LIMB MECHANICS AS A FUNCTION OF SPEED AND GAIT:

A STUDY OF FUNCTIONAL STRAINS IN THE RADIUS AND TIBIA OF HORSE AND DOG

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SUMMARY

Rosette strain gauges were attached to the midshaft of the radius and tibia of two horses and two dogs, which ran on a treadmill through their entire range of speed and gait. The relative magnitudes of the principal strains on the opposite cortices of each bone remained constant through the stance phase of the stride, and their orientation varied by a maximum of only 14° through the entire speed range. The maximum strain rate increased linearly with speed, but the peak strain magnitude was also dependent upon the gait used, increasing incrementally by up to 59% at the transition from walk to trot, and dropping by 42% from a trot to a canter. Force transducers attached to the shoes of one horse indicated similar changes in ground load.

The peak strains induced during vigorous activity are remarkably uniform in a wide range of animals. This suggests that the skeleton is scaled to provide constant safety margins between peak functional strains and those at which yield and ultimate failure occur.

INTRODUCTION

The primary role of the appendicular skeleton of terrestrial vertebrates is to provide rigid structures to withstand and transmit the loads involved in locomotion. The immediate consequence of these loads is to induce strains within the bone tissue. Since these strains can be recorded with strain gauges, suitably instrumented bones can be used as internal force transducers sensitive to the manner and magnitude of limb loading. However, since bone is a tissue which adjusts its architecture in relation to its functional strain environment, these strains also represent the structural objective of this adaptive process. This objective is assumed to be an appropriate compromise between the form, mass, strength, and need for tissue economy, within the appendicular skeleton.

In the study reported here, changes in bone strain were recorded *in vivo* from rosette strain gauges attached to the radius and tibia of horses and dogs. Recordings of bone strain were made during the complete range of these animals' gaits and speed while

running on a treadmill. These data are considered in relation to the mechanics locomotion, and the functional significance of bone form.

Bone strain, locomotor mechanics and gait change

Cursorial quadrupeds increase their speed by using different gaits in which the movements of the trunk, and the relative timing of the support and swing phases of the limbs, are altered. Although the sequence of movements involved in these gaits has been described in detail (Muybridge, 1957; Gambaryan, 1974; Hildebrand, 1959, 1965, 1976; Gray, 1968), the specific mechanical and metabolic benefits of each gait remain controversial. Many previous studies have centred on measuring total oxygen consumption (Taylor, Schmidt-Nielsen & Raab, 1970; Taylor & Rowntree, 1973; Fedak & Seeherman, 1979; Hoyt & Taylor, 1981), which gives little indication of the distribution of muscle activity within the body, on qualitative EMG recording (Tokuriki, 1973a, 1973b, 1974; Taylor, 1978; Goslow *et al.* 1981), which provides information relevant to the electrical activity of the muscle but not the amount of tension it develops; on cinematographic analysis of the moments and forces acting about joints (Alexander, Langman & Jayes, 1977; Alexander, Jayes &⁻Ker, 1980; Alexander & Goldspink, 1977), which relies heavily on theoretical assumptions; and on force plate analyses (Pratt, 1976; Heglund, 1979; Cavagna, Heglund & Taylor, 1977; Alexander & Jayes, 1978), which are confined to whole animal or single limb contact forces. Data revealed by each of these methods alone is limited and can disguise or misrepresent the mechanical and metabolic benefits of gait change. To investigate these benefits directly it is necessary to know at all times each muscle's energy consumption, or its tension and length, either of which would be difficult to achieve. However, one consequence of tension is that it loads the bones to which the muscles are anchored. The normal pattern of limb bone deformation therefore results from (and can be used as a measure of changes in) the internal forces caused by the muscles as they react with the externally imposed forces originating from the animal's contact with the ground. Any alterations in the absolute or relative magnitude of these forces should be detectable in terms of the size and pattern of strains engendered within the limb bones.

In the experiments reported here, the bone strain data, which were obtained from the radius and tibia of horses and dogs over these animals' complete speed range on a treadmill, are examined in relation to the load distributions which occur in the limbs during each gait, and at each gait transition.

Bone strain and the functional significance of bone form

Since the primary responsibility of the appendicular skeleton must be to support the animal and not break or suffer high levels of damage even under the extremes of normal loading, there are obvious advantages in each bone being as massive as possible. However, since bone tissue is also metabolically expensive, both to produce and, subsequently, to transport, there are conflicting advantages between bone structure being massive and so creating high safety factors to failure, and bones containing less tissue and therefore economical to transport, but having a higher risk of fracture.

The suitability of each bone for its structural role results from two major influences

■he overall shape and anatomical relationship of the bone are genetically determined and will develop in the absence of functional stimuli (Lanyon, 1980). However, its final form, mass, and detailed architecture are influenced by mechanical activity and are therefore a unique achievement for each animal. The features most greatly influenced by mechanical function are those with obvious structural significance, i.e. the presence and size of crests and tuberosities, the thickness of cortices, the amount and orientation of cancellous tissue, and the degree of curvature of long bone shafts.

Although the nature of the functional influences responsible for the production and maintenance of normal bone structure are not understood, the evidence suggests that they are derived from some aspect of the mechanical circumstances which the bone encounters (Wolff, 1870; Roux, 1895; Koch, 1917; Goodship, Lanyon & MacFie, 1979; Rubin & Lanyon, 1981; Hayes & Snyder, 1981; Lanyon *et al.* 1982). For the bones of cursorial quadrupeds, the predominant functional stimulus will almost certainly be provided by locomotion, and the structural objective of bone architecture in the limbs will therefore be related to the mechanical demands which this activity imposes. The strain data obtained from the experiments described here will be considered in relation to this structure–function relationship.

MATERIALS AND METHODS

Limb terminology during gaits

At any gait, each individual limb performs essentially the same action, slowing or increasing its relative motion according to the requirements of speed (Tokuriki, 1973*a*, 1973*b*, 1974). The difference between gaits depends primarily on the sequence in which the limbs are placed on the ground. During the walk the principal support phases occur between either diagonally opposite, or ipsilateral, fore and hind limbs. Between these two main support phases, there are transient phases when three, or even four, legs may be touching the ground, but at no time are there less than two feet with ground contact. As speed at the walk increases, the limbs move faster until the animal changes from a walk to a trot. This gait consists of alternating support by diagonally opposite fore and hind limbs moving in phase with one another. Each diagonal support phase is separated by an aerial (floating) phase.

During the canter, the footfall pattern is changed so that the legs of one diagonally opposite pair move out of phase with each other while those of the other pair remain 'in-phase'. A single stride of the canter begins with the lead ('out-of-phase') forelimb, which throws the animal into the aerial phase. The animal lands on the diagonally opposite (out-of-phase) hind limb. The contralateral hind limb and its diagonally opposite (in-phase) forelimb make ground contact simultaneously in the same way that they did in the trot. As the stance phase of these diagonally opposite in-phase limbs ends, the out-of-phase lead forelimb is placed to the ground and provides the animal's sole support before it is propelled into the aerial phase of the next stride.

As the animal's speed increases it will change gait from a canter to a transverse gallop. The difference in limb sequencing between these two gaits specifically concerns the relationship between the in-phase fore and hind limb which at the trot and ■■nter had been working synchronously. During a transverse gallop the previously

in-phase hind leg makes contact before the previously in-phase foreleg. A total
four independent limb contacts are thus made with the ground, and in some animals
the relationship of the previously synchronous (in-phase) pair of limbs becomes so
extended that there is a second aerial phase between them. Although other animals
use a variety of other gaits (e.g. rotary gallop, pace, bound, etc.), the four footfall
patterns described above were the gaits normally exhibited by the animals used in
these experiments.

Principles of strain measurement

When a structure is deformed, even in a very simple manner, the strain produced
within it is complex. If a solid cube of isotropic material is compressed between two
opposing faces, it will compress in that plane and stretch in the plane perpendicular
to it. The ratio of the change in any dimension to the original dimension is the strain.
At any point on the structure's surface there will be a principal compressive strain
and, at right angles to it, a principal tensile strain. In these principal strain directions
there is no shear strain. In any direction other than the principal directions there is a
component of shear which varies in magnitude, but is maximum at 45° to the direc-
tions of the principal tensile and compressive strains. If the loading pattern of the
structure is complex, and the material is anisotropic, the relative magnitude of the
principal strains will be affected as will be their orientation with respect to the direc-
tion of loading. Despite this, the direction of the principal tensile and compressive
strains will always remain at right angles to each other.

By attaching strain gauges to a structure's surface, the changes in dimension of
that surface can be measured. The type of strain gauge used in this and previous
in vivo studies on bone (Lanyon, 1973) is composed of an electrical conductor made
of metal foil arranged as a grid mounted on a thin supporting epoxy–resin base. The
base is glued to the bone surface so that the gauge element deforms with the structure's
surface. The resulting change in the conductor's dimensions alters its electrical
resistance and this change can be recorded. A single strain-sensitive element can only
respond to changes in strain from the surface of the structure to which it is attached,
and it is maximally sensitive to strains in the directions in which its grid is aligned.
This severe limitation of single element gauges makes it necessary to use rosette
strain gauges which are composed of three completely independent strain-sensitive
grids. These grids are stacked over the same area and are aligned at zero, 45 and 90°
relative to one another. Using the independent values of strain from these three
directions, the changes in the size and direction of the principal strains can be com-
puted using standard formulae (Dally & Riley, 1978). The alignment of the rosette
gauge relative to the bone's princpal strain directions (or the bone's geometry) is
unnecessary since the principal directions are calculated and corrected to the bone's
long axis using radiographs or the isolated bone post-mortem.

Calculation of bone loads

Each strain gauge provides data relevant to the small area of bone surface to which
it is adherent. By using rosette data from two sites opposite one another on the bone's
circumference, the loading situation of the bone can be approximated (Lanyon *et*

1981 *b*). The three components of load – axial force, bending moment, and torsion – can be calculated from the strains by using the natural and sectional properties of the bone. In this study, the primary loading conditions of the bone were assumed to consist of axial force and bending moment. To determine the magnitude of these loads, the principal strains were first converted through a coordinated transformation matrix into strains in the longitudinal and transverse directions. From the relationships of these, the proportion of the total strain due to bending or axial compression can be calculated. Through a reduced stress matrix, the isolated longitudinal stresses necessary to produce these strains can also be determined (Carter, 1978).

The cross-sectional shape, area, and second moment of area of the horse bones were assessed from anteroposterior and lateral radiographs of the limbs. The dogs were killed after the experiment, and the bone dimensions were measured directly. With this bone geometry, bending moments in one plane and loads due to axial force can be calculated (Crandall, Dahl & Lardner, 1977). The axial force can be transformed to the weight-referenced gravitational force, and stresses due to axial force or bending moment can also be determined. A value of 18·2 GPa is used for the longitudinal elastic modulus, 12·2 GPa for the transverse modulus, and 0·46 for the Poisson's ratio of longitudinal stress/transverse strain (Lanyon, Magee & Baggot, 1979; Schryver, 1978; Carter, 1978).

Experimental procedure

Bone strain was recorded from rosette strain gauges, attached to the cranial and caudal surfaces of the right radial and tibial midshafts of two adult dogs (29 and 32 kg) and two adult ponies (147 and 138 kg), during locomotion on a treadmill. The gauges were attached under general halothane anaesthesia using a single medial incision over the bone's diaphysis and reflexion of limb musculature, exposing the cranial and caudal gauge sites without any muscle disruption. The bone surface was prepared by removing a small (10 mm²) area of the bone's periosteum, drying the exposed surface, swabbing it with methyl-ethyl-ketone, and then gluing the gauge to the surface with isobutyl 2-cyanoacrylate monomer. The lead wires from the gauge passed through a small epoxy resin flange which was anchored to the bone's surface some 30 mm from the gauges by a 1·5 mm diam. stainless steel screw inserted into a tapped hole in the cortex. The leads were passed subcutaneously and emerged through the skin at a remote incision. The wound was closed, and the lead ends then connected to a series of strain gauge bridge amplifiers via a standard six pin plug connector. The orientation and position of the gauges were determined from cranio–caudal and lateral radiographs.

All the animals used were in good physical condition and had previously been trained to perform on the treadmill over their complete range of speed. Post-operative soreness had subsided sufficiently by 2 days after gauge implantation such that the animals were willing to run on the treadmill up to their previously determined maximum speeds without discernible lameness. While the dog radius and tibia were instrumented in separate operations, the ponies' tibias and radii were instrumented on the same occasion, allowing data from all 12 gauge elements to be recorded onto magnetic tape simultaneously. On at least one occasion, each animal's strain recordings were synchronized to cine film taken at 200 f.p.s.
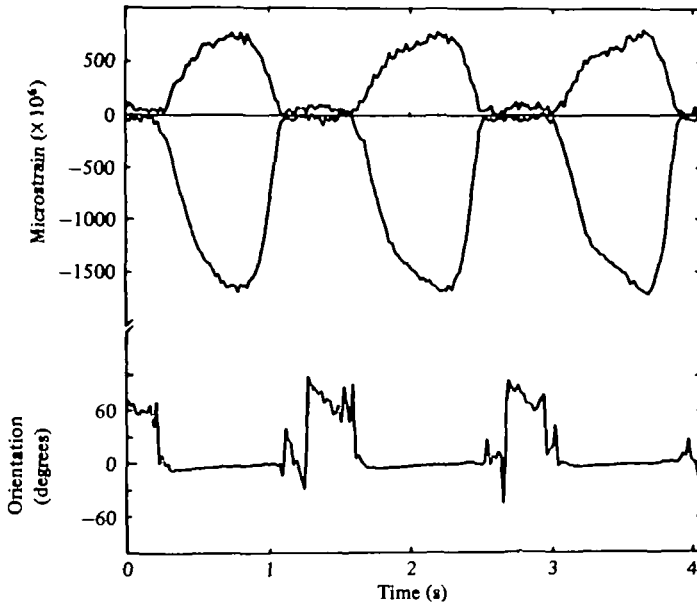
Fig. 1. Peak principal tensile (upper trace) and compressive (lower trace) strain on the caudal surface of the radius of dog B, together with the orientation of the principal compressive strain in relation to the long axis of the bone, taken while the animal walked at 4·2 kph. While both the tensile and compressive strain magnitudes change quickly during the stance phase of the limb, the orientation of the principal strains remains remarkably constant.

Analysis of bone strain data

Calculations of the magnitude and orientation of principal strains were made from the 'raw' (3-element) strain data of at least six consecutive strides. The analogue strain gauge data from the F.M. tape was digitized through an A–D convertor and entered into a microprocessor. From these data, principal strain calculations were made at each speed at 5 ms intervals, and the magnitudes of principal tensile strain (ϵ_t), compressive strain (ϵ_c), and their respective directions relative to the long axis of the bone ($\theta\epsilon_t$ and $\theta\epsilon_c$) were plotted. The location of zero strain from each channel of the changing strain gauge signal was adjusted to be zero volts by applying a suitable d.c. voltage off-set to the tape recorder output signal. Positions of zero strain from the gauge traces were taken to be the strain levels during the swing phase of the limb when the three gauges of the rosette showed little or no change in strain. These zero strain levels are identical to those occurring when the leg is lifted from the ground, or when the animals were anaesthetized and lying on their sides.

RESULTS

Changes in strain and strain orientation during a stride

The processed principal strain data analysed from the caudal surface of the radius of dog B while walking on the treadmill are indicated in Fig. 1. The features of these strain cycles were common to all gauges. During the swing phase, there is little or
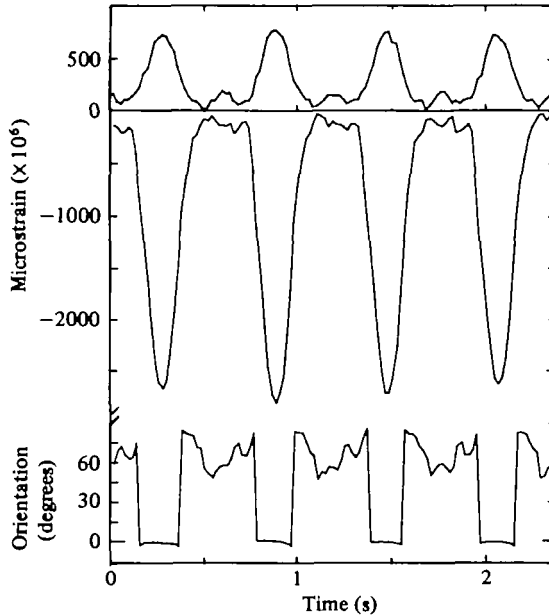
Fig. 2. Similar data to that shown in Fig. 1, from the caudal radius of horse A taken while trotting at 8·6 kph. The constancy of strain orientation is again maintained throughout the stance phase of the limb, and is similar to that at different gaits.

change in raw strain in any element of the gauges, and this flat portion in the gauge traces is taken to represent zero strain (Fig. 1). As the limb is placed to the ground and the bone is loaded, there is a sharp increase in both the principal tensile (ϵ_t) and principal compressive (ϵ_c) strains, which reach a peak approximately midway through the stance phase. Both components of principal strain then quickly return to zero as the leg again enters the swing phase. The orientation of the larger principal strain ($\theta\epsilon_c$) relative to the long axis of the bone is also shown. The direction of the smaller principal strain ($\theta\epsilon_t$) is always 90° removed.

In all the bones instrumented, the principal compressive strain was the larger principal strain on the caudal surface and was closely aligned to the bone's longitudinal axis. On the cranial surface the principal tensile strain was larger in magnitude and oriented more closely to the bones' longitudinal axis than the transverse compressive strain. In all cases, the peak principal compressive strain ($P\epsilon_c$) on the caudal surface was larger than the peak principal tensile strain ($P\epsilon_t$) on the cranial surface. This strain situation is consistent with the predominant loading mode of these bones, i.e. axial compression with superimposed cranio–caudal bending.

In contrast to the abrupt changes in strain magnitude which occurred throughout the stance phase of the stride, the strain direction remained constant. The change in strain orientation during the loading period was always less than 4° from its orientation at the instant when peak principal strain was developed (Figs. 1, 2).

Changes in strain orientation as a function of speed and gait

Since the strain direction changed so little during the stance period of the limb, its orientation at peak principal strain ($\theta P\epsilon_t$ or $\theta P\epsilon_c$) was considered to be representative
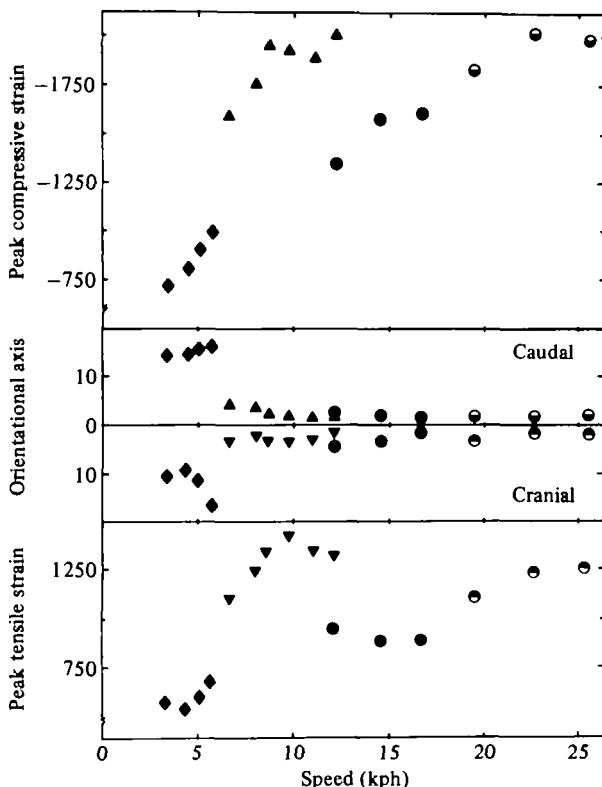
Fig. 3. Speed-related changes in the peak principal compressive strain on the caudal surface, and peak principal tensile strain on the cranial surface, of the tibia of dog A, together with their orientation to the bone's long axis. The peak strain magnitude increases 49 % from a walk (◆) to a trot (▲) at 5·7 kph, but drops 33 % from a trot to a canter (●) at 12·1 kph, when the instrumented hind limb is out-of-phase with its contralateral forelimb. The data points from the three fastest speeds were obtained with the animal galloping (◓), and it appears that the peak strain magnitude plateaus at these higher speeds. The strain orientation on both cortices shifts by 13° at the walk:trot transition, but remains aligned with the bone's long axis throughout the rest of the speed range.

of the strain direction throughout the stride. The largest change in strain orientation throughout the animal's speed range was that recorded from the caudal surface of the tibia of dog A, which changed by 16° (Fig. 3). In this animal, the strain orientation shifted from 10·8 ± (standard deviation) 1·7° proximal lateral to the bone's long axis at a slow walk (2 kph), to 16·3 ± 0·9° at the fastest walk (6 kph). At the same speed, transition to a trot reduced the longitudinal divergence to 3·7 ± 0·6° and steadily shifted toward the bone's long axis as speed increased, until, at the fastest gallop (25 kph), reaching an orientation actually aligned with the bone's longitudinal axis (0·9 ± 0·8°).

The principal strain direction on the caudal cortex of the tibia of horse B was furthest removed from the longitudinal axis of the bone. At a slow walk (3 kph), the angle of the principal compressive strain was 19·4 ± 2·3° (proximal lateral), shifting to 23·8 ± 1·1° at the walk:trot transition. This angle was reduced with increasing speed to 18·4 ± 2·3° at a fast trot, but rose again to 24·4 ± 0·9° during a fast canter.
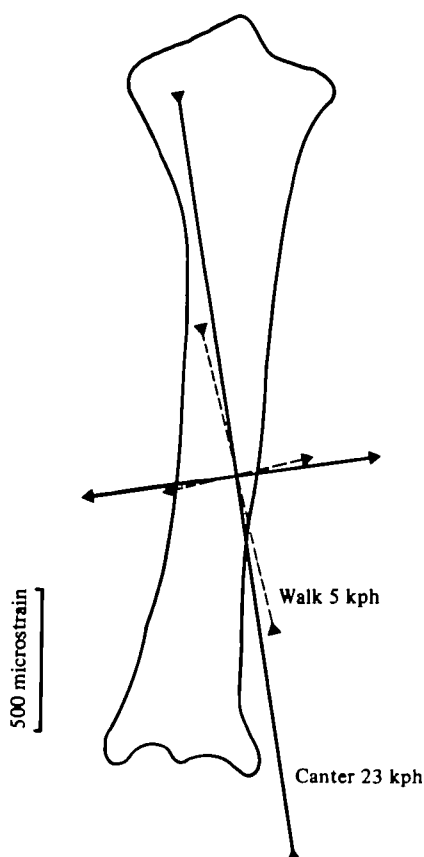
Fig. 4. Tracing from a cranio–caudal radiograph of the tibia of horse B. The size and orientation of the principal tension (◄——►) and compression (►——◄) strains at the gauge site on the caudal aspect are indicated. The increase in size, but relative constancy in orientation of these strains is evident.

The loading orientation of the other experimental bones diverged very little throughout the range of speed, and remained closely aligned with the longitudinal axis. The standard deviation of the variance in orientation produced at any given speed was no greater than ±2·3° for any animal (Fig. 4).

Changes in strain magnitude as a function of speed and gait

The peak strains referred to in the following sections are the larger of the two peak principal tensile or compressive strains on each cortex. In each case, these were also the strains aligned closest to the longitudinal axis of the bone (in tension on the cranial surface and compression caudally). However, the principal strains longitudinally oriented on the concave surface were always higher than those strains on the tensile surface and for this reason, the results will concentrate on these larger compressive strains.

Dog tibia

The peak principal strains of dog A's caudal tibia were compressive and increased from $-702 \pm$ S.D. 35 to -1059 ± 49 microstrain ($\mu\varepsilon$) during walking at speeds ranging from 2·5–5·7 kph (Fig. 3). At the walk:trot transition, strain magnitude increased 49% to $1580 \pm 37 \, \mu\varepsilon$ and increased with increasing speed to $-2006 \pm 63 \, \mu\varepsilon$ at the fastest trotting speed of 12·1 kph. This speed had been noted pre-operatively as the natural gait transition speed. At this speed, while cantering, the dog used a left leg lead, so that the instrumented right tibia was the 'out-of-phase' hindlimb. At the trot:canter transition, the peak principal strain dropped 33% to $-1348 \pm 79 \, \mu\varepsilon$, and then increased linearly with speed to $-2016 \pm 99 \, \mu\varepsilon$ at 22·5 kph, at which time the dog was galloping. At the animal's maximum speed (24·7 kph) the strain had dropped slightly to $-1998 \pm 50 \, \mu\varepsilon$. The peak principal longitudinal strain on the cranial surface of the tibia was tensile, but showed similar changes in magnitude with speed and gait.

Dog radius

The peak principal strain on the caudal surface of dog B's radius increased 19% at the transition from a walk to a trot (-1503 ± 63 to $-1800 \pm 22 \, \mu\varepsilon$ at 4·2 kph) and reached $-2384 \pm 49 \, \mu\varepsilon$ when trotting at the trot:canter transition speed of 11·4 kph. Following transition to a canter at this speed, there was a 13% drop in peak principal strain (to $-2087 \pm 22 \, \mu\varepsilon$) when this leg was the non-lead leg. During the canter, peak principal strain on this in-phase forelimb increased with speed to $-2248 \pm 41 \, \mu\varepsilon$ at the fastest speed of 14·5 kph.

Horse tibia

The peak principal compressive strains on the caudal surface of horse A's tibia ranged from $-939 \pm 36 \, \mu\varepsilon$ at a slow walk (4·1 kph) to $-3146 \pm 65 \, \mu\varepsilon$ at a fast canter (in-phase hind limb). During the walk, the peak principal strains increased with speed in a linear fashion to $-1295 \pm 47 \, \mu\varepsilon$ at 5·3 kph, the predetermined normal walk:trot transition point (Fig. 5). During trotting at this speed, peak strains were increased by 50% to $-1943 \pm 80 \, \mu\varepsilon$, and subsequently rose only slightly through the trotting speed range, reaching $-2395 \pm 93 \, \mu\varepsilon$ at 18·5 kph, which was the fastest trot attained.

Horse A had been trained to extend her gait and to change her lead legs. During trotting at 13·1 kph (4 kph below her normal trot:canter transition speed), the peak principal strain on the tibia was $-2363 \pm 56 \, \mu\varepsilon$. While cantering at the same speed, this dropped 31% to $-1637 \pm 127 \, \mu\varepsilon$ when the instrumented leg was diagonally opposite the lead forelimb (i.e. out-of-phase). The peak principal strains recorded while the tibia remained out of phase rose to $-2725 \pm 53 \, \mu\varepsilon$ at the fastest cantering speed of 25·2 kph. When the trot:canter transition transferred to the opposite lead leg, the instrumented tibia became in-phase whith the non-lead forelimb. The peak strains at 13·7 kph fell only 2% at the transition from $-2425 \pm 94 \, \mu\varepsilon$ during the trot to $-2391 \pm 130 \, \mu\varepsilon$ at the canter. The peak principal strains continued to increase with
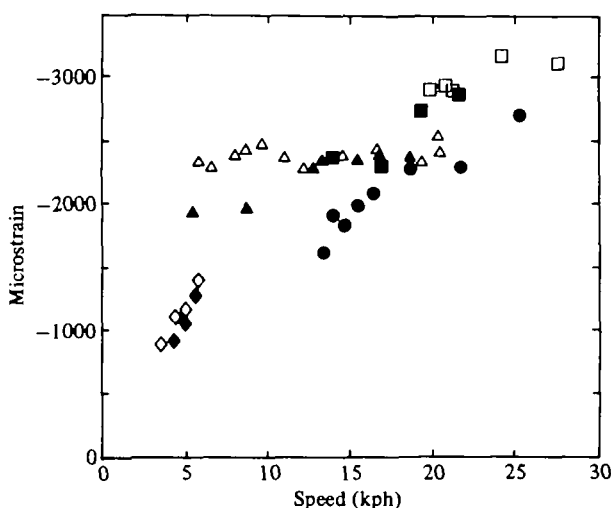
Fig. 5. Peak principal compressive strain from the caudal tibia of horse A (closed symbols) and horse B (open symbols). At 5·3 kph, both animals show a large increase in peak strains with the transition from a walk (◆) to a trot (▲). Strain levels remain fairly constant throughout the trot, despite an increase in speed from 5 to about 20 kph. Horse A was capable of extending each gait both above and below the normal gait transition speed. The data from this animal shows that at, or below, the normal transition speed (17 kph), there was no incremental change in peak strain when the animal changed from a trot to an in-phase canter (■) (the instrumented leg remaining in-phase with its opposite forelimb). However, above this transition speed there was a 10–15 % increase in peak strain when the animal changed from the extended trot to the canter. Horse B showed a similar incremental increase at the canter: extended trot transition. In both animals, peak strain levels appeared to plateau at high speeds. Horse A was trained to change lead legs as well as extend gaits. The lead change during the canter, such that the instrumented hind limb was out-of-phase with the lead forelimb, (●), caused a large decrease in peak strain, identical to that measured in the tibia of dog A (Fig. 3).

speed during the canter when the tibia was in phase, and reached $-3146 \pm 65\,\mu\varepsilon$ at 25·1 kph, which was the highest strain recorded for horse A. The peak principal tensile strain on the cranial surface of the tibia rose in a similar fashion to $+2350 \pm 44\,\mu\varepsilon$.

The strain changes in the tibia of horse B were similar to those in horse A, except for a small discrepancy during trotting at the lower speeds. The compressive strain of horse B's caudal tibia increased 59 % (-1400 ± 33 to $-2345 \pm 163\,\mu\varepsilon$) at the transition from a walk to a trot, and remained around this magnitude throughout the trotting range. Horse B would not change its lead leg, and during the canter the instrumented tibia was always diagonally opposite the non-lead forelimb (in-phase). The peak strain at the transition from a trot to a canter (20·3 kph) rose 14 % from -2570 ± 184 to $-2928 \pm 139\,\mu\varepsilon$. The highest strains recorded from any animal in this experiment were $-3185 \pm 73\,\mu\varepsilon$, recorded from this horse during a canter at 24·1 kph. The peak strain dropped slightly while galloping to $-3134 \pm 92\,\mu\varepsilon$ at the fastest recorded speed of 27·1 kph. The magnitude of all these strains from horse B are similar to those measured from horse A (Fig. 5).
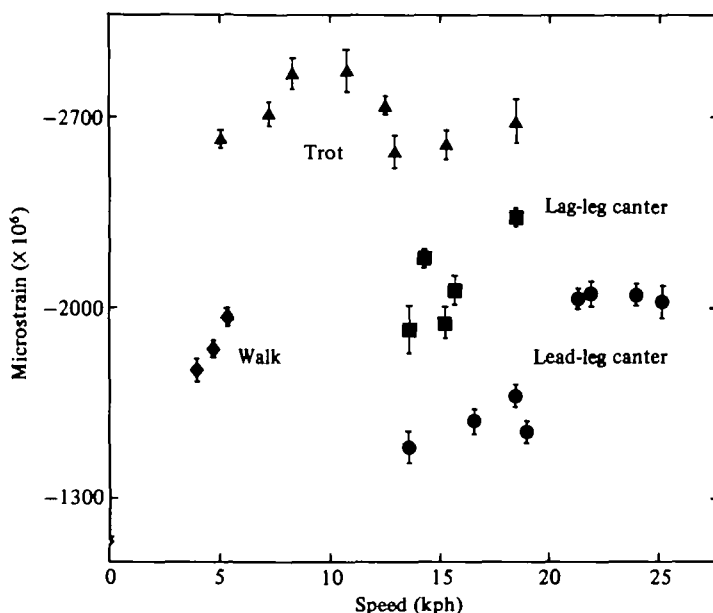
Fig. 6. Peak principal compressive strain (±S.E.) on the caudal radius of horse A (which would extend gaits and change lead). A 34 % increase occurred at the transition from a walk to a trot at the same speed, while there was practically no change over a 15 kph increase in speed at the trot. Transition from a trot to a canter involved a reduction of 26 % when the instrumented forelimb was the non-leading leg, and 42 % when it was the lead leg (see also force-shoe traces, Fig. 7). At this point, strains during the canter were actually 16 % lower than those which occurred at the slowest walk. Peak strains at higher speeds appeared to plateau.

Horse radius

As in the tibia, the larger principal strains on the caudal surface of the radius were compressive and almost longitudinal. At the slowest walk (4·1 kph), the mean peak principal strain on the caudal surface was $-1777 \pm 105\,\mu\varepsilon$ rising to $-1965 \pm 58\,\mu\varepsilon$ at the walk:trot transition speed (5·5 kph) (Fig. 6). When trotting at this transition speed, the peak strains increased to 34 % above the highest walking value ($-2626 \pm 73\,\mu\varepsilon$). Strains fluctuated around $-2700\,\mu\varepsilon$ throughout the speed range at the trot, the largest strains for the radius of horse A being recorded midway through that trotting range ($-2865 \pm 173\,\mu\varepsilon$ at 8·5 kph). At the fastest trotting speeds recorded (18·6 kph), the peak strains were $-2671 \pm 182\,\mu\varepsilon$. After transition to a canter at 13·7 kph, when the instrumented radius was the non-lead forelimb (in-phase), the peak strains dropped 26 % from -2567 ± 142 to $-1911 \pm 125\,\mu\varepsilon$, rising to $-2316 \pm 77\,\mu\varepsilon$ at 19 kph. When the gait transition was such that the instrumented leg was the lead forelimb (out-of-phase), the drop in peak strains between a trot and a canter (at 13·1 kph) was 42 %, to $-1494 \pm 129\,\mu\varepsilon$; i.e. 16 % lower than the strains recorded for the slowest walk. The peak strain values for the lead leg levelled at $-2041 \pm 99\,\mu\varepsilon$ (at 21·3 kph), dropping slightly while galloping to $-2007 \pm 139\,\mu\varepsilon$ at 25·2 kph.

The strains recorded from the radius of horse B were similar to those from horse A. Horse B went faster than horse A, but would not change his lead leg. The measure-ment of peak strain from the non-lead radius appeared to continue the upward rise
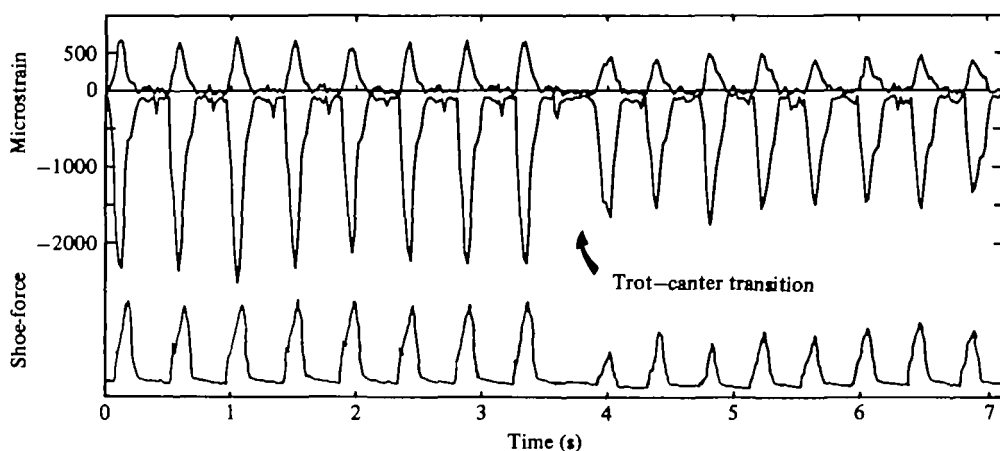
Fig. 7. The upper pair of traces are the principal strains of the caudal aspect of the radius of horse A, analysed as she changed from a trot to a canter at a constant treadmill speed. The lower trace is from the load-sensitive force-shoe attached to the same forefoot one year after completion of the strain gauge experiments. The animal's trot:canter transition for these two separate events is shown at the same speed, 16 kph. The 42 % decrease in compressive strain at the transition is reflected by a similar decrease in peak force recorded from the shoe.

peak strain value seen in horse A (which would not go faster) and reached $-2649 \pm 105 \, \mu\varepsilon$ at the animal's maximum speed of 27·1 kph (Fig. 6).

Change in bone load with speed and gait

The principal strain data from the two rosettes on each bone were used to approximate axial force and bending moment within the bone (DeLaura, Rubin & Lanyon, 1982). At the transition from a walk to a trot (at 5 kph) there was a 66% increase in the normalized axial force in the radius of horse A, while at the transition from a trot to a lead leg canter (15 kph) there was a 64% decrease. The comparable figures for the tibia of dog A were a 57% increase at the walk:trot transition, and a 57% decrease at the transition from a trot to an out-of-phase canter.

Estimation of ground forces with force shoes

Although there are several experimental advantages to treadmill locomotion, it has the disadvantage that ground force data is difficult to obtain from any floor mounted device. With horses, however, it is possible to incorporate load cells into modified shoes which can be nailed to the animal's foot in the normal manner (Pratt, 1980). A set of such shoes was constructed for the left forefoot of Horse A. These shoes had an epoxy-resin base attached to the ground surface into which 6 mm holes were drilled parallel to the ground at the metal/epoxy-resin interface. A split, hollow, stainless-steel cylinder with a strain gauge attached to its inner surface could be inserted into the hole, where it would be deformed proportionately to the loads applied to the ground.

Horse A was made to perform at the same speeds on the treadmill as she had done when recordings were made from her bone bonded strain guages. The force shoe experiment was performed 1 year after the strain gauge experiments. The magnitude
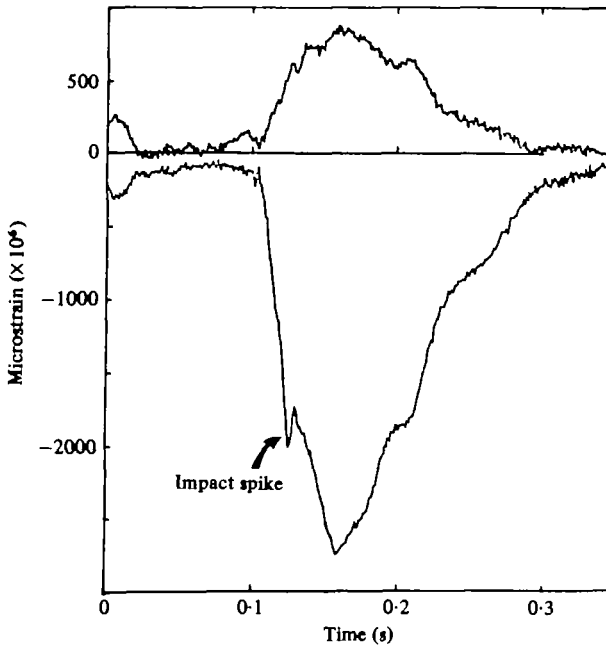
Fig. 8. Trace of the principal tension and compression strains from the caudal surface of the radius of horse A taken during one stride at the trot. This data was recorded at 15 in/s and analysed at 1 ms intervals to ensure no transient response was being missed. The strain reversal which occurs during the period of increasing strain is commonly referred to as the 'impact spike'. These spikes did not appear on the dog traces.

of the force shoe signal was primarily, although not uniquely, dependent upon the size of the vertical force between foot and ground surface. When running on the treadmill, the size of these recordings followed exactly the same pattern as those of the surface bone gauges. The 42% decrease in surface strain on the radius at the trot:canter transition was mirrored by a 42% drop in deflexion of the horse shoes (Fig. 7). At the walk:trot transition, the bone gauges showed an increase of 34% where the force shoes demonstrated an increase of 32%.

Impact spikes

At the trot and the canter, a transient strain 'spike' appeared immediately following impact on the traces from gauges attached to the horses' radius and tibia. The peak magnitude of the spike was approximately 75% of that of the actual peak principal strain (Fig. 8). While the 'spike' appeared on the analogue raw strain data, it was eliminated or attenuated on the processed principal data, which were taken at 5 ms intervals. Some high speed data from all animals and bones were taped at 15 ips and analysed at 1 ms intervals to ensure that no other transient response was attenuated on the FM tape. The 'impact spike' did not occur on the dog bones.

Loading and unloading strain rates as a function of speed

Peak loading strain rate was defined as the sharpest increase in principal strain magnitude over a 15 ms interval (3 data points) and always occurred at the initiation
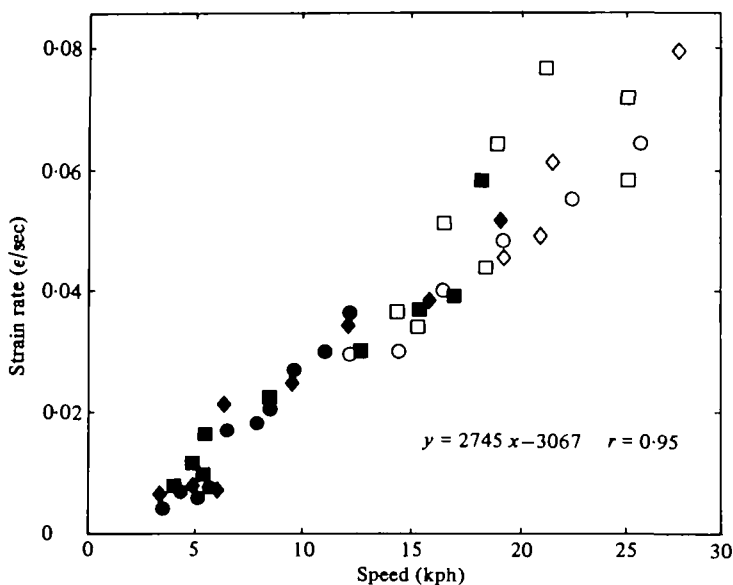
Fig. 9. The peak maximum strain rates (determined over 15 ms intervals) from the caudal surface of horse A's tibia (■), horse B's radius (♦) and dog A's tibia (●). The rates determined from cantering and galloping are shown as open symbols. These strain rates appear remarkably similar considering the different bones and the 5× difference in animal mass. Despite the discrepancies in peak strains which occur at the gait transitions, the increase in maximum strain rate appears to be linear. The equation determining the line is given.

of the stance phase. Peak unloading rate was the sharpest decrease in principal strain, and occurred as the foot was removed from the ground. The highest strain rates were consistently on the caudal surface of either radius or tibia, on all animals. The strain rates on the cranial surface were less, in proportion to the smaller strain magnitude on these cortices. At the change from a trot to a canter, there was no consistent change in strain rate similar to that measured in strain magnitude. Indeed, the loading and unloading strain rates appeared to increase in a linear fashion relative to speed. A linear regression was therefore calculated and, with only one exception (horse A's radius), these lines represented the data with a confidence limit of $P < 0.001$.

Fig. 9 demonstrates a typical relationship of strain rate vs. speed. For dog A's tibia the peak loading strain rate increased from 4479 $\mu\varepsilon.s^{-1}$ (microstrain per second) at the slowest walk, to 7721 $\mu\varepsilon.s^{-1}$ at the fastest walking speed. Transition to a trot at this speed increased strain rate 125 % to 17435 $\mu\varepsilon.s^{-1}$. After this incremental increase, strain rate increased linearly with no incremental change at the trot:canter transition to 64060 $\mu\varepsilon.s^{-1}$ at the fastest galloping speed (25 k.h^{-1}). The slope for this increase was determined by least squares fit to be:

$$y = 2649x - 2886, \quad r = 0.97.$$

(This slope represents all the rate points, including those from the walk. It is possible that because of the comparatively few speeds recorded for walking that there is relatively little effect from the transition discrepancy. This is true for all the bones.)

The data for the tibia of dog A are plotted together with the data from horse B's

radius. Again, a large discrepancy exists at the walk:trot transition (191 %), but the correlation of the sloped linear fit over the complete speed range remains high. The equation of the line is similar to that for the dog tibia:

$$y = 2671x - 2873, \quad r = 0.98.$$

Considering the different masses of the animals ($5x$), and the different bones, the combined data for both animals give a remarkably high correlation coefficient:

$$y = 2665x - 2938, \quad r = 0.96.$$

A very poor correlation of strain rate to speed existed for horse A's radius (loading $P < 0.025$; unloading $P < 0.1$), and is perhaps a result of the extended gaits. However, horse A's tibia correlates very well with the strain rates measured from the other animals. The representative equation as determined by these points is:

$$y = 2894x - 3450, \quad r = 0.91.$$

The regression equation for data from the three animals combined is:

$$y = 2746x - 3067, \quad r = 0.95.$$

Duty factor and stride frequency

There are various ways in which the decrease in peak strain and ground force seen at the trot:canter transition could be achieved without change in speed. During the canter, if each individual limb were to be in contact with the ground for a longer period relative to the entire stride cycle, this would allow more time for the necessary propulsive force to be applied, and thus the peak ground force would decrease proportionately. However, measurements of ground contact time from the treadmill cine records in these experiments are in agreement with previous reports by other investigators, who have shown that, although duty factor changes significantly from a walk to a trot, there is no such discrepancy from a trot to a canter (Jayes & Alexander, 1978) (e.g. time of ground contact at the gait transition for dog A's tibia: trot = canter = 0.175 s). It has also been suggested that the change in gait is made to increase the average number of feet on the ground per stride (Pennycuick, 1975), which would also allow the required propulsive force to be applied over a longer period of time. However, in this experiment at least, there was no change in the average number of feet on the ground at the trot:canter transition (e.g. dog A, average number of feet on ground: trot = 1.47; canter = 1.50).

An increase in stride frequency following the transition to a canter would also allow a decrease in load, since ground contact per second would be increased. However, our data confirm that although stride frequency changes significantly from a walk to a trot, no change occurs from trot to canter (Heglund, Taylor & McMahon, 1974).

Although the actual duty factor and stride frequency remain constant at the trot:canter transition, it would have been possible for the period in which significant load transfer occurred to be increased if the shape of the load curve were altered. However, the curve produced at the canter is similar in shape to that produced at the trot (Fig. 7).

It appears therefore that the decrease in peak vertical force which we observed at the trot:canter transition was most likely associated with a decrease in the vertical displacement of the animal's centre of mass which occurred while the feet were still in contact with the ground (Cavagna, Heglund & Taylor, 1977).

<div align="center">DISCUSSION</div>

<div align="center">*Bone Strain and the Functional Significance of Bone Architecture*</div>

The strategies available for achieving the best compromise between tissue economy and mechanical competence in the skeleton are: (1) to regulate the manner and magnitude of skeletal loading; (2) to adjust the material properties of the tissue; (3) to adjust the mass and alignment of tissue present.

(1) *Regulation of the manner and magnitude of applied loading*

In the limb bones which we have investigated, the orientation of the principal strains and the ratio of their magnitudes on opposing cortices were maintained constant during the limb's stance phase, indicating a consistent mode of loading throughout the limb's period of ground contact. This mode of loading was also maintained throughout the animal's complete range of speed, regardless of change in gait.

Although the orientation and manner of loading were uniform throughout the animal's range of speed and gait, the peak load magnitude, and thus the peak strains achieved, were dependent upon the gait used. Large increases in peak strains occurred at the walk:trot transition, while decreases occurred at the transition from a trot to a canter. Thus, while coordination of muscle activity and external forces confines the orientation of loading within the skeleton, the sequencing of limbs and redistribution of muscular activity that accompany gait change permit increases in ground speed with regulation of the loading magnitude.

(2) *Adjustment of tissue properties*

Although the bone tissue in deer antlers and the temporal bulla has become adapted for its particular role in these locations by adjustment of mineral content (Currey, 1979), it seems that in limb bones, which have a more traditional load-carrying responsibility, the material properties of the tissue remain fairly constant (Reilly & Burstein, 1974; Schryver, 1978; Lanyon, Magee & Baggott, 1979), and strain regulation is primarily accomplished by adjusting the mass and disposition of the bone in relation to its manner of loading (Woo *et al.* 1981). The result of this uniformity in the physical properties of bone tissue in animals of widely differing size and type would imply either that the functional strain levels engendered within the tissue are essentially similar, or that their bones are at a very different risk of failure. The margins which exist between customary strains and those which will cause yield or fracture are commonly referred to as the safety factors. These safety factors have no direct physiological relevance themselves, but reflect conflicting evolutionary pressures for bones to be light and economical, and yet to withstand a certain proportion of loading accidents. Using both experimentally and theoretically derived data, Alexander has suggested the range of skeletal safety factors to yield failure to be from

Table 1. *Peak functional strains measured from bone-bonded strain gauges in a range of animals, during their customary activity which elicited the highest recorded strains*

(The safety factors to yield and ultimate failure were calculated using values of 6800 and 15700 microstrain for yield and ultimate tensile strain, respectively (Carter *et al.* 1981 *a, b, c*).)

Bone	Activity	$P\epsilon_0$	Yield	Ulti-mate	Reference
Horse radius	Trotting	−2800	2·4	5·6	—
Horse tibia	Galloping	−3200	2·1	4·9	—
Horse metacar.	Acceler.	−3000	2·3	5·2	Biewener *et al.* (1982)
Dog radius	Trotting	−2400	2·8	6·5	—
Dog tibia	Galloping	−2100	3·2	7·4	—
Goose humerus	Flying	−2800	2·4	5·6	Rubin & Lanyon (1981)
Cockerel ulna	Flapping	−2100	3·2	7·4	Rubin & Lanyon (1982)
Sheep femur	Trotting	−2200	3·1	7·1	DeLaura *et al.* (1982)
Sheep humerus	Trotting	−2200	3·1	7·1	In preparation
Sheep radius	Galloping	−2300	3·0	6·8	O'Connor *et al.* (1982)
Sheep tibia	Trotting	−2100	3·2	7·4	Lanyon *et al.* (1982)
Pig radius	Trotting	−2400	2·8	6·5	Goodship *et al.* (1979)
Fish hypural	Swimming	−3000	2·3	5·2	Lauder (1981)
Macaca mandible	Biting	−2200	3·1	7·1	Hylander (1979)

one to eight (Alexander, 1981). However, peak functional strains recorded directly from a variety of animals indicate that these strains are remarkably similar throughout a wide variety of animals, and that the range of safety margins to failure is narrower than that previously predicted (2·1–3·1 safety margin to yield) (Table 1).

During normal activity, the skeleton is not only at risk from failure during single loading incidents, but also from fatigue damage following repetitive loading. The latest estimates of Carter *et al.* (1981 *a, b*), made after repetitively loading machined samples of bovine and human cortical bone over a strain range in excess of 5000 microstrain, suggest that the fatigue resistance of bone is poor and predict that a strain range of 3000 microstrain would elicit a fatigue life of approximately 100000 cycles. If Carter's suggestion is true, and the linear extrapolation of *in vitro* fatigue life into the physiological strain range is correct, then bone has no fatigue endurance limit, and the strain levels engendered during normal activity would cause sufficient damage to necessitate not only constant, but also substantial, intracortical and tra-becular remodelling in order to prevent complete fatigue failure. Although it seems probable that these fatigue predictions are too pessimistic, studies of peak functional strains and bone remodelling activity of migratory species, such as the gnu and gazelle which travel many thousands of miles in a few weeks, or swifts and geese which fly tens of thousands of miles every year, would be illuminating in this respect.

(3) *Adjustment of mass and alignment of bone tissue*

Because loads can be sustained with the smallest strains if they are applied axially, it would seem advantageous for bone remodelling to be directed towards achieving this favourable manner of loading. In fact, despite the apparent desirability of axial loading as a remodelling objective, in only one bone so far studied by us (metacarpus

Table 2. *The percentage of total strain due to bending and the axial force/body weight*
   (Gf) during locomotion in the tibia of animals of a widely varying size range

(Data from the horse and dog are those presented here, those from the buffalo and elephant
are extrapolated from Alexander (1979*b*). In each case the strains due to the bending moment
account for the largest proportion of the total strains. It appears likely therefore that bone
architecture (girth, cortical thickness and curvature) is adjusted in relation to bone length,
limb orientation, and style of locomotion in order to ensure similar strain magnitudes and
proportions in a variety of animals (see Tables 1 and 3.))

	% due to Bm	Gf
Dog	84·4 + 3·5	3·6
Horse	83·5 + 2·5	2·8
Buffalo	81	3·0
Elephant	89	0·8

has the amount of bending during steady state locomotion been small enough for
all cortical surfaces to be under greater or lesser degrees of compression (Biewener
et al. 1982). The more common situation is that seen in the radius and tibia where the
bones' neutral strain axes pass through the narrow cavity, thus placing the entire
thickness of at least one cortex into longitudinal tension, and the other cortex into
longitudinal compression. The percentage of total strain due to bending for the tibia
of four animals (Table 2) shows that as much as 89% of the total strain in this bone is
due to bending.

   Although external bending moments cannot be avoided, they could be minimized
if the longitudinal curvatures which many bones characteristically develop were
arranged so as to produce moments within the structure of an opposite sign to those
externally imposed. Even if complete flexural neutralization could not be achieved
by this means, any cancellation of bending moments should provide a definite struc-
tural benefit. However, despite the apparent desirability of flexural neutralization
by this means, the curvatures which many long bones have developed are not always
directed towards neutralizing bending, but in some cases actually appear to increase it
(Lanyon, 1980). In the horse radius at the time of peak strain, the bending moments
induced at the midshaft by the bone's curvature are in fact greater than those produced
by its eccentric loading and its angulation to the ground (Biewener *et al.* 1982). The
structural advantages to such longitudinal curvatures would be hard to determine if
the functional strains which bending creates were the purely deleterious phenomena
which they would be in an inanimate material. It is possible, however, that in living
bone intermittent strains may produce some physiological benefit, either to the
metabolism of the bone's cellular population, or to the maintenance of their matrix
on which the structural competence of the bone depends. Under these circumstances,
a certain level of intermittent strain might be desirable, and strain regulation could be
achieved by increasing or decreasing the bone's curvature according to its external
loading situation. The idea that any feature of bone morphology might be specifi-
cally designed to increase tissue strain is contrary to conventional ideas which have
concentrated on the advantages of tissue economy and structural safety. It appears,
however, that widely dissimilar weight-referenced axial loads, combined with different
cross-sectional geometries, thickness of cortices, and degree of longitudinal curvature,
conspire to produce similar levels of peak functional strain (Table 3).

Table 3. *Stresses calculated for the tibial midshaft of
four quadrupeds during fast running*

(The data for the elephant and buffalo are extrapolated from Alexander, the horse and dog
data were determined by our strain gauge experiments and are given from their fastest speed
on the treadmill. Values given are for stress due to axial compression (Ac), and stress due to
the bending moment (Bm); torsional loading is assumed to be insignificant. Although the
two methods of stress determination are completely different, the results they produce for
peak stress within the tibia of animals of widely differing size (80 ×) are remarkably similar.)

	σA_o	σM_b	σTotal
Elephant (2500 kg)	6 MPa	51 MPa	57 MPa
Buffalo (500 kg)	11 MPa	47 MPa	58 MPa
Horse (140 kg)	7 MPa	46 MPa	53 MPa
Dog (30 kg)	7 MPa	37 MPa	44 MPa

where σ is stresses,
MPa is megapascalls

In both the dog and the horse, maximum strains in the radius occur at a trot, and
in the tibia, the peak strain levels measured during trotting are achieved again only at
the animal's fastest gallop. The maximum strains for any speed within the dog and
horse tibia were used to determine the maximum stresses due to bending and axial
compression. These stress values were then compared with those which Alexander
et al. (1979*b*) calculated for large, fast running quadrupeds, using cinematography
and limb dissection (Table 3).

The similarity in these data suggests that peak functional stresses within bone are
more likely to be dictated by the requirements of the tissue than by any parameter of
animal size or locomotory function. It further suggests that the skeletons of vertebrates
are scaled to regulate peak functional stresses (a result of evolutionary pressure to
maintain similar safety factors to failure), rather than preserving geometric (length/
diameter) proportionality (Alexander *et al.* 1979*a*) or elastic similarity (McMahon,
1973, 1975).

Although relating bone architecture to peak functional strains appears the most
relevant (and convenient) measure in relation to a bone's structural competence, it
has been shown (O'Connor, Lanyon & MacFie, 1982) that the parameter of a strain
régime which has the greatest influence in regulating bone mass is the rate at which
the strain changes rather than the peak strains that are achieved. Thus, although the
maximum danger to the bone arises from peak strains, the predominant factor which
influences bone mass is the rate at which the strain changes. The association which
naturally exists between high peak strains and high strain rates will therefore result
in bone architecture being preferentially influenced by the strains encountered during
periods of vigorous, rather than more sedentary, activity.

Bone strain, locomotor mechanics, and gait change

The essentially linear relationship between the amount of oxygen an animal
consumes and its speed conceals the different mechanical strategies which are em-
ployed at each gait in order to increase speed and yet conserve energy. Hoyt &
Taylor (1981), using the same horses employed in this study, showed no discrepancy
in oxygen consumption at the animal's normal transition speeds. The large changes in
limb loading which occurred at these transitions could only be achieved for the same

xygen consumption if some method of energy conservation or redeployment were involved.

For locomotion at any speed, oxygen is necessary to enable muscles to develop tension. However, the relationship between the amount of oxygen used, the work done, and the tension developed, is not a simple one. Tension may be developed within a muscle while it is shortening and doing positive work, while it remains the same length, or while it is being stretched and doing negative work. Since positive work is metabolically far more costly than negative work, it becomes advantageous for any particular muscle to maximize the relative amount of negative work which it has to do (Abbot, Bigland & Ritchie, 1952). The energetic cost of developing any level of peak tension will then be less, and the number of active muscle fibres necessary to achieve this can be reduced. In addition to the benefits of obtaining high tension levels cheaply, negative work provides the advantage that the energy stored within the muscle and tendon during stretching can be recovered elastically and contribute to movement at no additional metabolic cost. The extent to which this particular energy conservation strategy is used varies according to the location of the muscle and the gait which the animal employs.

When an animal is walking, there is little or no useful recovery of energy stored elastically within stretched tendons and muscles. Instead, metabolic energy expenditure is reduced because of the smooth exchange between potential and kinetic energy as the animal's centre of mass rises and falls, accelerating and decelerating, at each step. The saving which results from this transition can account for as much as 70% of the propulsive energy required for forward movement during the walk (Cavagna, Thys & Zamboni, 1976; Cavagna *et al.* 1977).

At a trot in a quadruped or a run in a biped, there is an aerial period between each support phase. Maximum potential and kinetic energy are in phase at these gaits, thus eliminating the possibility of energy conservation by phasic interchange. However, on landing from the aerial phase, much of the animal's kinetic energy is converted to strain energy by stretching the tendons, ligaments and muscles within the limb. This strain energy is recovered elastically and contributes towards the propulsion into the next airborne phase. Presumably, it is the substitution of this form of mechanical energy conservation for that used in the walk which allows the transition to a trot to be accomplished without any incremental cost in oxygen consumption. This occurs even though the amount of work done increases due to an increase in the vertical displacement of the animal's centre of mass (Cavagna *et al.* 1977), which is clearly indicated by the substantial increase in skeletal strain at this transition.

In the canter and gallop there is only one floating phase per stride instead of the two at the trot. The decrease in ground force measured at this transition, by both the force shoes and the bone-bonded strain gauges, indicates a decrease in the amount of external work being done. This is presumably achieved by a reduction in the vertical excursion of the animal's centre of mass. Recruitment of the trunk at this time introduces another large active group of muscles (Taylor, 1978; Goslow *et al.* 1981) but, despite this, there is no incremental increase in oxygen consumption at the gait transition (Hoyt & Taylor, 1981). This can most readily be accounted for by a decreased use of the muscle groups within the limbs which were previously active

during the trot. The lack of any discrepancy in bone strain rate over the trot:cante■
transition, despite a 40% decrease in peak axial load, suggests that the muscle loading
rate, and thus also the fibre type population which is active, remains constant at that
time, but that the active fibre number is reduced. This supposition is supported by
glycogen depletion experiments, which demonstrate that some muscles in the limbs
actually do less work during the canter than the trot (Armstrong *et al.* 1977).

The reduced limb bone loading, which we have shown to occur at the trot:canter
transition in these experiments, reflects a coordinated reduction in both ground force
and tension within the limb muscles. This drop could be predicted from appropriate
substitution in the canine power output formulae published by Cavagna *et al.* (1977),
and is consistent with their observation of a decrease in external work between
cantering and trotting at the same speed. These bone strain and force shoe measure-
ments are further supported by ground-mounted force plate recordings near the
transitions, which also show a decrease in peak vertical force at the canter (Biewener
et al. 1981). For the ground force to decrease at the transition while the animal con-
tinues at the same speed implies a reduction in vertical movement of the animal's
centre of mass during the period of ground contact.

CONCLUSIONS

Limb bone loading is the result of forces engendered within the muscles and forces
originating from the ground. During treadmill locomotion these act together with the
following results:

(1) A constant loading orientation of the bone is maintained during the stance
phase of each limb and throughout the animals' complete range of speed and gait.
This restricted mechanical environment provides a unique requirement (and should
permit an economical solution) to the structural demands of steady-state locomotion.

(2) Peak bone loads increase incrementally at the walk:trot transition and decrease
substantially at the transition from a trot to a canter. This decrease is most marked in
the lead forelimb and the diagonally opposite hind limb. The decrease in limb bone
loading is accompanied by a decrease in ground force. Since the manner of loading
remains constant, this implies that fewer muscle fibres are active within the limbs at a
slow canter than at a fast trot. Although probably not the sole purpose of the gait
change, the decreased limb loading which occurs at this transition permits increased
speed without progressive erosion of the bone's safety factors to failure.

(3) The bone's rate of loading and unloading increases linearly with speed. The slope
and magnitude of maximum bone strain rate as a function of speed is similar in dogs
and horses, for both radius and tibia. Since the osteogenic potential of a strain régime
is determined primarily by this rate of change of strain rather than the peak strains
achieved, the architecture of the appendicular skeleton will be primarily related to the
loading situation during the animal's most vigorous activity.

(4) The maximum locomotor stress levels and the percentage of the total strain due
to bending from our experimental dogs and horses were similar to those quoted for a
buffalo and an elephant. Peak strain magnitude, measured directly by strain gauges
from a variety of animals, appears to range between 2000–3000 microstrain. In long

bones this regulation of peak functional strains is primarily achieved by adjustment of the bones' girth, cortical thickness, and longitudinal curvature in relation to their overall length. Scaling within the appendicular skeleton appears therefore to be related to peak functional strain levels within the bone rather than any criteria related directly to animal size, weight, or locomotory function.

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