MUSCLE FORCES DURING LOCOMOTION IN KANGAROO RATS: FORCE PLATFORM AND TENDON BUCKLE MEASUREMENTS COMPARED

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Summary

The muscle forces and stresses occurring during normal locomotor activity in kangaroo rats are compared with the peak isometric force developed by the same muscles in situ. Two methods were used simultaneously to determine the stresses (force/cross-sectional area) acting in the ankle extensors during steady-speed hopping and during jumps when animals were startled: a direct measurement using a force buckle surgically implanted around a tendon; and an indirect measurement using a force platform/cine analysis technique. We obtained essentially the same values with the two techniques. We found that at slow speeds (0.7 m s⁻¹) the ankle extensor muscles of kangaroo rats exerted 20% of the maximum isometric force developed when the muscles were stimulated via the tibial nerve. This increased to 53% at higher speeds (1.9 m s⁻¹). At the animal’s preferred hopping speed (1.5 m s⁻¹), peak force was approximately 40% of maximum isometric force. In jumps when animals were startled, peak forces as high as 175% of the maximal elicited isometric force were recorded. These high forces always occurred when the muscles were being stretched. It appears that kangaroo rats utilize nearly the entire range of muscle force possible during normal locomotor events (i.e. up to 175% of maximum isometric force when muscles are stretched).

Introduction

Muscles are biological machines for generating force. A basic similarity in the geometry of the proteins (actin and myosin) that generate the force results in similar stress (force/cross-sectional area) generation capabilities among vertebrate skeletal muscles: maximal isometric stress is approximately the same, independent of body size, mode of locomotion or athletic prowess (Close, 1972).

Key words: muscle, force, stress, locomotion.
One might anticipate that the stresses developed by muscles during equivalent locomotor activities would also be the same in all animals. In fact, this assumption was the basis of a discourse about how locomotor performance would change with body size given by A. V. Hill to the Royal Institution (1950), and was a consideration in calculating the maximal sustained power output by skeletal muscle (Weis-Fogh & Alexander, 1977). However, some allometric models of locomotion have muscle stress varying with body size (see McMahon, 1984).

We have argued that the magnitude and time course of force generation by limb muscles, rather than the mechanical work they perform, determine a wide variety of locomotor parameters, including the preferred speeds that animals use, the speed at which they change gaits, how fast they can run, and how much energy they use (Heglund et al. 1982; Taylor et al. 1980). Furthermore, we have suggested that muscle stress is the same under equivalent locomotor conditions (Biewener, 1983a; Taylor, 1978, 1985). The purpose of this paper is to measure the forces exerted by a muscle group over a range of locomotor activities to begin to test these ideas. Specifically, we ask how much of the potential for force generation is used for different locomotor tasks by comparing the forces developed during these activities with the maximum isometric force developed by the same muscles.

Muscle forces exerted during locomotion were measured simultaneously in two ways: directly, with a tendon force buckle technique, and indirectly, with a force platform/cine analysis technique. The force platform technique has been used by a variety of workers to calculate muscle forces (e.g. Alexander & Vernon, 1975; Biewener, 1983b; Biewener et al. 1981; Morrison, 1970; Zajac et al. 1981). This technique has the important advantages of being non-invasive and applicable to a wide variety of animals and muscle groups within an animal. However, it requires a number of assumptions (e.g. that antagonist muscles are not active, that one can identify precisely the point of application of force on the ground and on the skeletal elements of the limb, and that the distribution of stress within a muscle group is uniform). We felt that it was important to compare this indirect measurement of force with a simultaneous direct measurement to evaluate the magnitude of the errors introduced by these assumptions. Therefore, we surgically implanted a tendon force buckle around the Achilles tendon of kangaroo rats and compared the measurements of force provided by the two techniques. We chose the ankle extensors of this bipedal hopper because this muscle group offers an accessible tendon for implantation of the tendon buckle, the ankle joint is simple, and the animal has a symmetrical gait. The maximum force developed by these muscles was measured in situ in the same individuals for comparison with the magnitude of forces developed during normal locomotion.

**Materials and methods**

*Force platform recordings*

Five kangaroo rats (body mass, 94–125 g) were trained to hop down a 4×0.25 m runway with five independent force plates located in sequence midway along its
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length. The first, second, fourth and fifth force plates were 0.25 × 0.25 m in dimension. The third force plate was a 'split' plate, divided along its length (each half 0.25 × 0.125 m) to enable independent measurement of the reaction forces exerted on each hindlimb of the animal (Fig. 1B). The design and specifications of these plates have been described elsewhere (Heglund, 1981). Each plate is sensitive to forces in the vertical and horizontal (fore–aft) directions with less than 3% cross-talk between channels and less than 2% variation in sensitivity over the plate surface. The unloaded natural frequency was 180 Hz in the vertical direction and 200 Hz in the horizontal direction for the large plates and 400 Hz in the vertical and 300 Hz in the horizontal direction for the lighter divided plates. Both the vertical forces and the horizontal forces from all the plates were electrically summed and recorded. The vertical forces from the front and rear transducers of the divided plates were also recorded separately so that the point of application, or centre of pressure, of the ground reaction force exerted on each limb could be calculated when the animal stepped on the divided plate. Position of the reaction force, proportional to the force measured at one end divided by the total force measured by the plate, could be resolved to within ±0.5 mm for vertical forces of 1 N or greater (after correcting for cross-talk). The average hopping speed could be calculated from the time it took the animals to break two photobeams 0.5 m apart over the force plates.

High-speed ciné films (200 frames s⁻¹; Photosonics 1PI camera and Angineaux zoom lens) were made of the animals in lateral projection as they passed over the centrally located divided plate. The animals were shaved closely on their right side and the positions of the hip, ischium, ankle, fibula midshaft, tarsometatarsal and metatarsophalangeal joints marked with black ink. The reproducibility of determining joint position in these experiments, based on the standard deviations obtained from 10 repeated measurements of joint coordinates for a single run, was within ±0.7 mm. A correction was made for parallax errors in limb coordinates, but these were small, except when the animal was at the extremes of the camera field of view.

In vivo tendon force recordings

Following a series of control measurements in which ground reaction forces and limb positions were measured over a range of hopping speeds and jumping heights, each animal was anaesthetized (Halothane administered via a cone mask) and one small stainless-steel tendon buckle was implanted on both the plantaris and gastrocnemius tendons (Fig. 1A). Although the tendons were too small to place a separate buckle on each one, preventing the determination of the fraction of the force exerted by each of the two ankle extensors, the total force measured by the buckle could be compared with the force data from the force platform/ciné analysis. The soleus and its tendon were ignored in this analysis because the soleus is extremely small in kangaroo rats, comprising less than 2% of the total muscle fibre cross-sectional area of the ankle extensors (Biewener et al. 1981).

The tendon buckles were similar to the ‘E’ type tendon transducer described by
Loeb et al. (1985). Each transducer had a small (1×2 mm) metal foil strain gauge bonded to one side (Micrometricals, M-bond E610 adhesive). The tendons pass over and under the transducer arms, causing the transducer to bend in proportion to tendon tension (muscle force). Each buckle transducer was calibrated with flexible copper wire (0.5 mm diameter) before and after implantation to ensure that its sensitivity had not changed during the experiment.

The lead wires from the tendon force transducer (36-gauge Teflon-insulated,
Micromeasurements) were passed subcutaneously from the hindlimb, over the animal's back to its head. The wires were externalized at the base of the skull and soldered to a light-weight connector cemented to the animal's skull with dental acrylic. The incisions were sutured with 3-0 silk. A lightweight shielded cable suspended from the ceiling via a long compliant elastic cord was used to connect the animal to a Wheatstone bridge amplifier (Micromeasurements model 2120), while minimizing any disturbance to the animal during hopping.

We encountered two problems when attempting prolonged (5-day) recordings of in vivo tendon forces, although other investigators (Griffith, 1984; Loeb et al. 1985; Sherif et al. 1983; Walmsley et al. 1978) have reported successful long-term (4 weeks or longer) implantation of similarly designed buckle transducers. First, in two of three animals the much thinner plantaris tendon (0.41 ± 0.11 mm² versus 1.11 ± 0.20 mm² for the gastrocnemius tendon) was found ruptured. In the third animal the tendon was clearly worn and damaged. This occurred with no obvious lameness over the course of the experimental recordings (i.e. no significant reduction in ground reaction forces were observed for the experimental limb). Second, significant fibrous tissue formed over the buckle, potentially altering the buckle's sensitivity. This response is expected, and over longer time periods may lead to the buckle becoming completely ensheathed (Griffith, 1984; Loeb et al. 1985). The following experimental protocol was used to avoid these problems. The animals were allowed 2–3 h to recover from the surgery to implant the tendon buckle and mount the head connector. The animals recovered from the anaesthesia extremely quickly, and exhibited no negative effects from the surgery. The recovery period was followed immediately by the experimental procedures, which took 6–8 h. Following the in vivo recordings, the animals were anaesthetized with pentobarbitol sodium (35 mg kg⁻¹, intraperitoneally) and the buckle force transducers were calibrated in situ on the tendons. The data reported here are for five animals studied in this fashion.

The force buckle output, the vertical and horizontal outputs of the centrally located divided force plates, the summed vertical force and horizontal force for the whole force platform, the photocell outputs, and the camera shutter correlation pulse were sampled at 1000 Hz by a microcomputer and stored for later analysis. The force signals were zeroed and filtered with a 100 Hz digital low-pass filter (Winter, 1979).

The animals were shocked lightly using a small electrical grid placed on the surface of each divided force plate to elicit jumps. The weight of the grids reduced the natural frequency of the plates by 5–7 % but did not impair resolution of the ground reaction forces. Jump height was recorded by estimating the height change of the pelvis as it rose up a calibrated wall.

In situ muscle force recordings

The buckles were calibrated in situ immediately after the in vivo recordings. The gastrocnemius and plantaris muscles were stimulated via the tibial nerve, with the femur and tibia held rigidly by clamps. The tendons of the gastrocnemius and
plantaris were connected to a force transducer (Kistler, model 9203) with a double strand of 0-silk suture tied just above the calcaneus. Force was measured as a function of muscle length by adjusting the clamps holding the femur and tibia; isometric force was determined as the peak isometric force at the optimal muscle length.

The stimulation frequency and voltage were increased to levels (100 Hz, 1 V) where further increases did not elicit higher forces. Maximum isometric force was measured at a stimulation frequency of 100 Hz and 2 V, to ensure full recruitment of the muscles. The buckles used in this study gave linear responses to within 3% over the full range of recorded forces (Fig. 2A). A slight hysteresis was observed between loading and unloading phases of the curve due to the viscoelastic properties of tendon. The dynamic response properties of the transducer faithfully recorded the changes in force developed in the tendon, as illustrated in Fig. 2B. The force buckles were calibrated by doing a least-squares fit linear regression of the digitally sampled change in force (measured by the Kistler force transducer at 0-2-s intervals) versus the voltage output of the buckle transducer during short tetani. The correlation coefficients of the calibration regressions all exceeded 0.99, with their 95% confidence intervals less than 2% of the slope. The buckles were calibrated at forces greater than the peak isometric force by pulling directly on the tendons.

Following the buckle calibration, the muscles were removed from the animal and their masses, mean fibre lengths (N = 10) and mean pinnation angles were measured in order to calculate the muscles’ cross-sectional areas (Table 1) according to the technique of Alexander (1977). The moment arms of the tendons and lengths of limb segments were measured with Vernier calipers to ±0.1 mm. These measurements were used in the force platform/ciné analysis to calculate muscle forces.

**Results**

**Steady-state hopping**

Direct and indirect measurements of muscle forces were in close agreement over the entire range of hopping speeds. Fig. 3 illustrates typical records of the force measurements using the two techniques when a kangaroo rat hopped at a constant speed (left) and during a stationary jump (right). The top panels plot the force recorded from the tendon force buckle and the lower panels plot the ground reaction forces measured simultaneously by the force platform. The vertical ground reaction force from both feet is shown during five hops (second panel from top on left). In this tracing the animal lands on the divided plate on its fourth hop. Both vertical and horizontal components of ground reaction force recorded from a single limb by the divided force plate are shown for this hop (third and fourth panels from top). On the right, the force buckle and force platform recordings are shown for a stationary jump of 30 cm height. The force platform data are used
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Force (N)

Twitches: 2-5 Hz

Tetanus: 100 Hz

Time 200 ms

Fig. 2. (A) Representative in situ force calibration of one of the tendon buckles, showing the loading (upper line, closed squares) and unloading (lower line, open triangles) functions. These calibrations were generated by digitizing a dynamic loading test of the buckle (either by eliciting maximum tetanic force or by pulling directly on the tendon via the force transducer connection) and regressing the force versus the buckle’s voltage output at 0-2-s intervals. The regression slope was then used as the calibration for each buckle transducer (the 95% confidence interval of the regression was always less than 2% of the slope). Note the small, but detectable hysteresis. (B) Recordings of isometric twitch and tetanic muscle force and the corresponding outputs recorded from the buckle transducer in situ during representative dynamic loading tests.

together with the limb positions (obtained from the high-speed films) and the anatomical data contained in Table 1 to calculate muscle force.

Fig. 4A compares the muscle forces measured with the two techniques during one hop as the animal moved across the platform at a constant average speed.
Table 1. Anatomical data for the ankle extensor muscles

<table>
<thead>
<tr>
<th>Animal (body mass)</th>
<th>Gastrocnemius (M, g)</th>
<th>(L, mm)</th>
<th>(A, mm²)</th>
<th>Plantaris (M, g)</th>
<th>(L, mm)</th>
<th>(A, mm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kangaroo rat no. 1 (100 g)</td>
<td>1.26</td>
<td>8.6</td>
<td>138.5</td>
<td>0.31</td>
<td>7.5</td>
<td>39.5</td>
</tr>
<tr>
<td>Kangaroo rat no. 2 (90 g)</td>
<td>0.94</td>
<td>11.1</td>
<td>79.5</td>
<td>0.28</td>
<td>7.9</td>
<td>33.9</td>
</tr>
<tr>
<td>Kangaroo rat no. 3 (125 g)</td>
<td>1.10</td>
<td>9.9</td>
<td>106.5</td>
<td>0.36</td>
<td>8.2</td>
<td>40.7</td>
</tr>
<tr>
<td>Kangaroo rat no. 4 (101 g)</td>
<td>1.06</td>
<td>8.0</td>
<td>127.0</td>
<td>0.25</td>
<td>10.0</td>
<td>23.1</td>
</tr>
<tr>
<td>Kangaroo rat no. 5 (113 g)</td>
<td>1.27</td>
<td>8.1</td>
<td>147.0</td>
<td>0.33</td>
<td>8.4</td>
<td>37.2</td>
</tr>
</tbody>
</table>

M, muscle mass; L, mean fibre length (10 measurements made per muscle); A, muscle fibre cross-sectional area.

There was no consistent difference between the forces measured with the two techniques as the force rose to its highest value during each stride. However, the direct measurement of force was slightly higher (2–25%) during the time the force was falling. This difference might be explained either by antagonist muscle activity or by inertial forces which were not taken into account with the force platform technique.

The peak force recorded during a stride increased with increasing hopping speed. At the slowest speeds (0.7 m s⁻¹) force/cross-sectional area of the ankle extensors (stress) was about 38 kPa and this increased by 2.5-fold to 105 kPa at the highest speed (1.9 m s⁻¹). There was excellent agreement between the magnitude of peak stress measured with the two techniques over the entire range of speeds. This is illustrated in Fig. 4B which plots the peak stress measured from the force platform against peak stress recorded simultaneously from the tendon buckle. The slope of 1.04 clearly demonstrates that the two techniques yield similar values during steady-speed locomotion. Averaging all the measurements included in the graph, we find that peak stresses measured using the platform were 4.6 ± 6.6% (mean ± s.d.) higher than those recorded directly with the force buckle, and not significantly different.

Jumping

Fig. 5A compares the forces measured with the two techniques during a vertical jump from the plate by an animal when it was startled. As with steady-speed locomotion, the time course of force development and decay was very similar for both the direct and indirect force measurements; however, there was more variability between the two techniques. The force buckle gave a 10 ± 15% (mean ± s.d.) higher value of peak force. This is illustrated in Fig. 5B, which plots
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Fig. 3. (A) Comparison of the force recorded using the direct and indirect techniques during five hops along the force platform. Representative tracings are shown of the force recorded from the gastrocnemius and plantaris muscles by the tendon force buckle (top panel), total summed vertical force exerted by both hindlimbs on the series of four force plates (second panel), and the isolated vertical (third panel) and horizontal (fourth panel) components of the ground reaction force on the experimental limb when it landed on the divided plate. (B) Comparison of forces recorded by the two techniques during a jump to a height of 30 cm. The force measured by the force buckle is shown in the top panel, the vertical force acting on one hindlimb measured by the split force plate is shown in the middle panel, and the horizontal force measured by the split force plate is shown in the bottom panel. The period of constant force at the beginning of the recordings is when the animal was standing quietly on the plate prior to jumping.

Peak stress measured from the force platform against peak stress recorded by the force buckle. The stresses recorded during jumping reach values four times greater than those measured during steady-speed hopping, and the slope of 0.95 again
Fig. 4. Comparison of forces in the ankle extensors during steady-speed hopping in a kangaroo rat measured using the tendon force buckle (□) and the force platform/ciné analysis (▲) techniques. (A) demonstrates the close agreement in the force measured using the two techniques during the entire time the foot is in contact with the ground. (B) The peak stresses during a stride measured with force platform/ciné analysis technique as a function of the peak stress measured simultaneously with the tendon force buckle technique, over the entire range of stresses obtained during steady-speed hopping. The equation obtained by reduced major axis (model II regression) is: platform/ciné stress (kPa) = 1.04 x tendon force buckle stress (kPa) + 1.55 kPa; r = 0.95.

Fig. 5. Comparison of forces developed during a stationary jump by the ankle extensors of a kangaroo rat, measured simultaneously by the tendon force buckle (□) and the force platform/ciné analysis (▲) techniques. (A) demonstrates the close agreement in the forces measured with the two techniques during the entire time the foot is in contact with the ground. (B) The peak stresses during a stationary jump measured with force platform/ciné analysis technique as a function of the peak stress measured simultaneously with the tendon force buckle technique, over the entire range of stresses obtained during jumps. The equation obtained by reduced major axis (model II regression) is: platform/ciné stress (kPa) = 0.95 x tendon force buckle stress (kPa) + 1.89 kPa; r = 0.93.
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Fig. 6. A histogram of peak muscle stresses exerted during jumps of 20–50 cm and steady-speed hopping at the preferred speed of 1.6–1.9 m s\(^{-1}\) are compared with peak stress measured during maximal isometric stimulation (stippled bar). Mean values obtained using both the force platform/ciné technique (solid bars) and the tendon force buckle technique (hatched bars) are shown; the standard deviation of the mean is indicated at the top of the bars.

Reflects that the good general agreement between the two techniques extends to very high levels of force.

In situ measurements of maximal isometric force

The maximum isometric force measured for the ankle extensor muscles was 200 ± 23 kPa for the five animals included in this study. This compares with in vivo values of 89 kPa in these same muscles measured during steady-speed hopping at the preferred hopping speeds of 1.6–1.9 m s\(^{-1}\), and 350 kPa during maximal jumps to a height of 50 cm (Fig. 6).

Muscle length changes

Jumps to heights greater than 30 cm involved muscle stresses greater than maximum isometric stress. The ankle extensors must have been actively stretched to have achieved such high stresses (Katz, 1939). However, the magnitude of stretch undergone by these muscles is quite small (less than 1.5 mm) and difficult to demonstrate. Jumps greater than 30 cm in height involved the animal landing from a prior jump, providing the means to stretch the active muscle.
Discussion

Direct and indirect measurements of muscle force were in close agreement over the entire range of forces generated by the ankle extensors of kangaroo rats during locomotor activity. The agreement between the direct in vivo buckle recordings and indirect measurements of muscle force shows that antagonist muscle activity and inertial forces have little effect on the forces generated by limb muscles during the support phase of the stride. These data indicate that accurate estimates of muscle force (and stress) can be made using a force platform/ciné free-body analysis of a limb joint, particularly when the point of application of the ground reaction force acting on the base of the foot is known and the joint mechanics are relatively simple. The advantages of this approach for studying the mechanics of gait and body support are that it is non-invasive and more easily applied to a wider size range of animal species. Further, because there is no possibility of injury a broader range of normal locomotor activity may be studied. A limitation of this approach, however, is its inability to resolve forces exerted by individual muscles. Often, particularly for more proximal joints in the limb, this leads to an indeterminate solution (Morrison, 1970; Winter, 1979), and the relative distribution of muscle forces must be assumed.

Alternatively, use of the tendon buckle force transducers enables independent measurement of the forces exerted by antagonist muscles. We were unable to accomplish this in the present study owing to the extremely small size of the tendons of the kangaroo rat. Use of implanted force transducers also has serious limitations: (i) it is an invasive technique that has potential for causing injury; (ii) it can only be used on the relatively few muscles that have long and free tendons available for the implantation of buckles; and (iii) tissue reaction to the transducer may alter the transducer sensitivity over the course of its use.

One of the most interesting findings of this study was that the forces measured during the highest jumps (50 cm) exceeded the maximum isometric force of these muscles by as much as 75%. Forces greater than peak isometric force can only be achieved by stretching fully activated muscles.

It is also possible that our value for maximum isometric stress is low. However, our whole-muscle value for maximal isometric stress (200 ± 23 kPa) appears to be consistent with values of 180–200 kPa reported for soleus and gastrocnemius in rat and other rodent species (see Close, 1972; Prosser, 1973 for reviews), 190–240 kPa for cat soleus and gastrocnemius (unpublished data from our laboratory), and 200 kPa for frog sartorius muscle (Hill, 1970). Wells (1965) has reported maximum isometric stress values of 270–320 kPa for rat soleus and anterior tibial muscles. However, his higher values of muscle stress probably reflect in part an underestimate of muscle fibre cross-sectional area, which was calculated using a standard ‘whole-muscle’ estimate of fibre length, ignoring individual muscle fibre lengths and pinnation angle. It should be noted that the volume density (and hence cross-sectional area) of mitochondria and capillaries is 13–15% in the locomotor muscles of 0.1 kg (kangaroo rat-size) mammals, decreasing to about 5% in 25 kg mammals (Mathieu et al. 1981; Hoppeler et al. 1981). Hence, the value of maximal
isometric stress for the myofibrillar component of the kangaroo rat ankle extensors is probably 10–15 % greater than the 200 kPa we measured.

In vivo forces exceeding maximum isometric force were observed for jumps greater than 30 cm in height and involved active stretching (ankle flexion) of the muscles. Therefore, it seems likely that the muscles were fully activated for the highest jumps we recorded and operated on the lengthening region of their force–velocity curve. In vivo forces 1.5–1.8 times maximum isometric are consistent with the maximum forces generated by isolated muscles when they are rapidly stretched (Katz, 1939; Harry et al. 1987).

The ankle extensor muscles may also operate as springs at much lower forces (i.e. undergoing active stretching before rebounding: Cavagna et al. 1977; Goslow et al. 1981; Heglund & Cavagna, 1987). This would reduce by up to 33–55 % the fraction of muscle needed to generate this force. For example, at the preferred hopping speed of these animals (1.5–1.7 m s⁻¹; Perry et al. 1988) forces measured in the tendons were about 35 % of maximal isometric force. If the fibres recruited in these muscles were actively stretched and then recoiled during a hop, as little as 20 % of the muscle would need to be active to exert the peak force measured. Although the magnitude of energy stored during steady-speed locomotion is low in kangaroo rats compared with much larger hoppers, the ankle extensor muscles are typically stretched before shortening over a range of hopping speeds (see fig. 4, Biewener et al. 1981).

In conclusion, the force platform/ciné analysis and tendon buckle technique yielded similar values of muscle stress over nearly the entire range of forces generated by the ankle extensors of kangaroo rats (20–175 % of maximum isometric force). The accuracy of muscle force estimates determined from measurements of joint moments depends greatly on knowledge of the point of application of the ground reaction force on the animal’s foot. Moreover, the ankle extensors appear to be fully recruited and actively stretched to achieve the exceedingly high forces (75 % greater than isometric) observed at the limits of this range of in vivo muscle force generation (during jumps of 50 cm).

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References


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