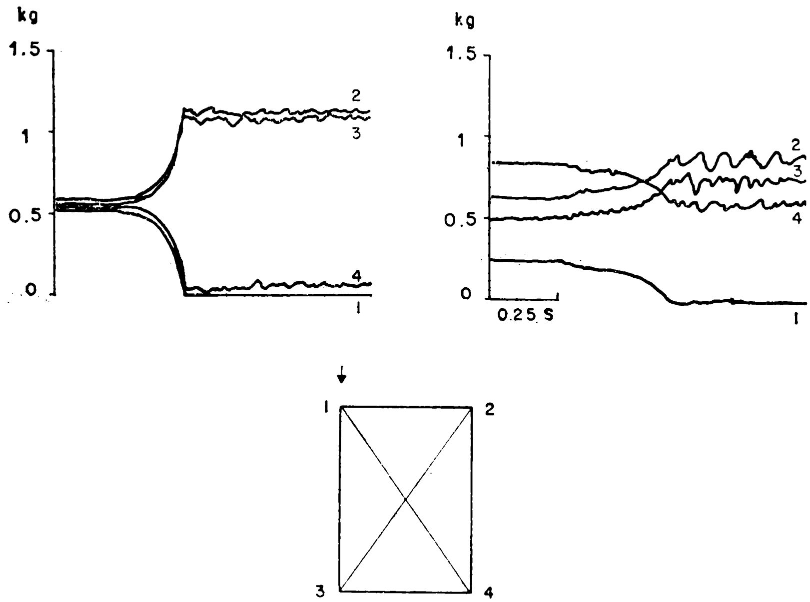

Fig. 2. Changes in weight distribution of a rigid object. The recordings were obtained with a table supported by four legs on the four platforms. The diagram at the bottom of the figure shows the position of the four supporting trays from which the vertical forces represented in the upper part of the figure were recorded. The arrow indicates the platform which is dropped (left foretray). On the left, the initial weight distribution is equal for the four trays; on the right, unequal. Notice that in both cases the same amount of weight is added or substracted to the four limbs (diagonal differential index equal to 1).

Let us now examine the case of a rigid object with unequal distribution of the weight on the four trays. Initial weights, as a percentage of the total are for limb 1 : 12%, for limb 2 : 29%, for limb 3 : 22% and for limb 4 : 37%. The initial values of A-P and L are different from 0. In the case presented in Fig. 2 right side, the following values were measured: A-P = −0.18, L = +0.32 and T = 0. The final weights are for limb 1 : 1%, for limb 2 : 40%, for limb 3 : 32% and for limb

4 : 27%. A-P and L values do not change because the center of gravity remains in the same position, but the absolute value of T increases (T = −0.44) although not to the maximum as in the previous case.

In both cases however, the weight distribution on the four supporting legs was modified in the same way. The same amount of weight was gained or lost by the four supporting legs, i.e. lost by both the one from which the support was dropped and the diagonally opposite leg, and gained by the other pair of diagonally opposing legs. Therefore a differential index was elaborated [1] to calculate quantitatively this diagonal pattern, for differing initial conditions, and/or when the limb flexion was isometric (i.e. force measured from limb did not reach zero).

This differential diagonal index (see Methods) is equal to 1 when the weight change is equal for each of the four limbs but of opposite sign for the two diagonal pairs. The index is zero when only the forelimbs (or only the hindlimbs) show a weight change (see Fig. 4). This latter situation was not encountered with the rigid object but was seen with the experimental animals where the strength of the link between forelimb and hindlimb can be changed by the nervous system.

A second differential index (antero-posterior index described in Methods) permitted evaluation of the contribution of the forelimbs and of the hindlimbs to the redistribution of weight.

With this index, a value of 0 indicates an equal contribution of fore- and hindlimbs to the weight change, a value of 1 corresponds to weight changes of forelimbs exclusively and −1 to weight changes of hindlimbs exclusively (see Fig. 5).

PHASIC MOVEMENT

Changes in instantaneous indices and values of differential indices during phasic movements will be successively analyzed.

Instantaneous indices (Fig. 3). The *antero-posterior index* is the one which changes the least whatever the experimental conditions or animals. The initial values of A-P index were from −0.04 to +0.16 in the cat and from +0.23 to +0.5 in the dog. This indicates a tendency for the center of gravity to be localized nearer the forelimbs than the hindlimbs as already noticed by Gray (8) in many quadrupeds. Forelimbs movements were usually accompanied by a slight backward shift of the center of gravity. Maximal change in A-P index value was of 0.2 that is 10% of the animal's weight being displaced backwards. Hindlimb movements were accompanied by the slighest A-P shift.

[1] The authors are indebted to Dr. A. A. Frolov who proposed this index.

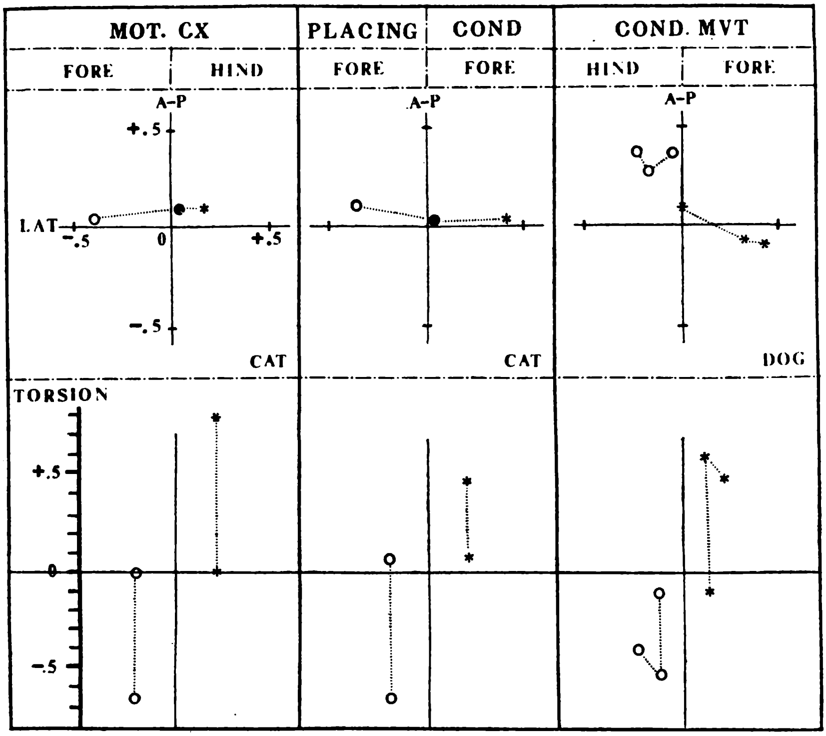

Fig. 3. Examples of anteroposterior, lateral and torsion instantaneous indices before movement (initial values closest to zero) and at the time of lift-off are represented. Three categories of samples are shown, each one corresponding to the mean values obtained during one experimental session. On the left, forelimb and hindlimb movement elicited by cortical stimulation in the cat (movements with lift-off), in the middle, forelimb placing movement and conditioned lift-off movement of forelimb in the cat, and on the right fore- and hindlimb conditioned movement in the dog. For these last movements, a third value is given which corresponds to the final maintained position of the limb. The AP and L indices are combined, and thus indicate the position of the center of pressure (projection of the center of gravity under static conditions). In each graph, results from two different sessions are represented and symbolized one by a circle, the other by an asterisk. Torsion is represented separately at the bottom. Notice the restricted AP displacement, the more important lateral displacement (except for hindlimb cortically induced movements) and torsion.

The *lateral index* was in all cases modified during movements. Movements of a left limb were accompanied by a shift of the center of pressure (resultant of the vertical forces exerted by the limbs) from a midline position towards the right. At the time of lift-off, the center of pressure was always located inside the triangle formed by the three remaining supporting limbs. The L index shifted from 0.2 to 0.5, which would correspond under static conditions to a displacement of the body weight from 10 to 25%. This lateral displacement is seen in dogs as well as in cats for all types of movements. However, hindlimb cortically elicited movements were an exception since very little lateral shift of the center of pressure was seen.

Torsion was the index showing the largest change during movement. Starting from an initial value near zero in most cases, the index rose 0.4 to 0.8 at lift-off time. This means that from 70% to 90% of the weight was supported by one pair of diagonally opposite limbs at the time of lift-off.

Differential indices (Figs. 4 and 5). Some interesting observations can be made by analyzing the differential indices, based on the differences in weights between the final values (time of lift-off) and initial values.

The *diagonal index* estimates in fact the forelimb and hindlimb contribution to the diagonal postural adjustment which takes place during movement (Fig. 4). The highest values were seen for movements produced by cortical stimulation, those for hindlimb movements (0.7–0.9) being higher than those for forelimb (0.4–0.7). No significant differences were noticed when comparing the series with cortical stimulation adjusted for a movement of 4–5 cm above the supporting tray and the series subthreshold for lift-off. The values obtained with cortical stimulation were actually the closest to those observed with a rigid object. Intermediate values were seen for placing movement, and the lowest indices were obtained for forelimb and hindlimb conditioned movements in the cat, where the weight changes are restricted almost exclusively either to forelimbs or to hindlimbs (see Fig. 4). For conditioned movements in the dog, values from 0.3 to 0.6 were observed, which are more comparable to those values from cats performing placing movements rather than conditioned lift-off movements.

The *antero-posterior index* also estimates the relative contribution of forelimb and hindlimb to the postural adjustment associated with movement (Fig. 5). The highest positive or negative values were observed for cat's conditioned forelimb or hindlimb movements (highest contribution of forelimbs to the postural adjustments with forelimb movement and from hindlimbs to adjustments of posture associated with hindlimb movement). The lowest values were seen for movements induced by cortical stimulation (almost equal contributions of fore- and hindlimbs to postural adjustment). Intermediate values were recorded for placing movement in the cat and for limb movement in the dog. The results obtained with the antero-posterior index are thus in good agreement with those furnished by the diagonal one. In addition, this index shows

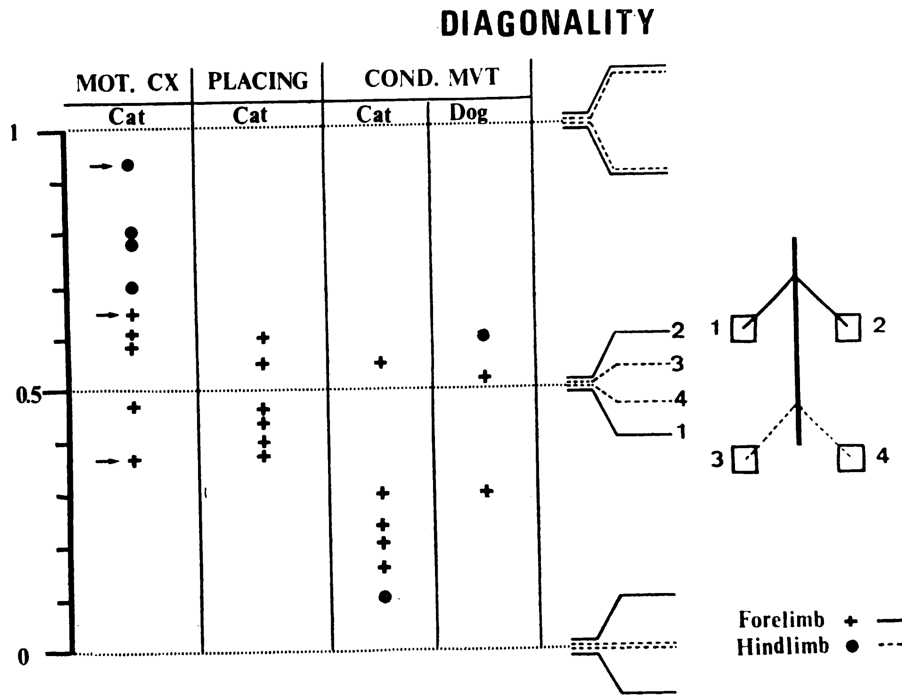

Fig. 4. Values of differential diagonal index during different types of limb movements: motor cortical stimulation in the cat (Mot Cx), placing movement in the cat (placing) and conditioned movement in cat and in dog (cond MVT). Each symbol represents the mean value obtained from one experimental session. For cortical stimulation, the results are from three cats each one having stimulating electrodes in the forelimb and in the hindlimb motor cortical area. Placing movements are obtained from 3 cats, with results from left and right placing movements. The conditioned movements in the cat were obtained from 4 animals, two trained to perform the lift-off movement of forelimb on the right and left side, one performing forelimb movement on the left side and one performing hindlimb movement of the left side. Three dogs were used, two with forelimb movement, one with hindlimb movement. On the right, diagrammatic representation of quadruped with the paws resting on four trays. The force changes which would be observed for different index values (+1, 0.5, 0) are represented. When limb 1 corresponds to the moving limb, the force exerted by it falls to zero (see for comparison Fig. 2). The lower traces, at the time of lift-off, are 1 and 4 and the upper traces are 2 and 3. The representation of force changes for the different values of the index is only an approximation based on the hypothetical case in which no shift of the projection of the center of gravity occurs during movement. On the left, values of the diagonal index. For motor cortical stimulation two sets of values are represented. Those without arrow correspond to sessions without lift-off, and those with arrow to sessions where cortical stimulation was adjusted for raising the limb 4–5 cm above the supporting tray. For the comments on the figure see text.

a result, at first sight surprising, concerning the hindlimb movement elicited by cortical stimulation. In this case, the value of the index is greater than or equal to zero (−0.02 to +0.3) which means that the postural adjustment associated with hindlimb flexion has a forelimb

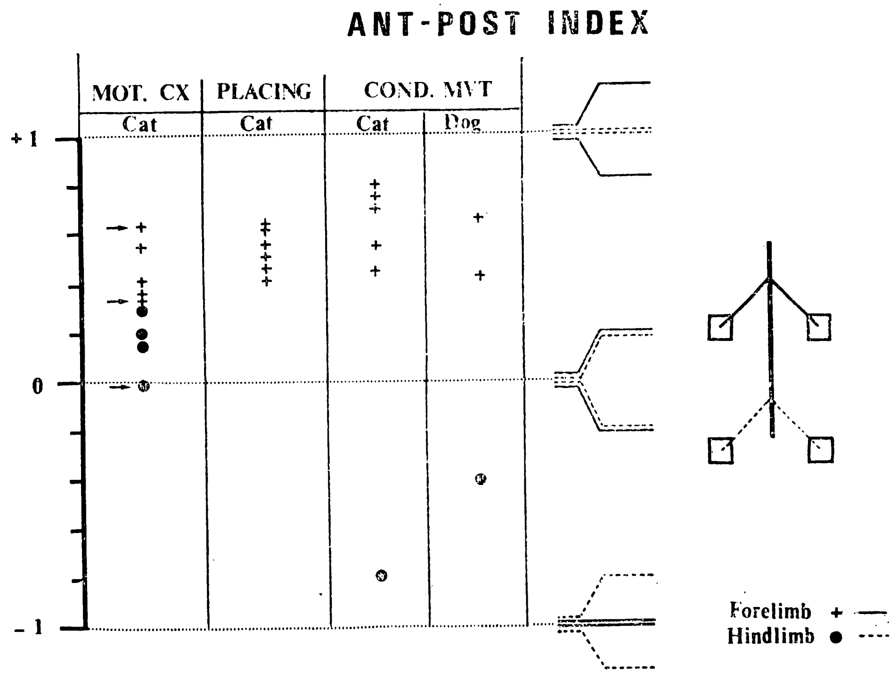

Fig. 5. Differential antero-posterior index measured from the same animals and sessions as those represented in fig. 4. On the right, diagrammatic representation of quadruped with the paws resting on four trays. The force changes which would be observed for different index values (+1, 0, −1) are illustrated. Two different sets of trials are represented for cortical stimulation as in Fig. 4.

component greater than or equal to the hindlimb contribution. This can be explained by the fact that the initial position of the center of gravity is located nearer to the forelimbs than the hindlimbs and thus a higher isometric weight change of forelimbs with respect to hindlimbs is possible.

MAINTAINED POSITION

The experimental procedure used to elicit a conditioned limb movement in the dog permitted comparison of two situations. One corresponds to the time of lift-off, that is the moment when the moving limb leaves the supporting tray. The second, a more static situation, corresponded to the maintained posture of the limb in the flexed position.

TABLE I

Comparison between diagonal differential indices during phasic movements and maintained position in the dog. The diagonal differential index was measured between lift-off and initial position and between final and initial position. Notice the lower value of the index at the time that the final position is reached

Dog	Difference between lift-off and initial	Difference between maintained position and initial
LIT (Forelimb)	0.52	0.31
POL (Forelimb)	0.29	0.1
TIM (Hindlimb)	0.57	0.36

Both instantaneous and differential indices were compared for the two situations. The main difference between the dynamic phase of the movement and the maintained posture was reflected in the diagonal differential index (Table I). This index was clearly lower during the postural fixation of the limb. At the same time, the lateral displacement of the center of pressure was increased and torsion was reduced (Fig. 3).

These results indicate that the support of the body on the two diagonal limbs was maximal during the dynamic phase of the movement, but this diagonality was less during the maintained posture of the limb in a flexed position.

DISCUSSION

One of the main objects of the experiments reported in this paper was to analyze the postural support accompanying movement in the standing quadruped. Two questions were raised. First, is this postural support qualitatively or quantitatively different in two different species of quadruped such as dogs and cats. Second, are there qualitative or quantitative differences in the postural support for movement according to the way that the movement was elicited. For this comparison, forelimb and hindlimb movements evoked by cortical stimulation, forelimb placing movements and fore- and hindlimb conditioned movements with or without maintained position were analyzed.

A first general conclusion is that qualitatively the different types of movement performed in the two species were supported by a diagonal stance using one forelimb and the opposite hindlimb. This diagonal pattern is similar to that observed when a rigid object supported by four legs loses one of its supports (Fig. 2). It is also used during locomotion, especially during trotting, where alternate supports on two diagonally opposite limbs are observed in succession (8, 9, 14, 16).

A second observation concerns the quantitative analysis of the diagonal support. It appears that the quadruped does not behave as a rigid object and that the contributions of each of the four limbs to the weight changes during movement are not equal. The analysis of the quantitative measurements of the forelimb or hindlimb contribution to the postural support has revealed that a hierarchy exists in the cat in the way that postural adjustment associated with movement is organized. The cortically evoked movements have the highest diagonal index, i.e. the closest to a rigid object where an equal contribution of fore- and hindlimb to the diagonal support are observed. An intermediate state is found with the forelimb placing movement, where the forelimb contribution to the postural support is higher than that of the hindlimb. Finally, the postural support for conditioned lift-off movement is the furthest from what is seen with a rigid table. There is a tendency that only forelimbs for forelimb movements and only hindlimbs for hindlimb movements participate in the postural adjustment associated with movement.

In attempting to explain these quantitative differences in the postural support in quadrupeds for the various types of movement, several factors may be considered. The first is the effect of the amplitude of the particular movement; two experimental series with cortical stimulation were compared, one without lift-off of the limb, the other with the leg raised 4–5 cm above the tray. The results obtained from both series were comparable. Thus, amplitude of movement does not seem to be an important factor contributing to the differences. A second possible mechanism could be the speed of force changes. In fact, for cortical stimulation where a high diagonal index is observed time to lift-off was less than 0.1 s, whereas for placing, with an intermediate diagonal index, the time was 0.18 to 0.35 s, and for conditioned movement with the lowest diagonal index 0.4 to 0.5 s. Thus the factor of speed of force changes cannot be excluded. However, it must be mentioned that the low diagonal index obtained for lift-off movements is only observed after learning is achieved, and that during learning the diagonal index is much higher, notwithstanding the fact that force changes are performed slowly. Thus differences in the central command according to the types of movement are probable. Concerning the movement elicited by cortical stimulation, the short latency of the force changes suggest that the command may have a direct access to the network which is responsible for the diagonal support. This network could be located at the spinal cord level, as suggested by experiments reported by Sherrington (15), who gave evidence for the existence at that level of a neural basis for a link between flexors and extensors of diagonally opposite limbs.

The changes in the supporting pattern according to the type of movement are clearly apparent in the cat, but the question remains open for the dog where results are available for only one type of movement, a conditioned limb movement. The measures of the diagonal index at the time of lift-off made on three dogs indicate that no values were observed as low as those in the cat. This suggests that the dog may not be able to produce postural support during movement limited to the two forelimbs or to the two hindlimbs as does the cat. The dog would thus behave more "rigidly" which is not a surprising result. However, before conclusions can be drawn, more data must be collected, using the same types of movement in both species.

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REFERENCES

1. ALEXEIEV, M. A. and NAIDEL, A. V. 1973. Rapports entre les éléments volontaires et posturaux d'un acte moteur chez l'homme. Agressologie 14B: 9–16.
2. BELENKIY, V. E., GURFINKEL, V. S. and PALTSEV, E. I. 1967. On elements of control of voluntary movements (in Russian). Biofizika 12: 135–141.
3. BROOKHART, J. M., PARMEGGIANI, W. A., PETERSEN, W. A. and STONE, S. A. 1965. Postural stability in the dog. Am. J. Physiol. 208: 1047–1057.
4. BURLACHKOVA, N. I. and IOFFE, M. E. 1978. A study of the effector structure of learned coordinations in the dog. Neuroscience 3: 125–127.
5. BURLACHKOVA, N. I. and IOFFE, M. E. 1979. The analysis of the postural adjustment accompanying a local movement. Agressologie 20B: 141–142.
6. COULMANCE, M., GAHÉRY, Y., MASSION, J. and SWETT, J. E. 1979. The placing reaction in the standing cat: A model for the study of posture and movement. Exp. Brain Res. 37: 265–281.
7. GAHÉRY, Y. and NIEOULLON, A. 1978. Postural and kinetic coordination following cortical stimuli which induce flexion movements in the cat's limbs. Brain Res. 155: 25–37.
8. GRAY, J. 1968. Animal locomotion. Weidenfeld and Nicolson, London, 479 p.
9. GRILLNER, S. 1975. Locomotion in vertebrates: central mechanisms and reflex interaction. Physiol. Rev. 55: 247–304.

10. GURFINKEL, V. S. and ELNER, A. M. 1973. On two types of static distrubances in patients with local lesions of the brain. Agressologie 14D: 64–72.
11. IOFFE, M. E. and ANDREYEV, A. E. 1969. Inter-extremities coordination in local motor conditioned reactions of dogs (in Russian). Zh. Vyssh. Nervn. Deyat. im. I. P. Pavlova 19: 557–565.
12. KORIAKIN, M. F. 1958. Contribution of postural excitations in patterning the conditioned defensive motor reflex in the dog (in Russian). Fiziol. Zh. SSSR im. I. M. Sechenova 44: 393–403.
13. POLIT, A. and MASSION, J. 1979. Patterns of postural support during limb movement. Soc. Neurosci. (Abstr.) 5: 382.
14. ROBERTS, T. D. M. 1967. Neurophysiology of postural mechanisms. Butterworths, London.
15. SHERRINGTON, Sir Charles. 1947. The integrative action of the nervous system. 2nd ed. University Press, Cambridge.
16. SHIK, M. L. and ORLOVSKY, G. N. 1976. Neurophysiology of locomotor automatism. Physiol. Rev. 56: 465–501.
17. SHUMILINA, N. I. 1945. On the duplex nature of motor excitations in the central nervous system (in Russian). Fiziol. Zh. SSSR im. I. M. Sechenova 31: 272–282.

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