

COMPENSATION FOR SUBSTRATE ELASTICITY IN THE KINEMATICS OF LEAPING BY INFANT PIGTAILED MACAQUES (*MA CA CA NEMESTRINA*)

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Abstract:

The means whereby animals adapt their locomotor behavior to variation in environmental conditions is an important and neglected problem in the area of motor control. To investigate this problem, young (3-month-old) pigtailed macaques (*Macaca nemestrina*) were filmed leaping a fixed distance from both rigid and elastic take-off supports. Sixteen of 17 subjects exhibited substantial invariance in the trajectories described by the major joints of the hind limb (hip, knee and ankle) during the leap. By contrast, the patterns of angular joint movement varied between performances involving the rigid and elastic supports. Maintaining invariant joint trajectories may enable the leaping animal to land safely at the target and prepare for subsequent action, and requires compensation for substrate elasticity. This compensation is effected, in part, by changing the patterns of joint flexion¹³ and extension.

Key words: locomotion, leaping, kinematic tuning, *Macaca nemestrina*

Article:

INTRODUCTION

As an animal moves through its environment, variation in external conditions such as the slope, roughness and consistency of the substrate requires that it constantly adjust, or tune^{4,9,18}, its locomotor performance. Tuning in regard to external conditions is clearly an essential requirement for any system controlling locomotion in a natural, variable environment^{6,18} and has emerged, in various formulations, as an important component of much current theory of motor control^{4,5,9,10,15,17,18}. There are, however, rather few experimental studies of the ways in which locomotion changes to accommodate environmental variation.

The requirement for a locomoting animal to vary its behavior in this manner is a special instance of a more general problem in the domain of motor control. Discussing this problem, Bernstein² noted that because of the varying external forces that act on the body in the course of movement, there cannot be an unequivocal relationship between the activity of muscles and the resulting movements. In order to produce invariant movements, muscle forces must be tuned to compensate for variation in external forces. Evidence for compensatory tuning is also to be found in a purely kinematic analysis of performance. If the limb movements of a dog running at a constant speed on a level and on an inclined treadmill are compared, the amplitude of the angular joint movements is found to increase with ground slope.¹³ The additional power thus developed by each step compensates for the increase in ground slope, maintaining a constant forward velocity. Prost and Sussman¹⁶ likewise found that changing the slope of the ground plane altered the footfall patterns of vervet monkeys (*Cercopithecus aethiops*), a change that may again reflect compensation for the altered distribution of forces acting on the animal's body on an inclined surface.^{7,8}

This paper describes an example of kinematic tuning of motor performance in young pigtailed macaques leaping a fixed distance from both rigid and elastic take-off supports. Elasticity was chosen as a suitable parameter to manipulate since it is a normally varying property of the substrates, such as tree branches,

available to tile macaques in their natural habitat. Films of leaping performance were analyzed to determine some of the invariant and variant kinematic properties of the leap.

MATERIALS AND METHODS

Subjects

Seventeen infant pigtailed macaques (*Macaca nemestrina*), weighing 960- 1340 g at the time of testing, were hand-reared in incubators until about one month of age when they were transferred to individual wire cages in a large colony room. To aid normal development, small groups of animals exercised for up to 1 h daily in a large playroom. All subjects played freely and vigorously during these play sessions and displayed no locomotor or other abnormalities. Except where noted, subjects received ad libitum water and Purina monkey chow in their home cages for the duration of the experiment.

Apparatus

All training and testing was carried out in a large (218 x 70 x 53 cm), upright wooden cage, illuminated from above and below by fluorescent lighting and with a glass front through which the subjects' performance could be observed and recorded. The target for leaping was a shelf, 99.7 cm above the cage floor, where diluted apple juice was available from a dispenser. The take-off support was a platform, 25.4 cm long, bolted to the opposite side of the cage at a height of 64.5 cm and accessible via a vertical ladder attached to the cage wall. Subjects were required to leap a distance of 36.2 cm vertically and 45.1 cm horizontally to reach the target shelf (Fig., 1a). To record leaping from a rigid support, the take-off platform consisted of three tubular aluminum cross-bars attached to two rigid stainless steel bars, 25.4 cm long and 1.3 cm in diameter. To provide an elastic take-off support, the stainless steel bars could be replaced by two nylon rods of the same dimensions. Analysis of film records revealed no detectable deflection of the rigid support, and a downward deflection of 3-5 cm in the elastic support, as the animal leapt. Since this study was concerned solely with the kinematic aspects of performance, the dynamic properties of the elastic support were not systematically investigated.

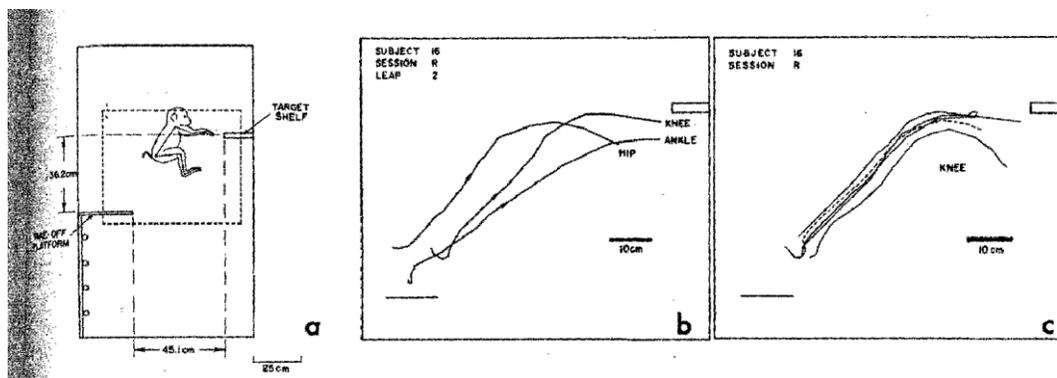


Fig. 1. a: the arrangement of the experimental leaping task. During adaptation, an inclined ladder (not shown) led from the bottom left-hand corner of the cage to the target platform, allowing the subjects to locate the source of apple juice reward. During training, the 25.4 cm rigid take-off platform (illustrated) could be replaced by longer ones (62.9 or 41.9 cm) to make the task easier. The broken rectangle shows the approximate area recorded on film. **b:** trajectories of the three major hindlimb joints during a single leap, constructed by connecting the joint positions in successive frames. **c:** the knee joint trajectories of the first 4 leaps of a single session are shown superimposed (solid lines). The mean trajectory (broken line) was computed from all leaps in the session by the method described in the text.

Procedures

At about three months (84 days) of age, each subject began adaptation to the apparatus by being placed in it for 15 min daily and allowed to explore freely. When the subject showed that it was accustomed to the cage by moving about in a relaxed manner and drinking apple juice regularly (after 10-38 days) the training period began. Each subject, was initially required to leap from a long (62.9 cm) take-off platform that was replaced by successively shorter ones until it would leap repeatedly and without hesitation from the test platform (25.4 cm). Training required from 4 to 49 days and was facilitated by 6 h of water deprivation before each day's session.

Each animal was tested as soon as it completed the training period. Prior to testing, a small area over each limb joint on one side of the animal's body was shaved, the joint center determined by palpation and marked on the skin with indelible ink to facilitate the determination of joint positions during the data processing. On the first day of testing the subject was filmed leaping from the rigid take-off platform (test session R); 8-12 leaps were filmed. On three subsequent days the rigid take-off platform was replaced by the elastic one and 8-12 leaps filmed on each day (test sessions E1, E2 and E3). Some subjects that became uncooperative and refused to leap on one or more days were filmed as often as they would leap on each day.

Data collection and analysis

Leaps were recorded on 16 mm black and white reversal film (Kodak 4X) at 64 fps with a Bolex H- 16 movie camera using an 18 mm, f 2.5 wide angle lens. Ambient lighting provided adequate illumination. The camera was mounted on a tripod 1,8 m in front of the cage, with the film plane parallel to and at the same height as that of the leap. No attempt was made to track the animal during filming; the camera remained stationary and was triggered manually at the onset of each leap. The approximate area recorded on film is indicated by the broken rectangle in Fig. 1a. The films were analyzed by means of a Grafpen digitizer, consisting of a square glass plate with two sound sensors placed along orthogonal sides. A stylus locates points on the plate by emitting a click that is detected by the sensors. The rectangular coordinates of the point touched are read out of the digitizer with 10-bit accuracy (one part in 1024), corresponding to an accuracy of ± 0.12 cm in the space of the leaping task. Using a Bell and Howell motion projector, the films were rear-projected, one frame at a time, on to the digitizer plate. On each frame the coordinates of the 7 major limb joints (shoulder, elbow, wrist, hip, knee, ankle and foot) and the finger- and toe-tip on the side of the body facing the camera were recorded. The coordinates of a fixed point in the back-ground were used to register data from successive frames. The data were read out of the digitizer by an Imsai 8080 microprocessor and stored on magnetic disk for subsequent analysis.

RESULTS

Two kinematic aspects of performance will be described : the trajectories of the major limb joints during the leap and the angular movements of those joints. Limb joint trajectories specify a relationship between the animal and the task situation and determine its posture and position during the leap and on landing. The trajectories cannot, however, be specified directly by the leaping animal but must result from an interaction among muscle forces, the inertia of limb segments and the substrate properties. Angular movements of joints can be specified more directly, but to attain the required result (a suitable trajectory) the specifications must be tuned to take account of the reactive forces with which they will interact. Effective tuning will appear as variation in joint angular movements to obtain relatively invariant trajectories when leaping performance under rigid and elastic conditions is compared. The analysis to be presented focuses on the kinematics of hindlimb movements since these, unlike the forelimb movements, were made almost entirely in the plane of the camera.

The general form of the leap

Different individuals employed different leaping styles but some characteristics were common to all. The subject crouched on the end of the take-off platform, looking upwards toward the target shelf. After a brief interval, the subject leapt upwards and out-wards; the great majority of leaps were symmetrical (both hindfeet left the platform together). As the hindlimbs extended, the forelimbs were swung forward and upward, so that the subject left the platform in a fully extended position, after which both forelimbs and hindlimbs were flexed. In landing, the subject grasped the target shelf with its hands, striking either the shelf or the wall below the shelf with its feet. It then scrambled on to the shelf to obtain a reward. Although individual differences were not systematically investigated in this study, they appeared to involve primarily the position of the feet when the subject landed. With one exception (see below), each subject was remarkably consistent in its overall style of leaping throughout the experiment. The angular movements of the hindlimb joints during the take-off thrust were similar to those described in the Cat^{22,23} and the vervet monkey²¹. Extension of the hip was most rapid at the start of the thrust and slowed toward the point of take-off, whereas knee extension began slowly and increased towards take-off (see Fig. 3).

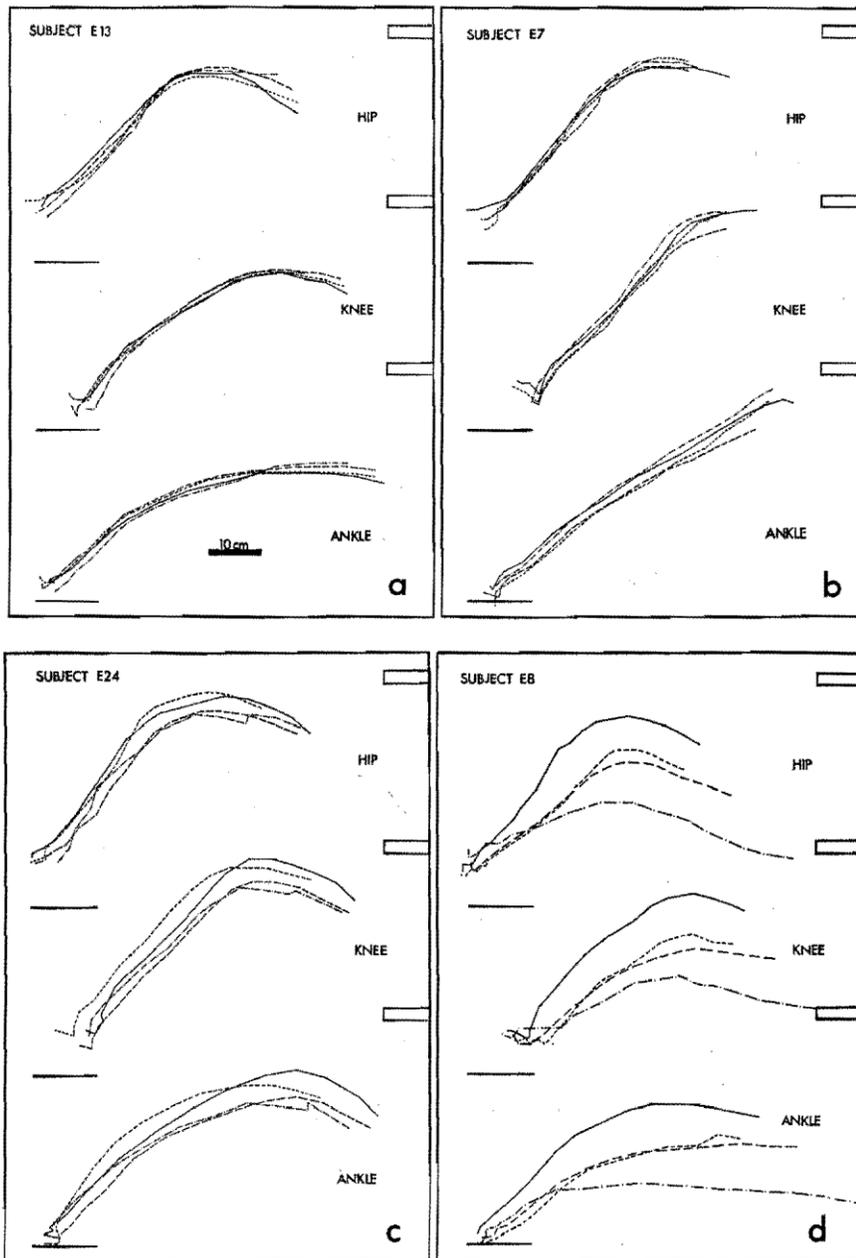


Fig. 2. The mean trajectories of the hip, knee and ankle joints from all 4 sessions are shown superimposed for each of four subjects. a-c: session mean trajectories of three subjects representative of those with invariant trajectories across sessions. d: mean trajectories of the one subject that showed great inter-session variability. Solid lines are means of rigid session (R). Broken lines are means of elastic sessions: -----, E1; - - - - - , E2; - · - · - · , E3. Scale is shown in a.

Mean limb-joint trajectories

In order to determine the effect of substrate elasticity on the trajectories of the major hindlimb joints (hip, knee and ankle), a mean trajectory was computed for each joint of each subject in each of the 4 testing sessions: the rigid session (R) and the three elastic sessions (E1, E2 and E3). Fig. 1b shows the trajectories of these three joints during a single leap. In Fig. 1c, the trajectories of the knee joint during the first 4 leaps of one session are superimposed (solid lines). The mean trajectory (dashed line) was calculated as follows. All of the leaps of a single session were registered with respect to the take-off frame (that on which the foot first left the support). Mean X and Y coordinates were computed for each of the 10 frames preceding take-off, for the take-off frame and for the 10 frames following take-off. The mean coordinates were then used to construct a mean trajectory.

Sixteen of the 17 subjects exhibited very similar joint trajectories, whether leaping from the rigid or the elastic substrate. Results from three representative subjects are shown in Fig. 2a, b and c. Only one subject (E8, Fig.

2d) displayed any great variation in its trajectories and indeed employed widely different styles of leaping on different occasions.

Mean angle-angle diagrams

In order to examine the behavior of the hindlimb system in an integrated fashion, the joint angle data were plotted as angle-angle diagrams^{3,12}, which show the relationship between two joint angles throughout an action and allow the change in this relationship when the animal performs under different conditions to be easily compared.

Mean angle-angle (hip-knee) diagrams for each session of each subject were computed by the technique previously described. Fig. 3 shows the diagrams for the three subjects whose trajectories are shown in Fig. 2a-c. One way in which variation in angular movement might appear, as tuning in regard to substrate elasticity, is in the relative rankings of the invariance of the trajectories and of the angle-angle diagrams.

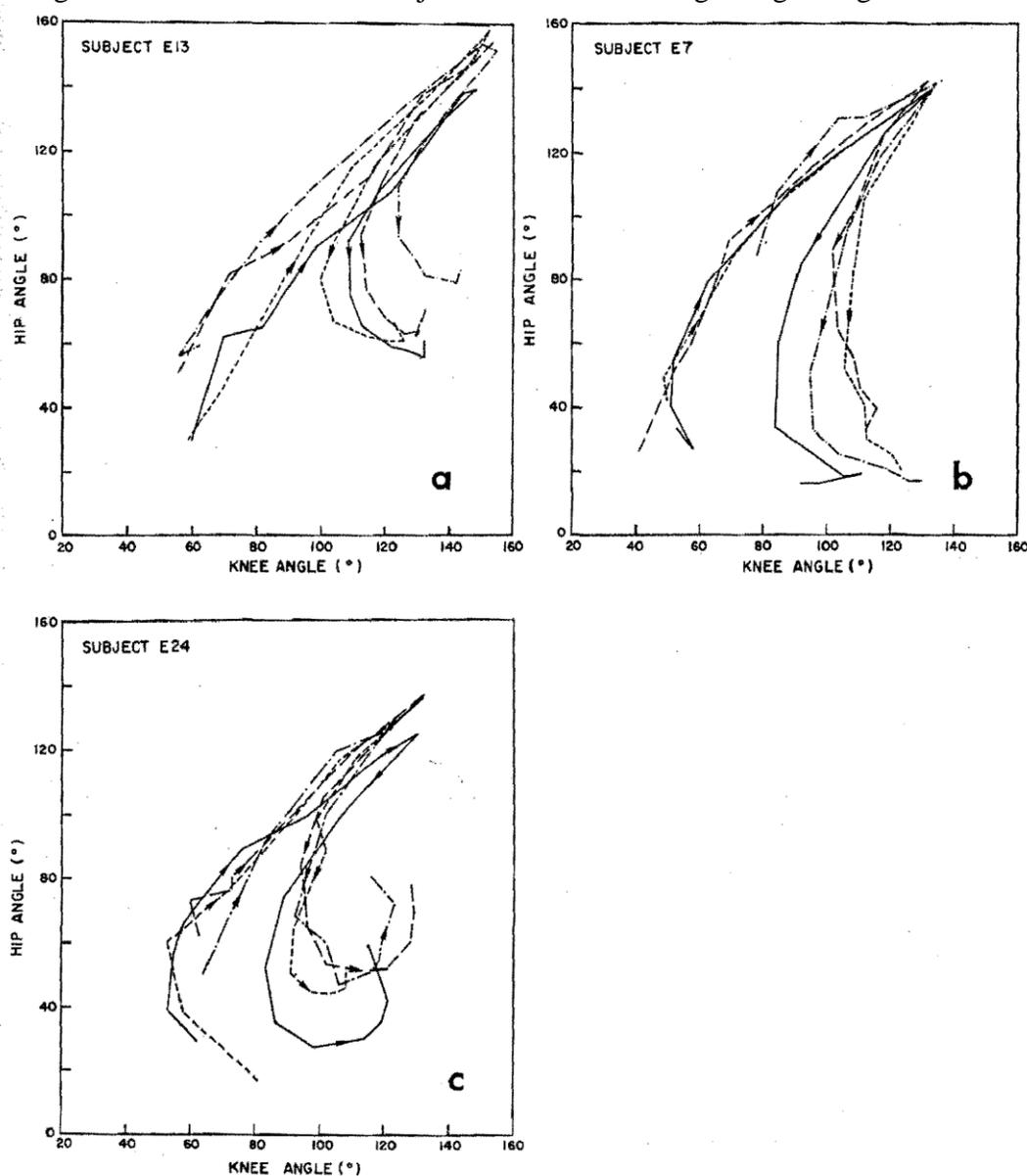


Fig. 3. Mean angle-angle (hip-knee) diagrams from all 4 sessions for the three subjects whose mean trajectories are shown in Fig. 2a-c. In each diagram, the leap originates (before take-off) at the lower left (approximately hip 40°, knee 60°). The limb extends to the take-off (the 'point' of each diagram at upper right) and then flexes after take-off, shown by the descending branch of each diagram towards the lower right. The up-curving 'tail' of the flexion phase in a and c is typical of subjects whose feet struck the wall below the shelf; the more symmetrical diagram in b is typical of those whose feet struck the target shelf itself. The overall similarity in leaping style maintained by each subject is readily apparent. Other conventions as in Fig. 2.

Subjects whose trajectories were most invariant across sessions might be expected to show the least invariance (most compensatory variation) in angle-angle diagrams.

To investigate this question, the mean limb joint trajectory plots and the neat angle-angle diagrams for all subjects were ranked, by the author and by three independent judges, in order of their coherence across sessions. The Kendall coefficient of concordance, W , was used to measure agreement between judges. For ranking, of the trajectories (hip, knee and ankle together), $W = 0.972$; for the angle-angle diagrams, $W = 0.806$. The correlation between the two mean rankings is 0.418 (Spearman rank correlation coefficient) which is not significantly different from zero [$t(15) = 175, 0.2 > p > 0.1$].

Comparison of matched pairs of single leaps

Although from the preceding analysis it appears that tuning is not being effected by changing the patterns of angular joint movement, there are several alternative explanations for this non-significant result. In particular, if an animal adopts slightly different compensatory strategies on different occasions, or if the time-sampling, imposed by filming the leap does not sample successive leaps at precisely the same stages of their execution, then the procedure of averaging across frames of film may tend to obscure or distort the evidence for compensatory variation in angular movement. This difficulty may be overcome by comparing individual leaps, rather than session means.

From the data for each subject, pairs of leaps were selected in which one leap was from the elastic and one from the rigid substrate and in which the joint trajectories of the two leaps were closely similar. If tuning is being effected by varying joint angle movements, then the angle-angle diagrams for such matched pairs should differ. In order to reduce the search of some 3300 possible pairs of leaps to one of manageable proportions, only the hip trajectories of the leaps were compared. Preliminary analysis revealed that the hip trajectory is a reliable index of overall hindlimb performance at this level of description: If two leaps have similar hip trajectories, their knee and ankle trajectories will also be similar.

Matched pairs of leaps representative of the closest trajectory matches found are shown in Fig. 4. Inspection of the hip trajectories of each pair (top diagram in each case) reveals that, although not identical, the pairs selected are extremely close. In view of the absence of any gross physical constraints on the subjects' performance, the closeness of the matches is indeed impressive. The first 6 pairs of leaps (Fig. 4a-f) show one apparent compensatory strategy, in which the flexion phase of the angle-angle diagram, representing the portion of the leap after take-off (see legend to Fig. 3) is shifted up and left (heavy arrow) in the leap from the elastic substrate. The two flexion phases parallel each other for most of their duration so the joint angle changes that arc.. responsible for this shift must occur before or very shortly after take-off. There are a number of changes that could have the observed effect and among which the present data cannot discriminate. In general, these all involve decreasing the ratio rate-of-hip-flexion/rate-of-knee-flexion, just after take-off. The last two pairs (Fig. 4g and h) illustrate what seems to be an alternative compensatory strategy in which the flexion phase of the angle-angle diagram is shifted down and right (heavy arrow) in the leap from the elastic substrate. To achieve the observed effect, the ratio of hip/knee flexion must be increased just after take-off.

The data presented in Fig. 4 support the hypothesis that invariance of hindlimb joint trajectories under environmental variability is achieved by variation in joint angular movement. However, the trajectories in these pairs of leaps, though very similar, are not identical. It is possible to argue that the differences between the angle-angle diagrams are just sufficient to account for the small differences that exist between trajectories and that no compensation is taking place. This criticism may be answered by comparing matched pairs in which both leaps are from the same substrate. For such pairs the angle-angle diagrams should be more closely similar than for pairs in which the two leaps are from different substrates. Since the data already presented suggest that more than one compensatory strategy may be available, so that even very similar leaps from the elastic substrate might have quite different angle-angle diagrams, pairs of leaps with similar trajectories were selected from the rigid session for each animal.

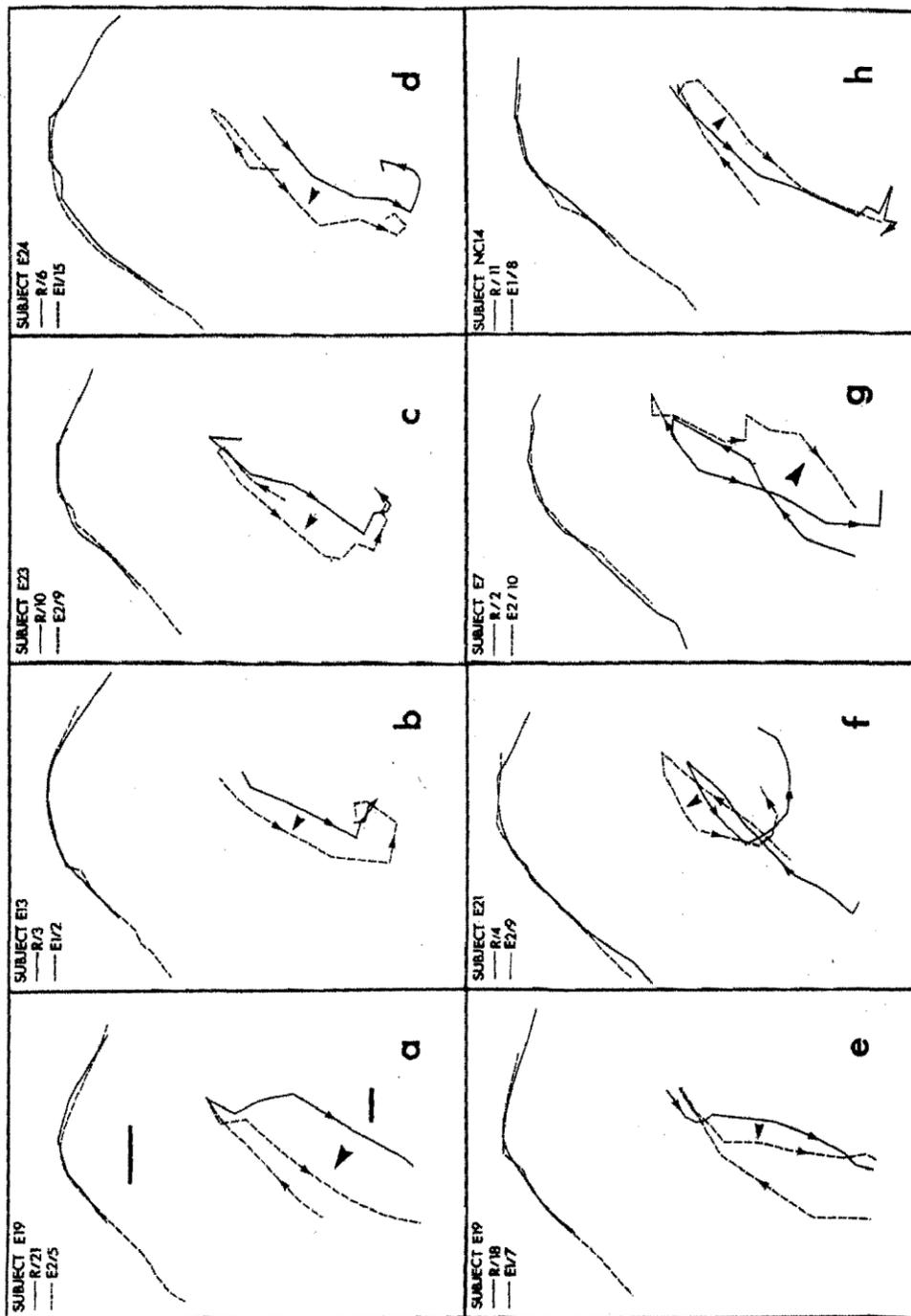


Fig. 4. Matched pairs of leaps, one from the rigid substrate (solid lines), one from the elastic substrate (broken lines). In each panel, the upper pair of lines are hip trajectories, the lower pair are angle-angle (hip-knee) diagrams. Scale is shown in a: upper pair, bar = 10 cm; lower pair, bar = 10°. See text for discussion.

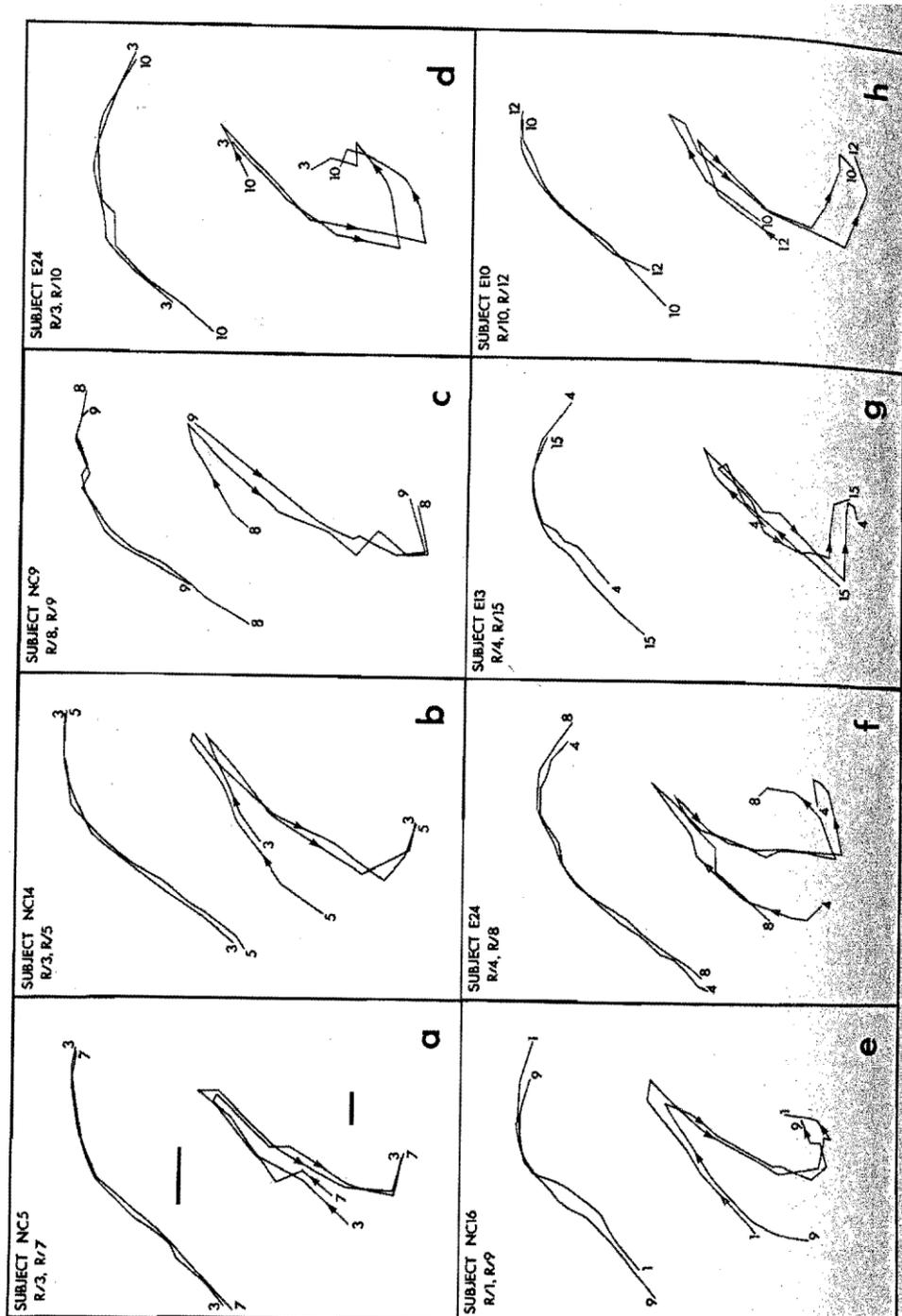


Fig. 5. Matched pairs of leaps both from the rigid substrate. Scale and conventions as in Fig. 4. See text for discussion.

Eight representative matched pairs from the rigid substrate are shown in Fig. 5. Inspection of this figure, and comparison with Fig. 4, shows quite clearly that the angle-angle diagrams of the pairs from the rigid substrate are much more similar than are those of pairs from the rigid and elastic substrates. Fig. 5h is a partial exception, since the two diagrams diverge markedly toward the end of the leap, but this may reflect compensation for an earlier divergence that can be observed just before take-off.

In searching the data base for these matched pairs of leaps, a very few matched triplets were discovered. These comprise three leaps, two from the rigid and one from the elastic substrate, all with very similar trajectories. In these cases, two comparisons are possible, one between the angle-angle diagrams of the two rigid leaps and one

between the diagrams of these two and that of the elastic leap. Those of the rigid leaps should be closely similar to each other and different from that of the elastic leap. Three such triplets are shown in Fig. 6 and it can be clearly seen that they confirm the prediction.

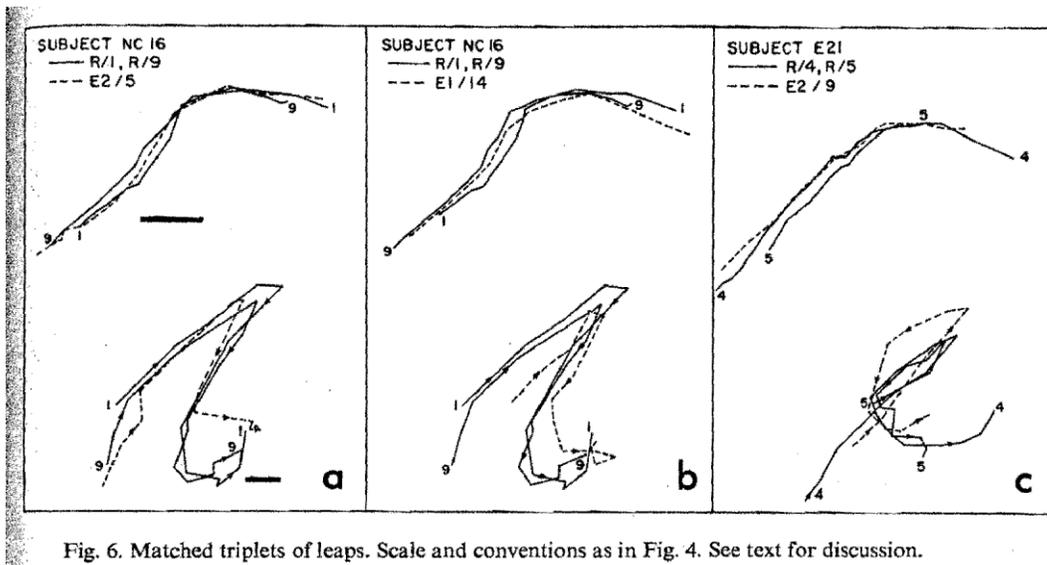


Fig. 6. Matched triplets of leaps. Scale and conventions as in Fig. 4. See text for discussion.

DISCUSSION

The behavior of the hindlimb subsystem of a leaping primate, as described in 11) report, shows many of the characteristics of a system proposed by Weiss¹⁹: Pragmatically defined, a system is a rather circumscribed complex of relatively bounded phenomena, which, within those bounds, retains a *relatively stationary pattern of structure in space or of sequential configuration in time in spite of a high degree of variability in the details of distribution and inter-relations among its constituent units of lower order*. Not only does the system maintain its configuration and integral operation in an essentially constant environment, but *it responds to alterations in the environment by an adaptive redirection of its componental processes in such a manner as to counter the external change in the direction of optimum preservation of its systemic integrity'* (p. 11-12: emphasis added).

This study has revealed some, though doubtless not all, of the 'relatively stationary pattern' of the subsystem's behavior that is maintained despite a change in the elasticity of the take-off support. It is of some interest that the trajectories of the major hindlimb joints should remain invariant under such a change, rather than only a much cruder specification of performance (that corresponding to a successful leap, for example). That such invariance is not imposed on the leaping animal by the geometric constraints of the task is clearly shown by the performance of one subject (E8..Fig. 2d) who succeeded in reaching the target on each leap with a wide variety of leaping styles.

Similarly, the data indicate at least some of the 'adaptive redirection of componental processes' that permit the invariance of the trajectories to be maintained. Other aspects of the subjects' performance that were not clearly revealed by this analysis, such as the forelimb movements and its behavior in the preparatory phase before take-off, may also contribute to the kinematic tuning of the leap.

Why should the subjects' behavior be so closely constrained at the relatively line-grain level of limb joint trajectories, when this is not apparently a mechanical requirement of success in the task? One answer undoubtedly lies in the principle, based on Bernstein's² early insights, that during locomotion, the maximum number of kinematic variables are kept independent of external conditions^{1,14}. The advantages of a style of motor control that incorporates such a principle have been widely discussed in the literature^{4,15,17,18}. A second reason for invariance in joint trajectories may be discerned in the demands placed on a leaping animal by the nature of the task. When an animal leaps at a target, it is not enough for it to simply adjust the magnitude and direction of forces applied during take-off. Although such adjustments ensure that the animal's center of mass

reaches the vicinity of the target, and help to reduce energy expenditure. they cannot guarantee that the animal will land safely and in a stable position for sub-sequent action. On reaching the target, the animal must grasp it securely and regulate the stiffnesses of its limb muscles so as to absorb the force of impact. This requires correct positioning of the limbs prior to landing, followed by a presumably complex series of changes in muscle activity that arrest the animal's forward motion and leave it in a stable position on the new support.

On the basis of these considerations, I conjecture that the invariance observed in joint trajectories reflects an optimally efficient (in some sense) solution to the problem of preparing for a safe landing at the target. (Since each animal produced a different set of trajectories, the optimum prescription depends presumably on individual capabilities as well as on the demands of the leaping task.) In order to permit this solution to be implemented when leaping from both rigid and elastic supports, fine tuning of the relationships among the joint angles is required. Previous biomechanical analyses of primate leaping^{11,20,21} have focused on the initial take-off phase of the leap, since it is here that the trajectory of the center of mass is determined and where, presumably, the greatest minimization of energy expenditure can be effected, This approach, however, neglects the overall ecological context of the task, which includes not only a geometric specification of the environment, but also a specification in terms of the physical objects with which the animal must interact both at take-off and on landing.

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