# Influence of rotational inertia on turning performance of theropod dinosaurs: clues from humans with increased rotational inertia

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## Summary

The turning agility of theropod dinosaurs may have been severely limited by the large rotational inertia of their horizontal trunks and tails. Bodies with mass distributed far from the axis of rotation have much greater rotational inertia than bodies with the same mass distributed close to the axis of rotation. In this study, we increased the rotational inertia about the vertical axis of human subjects 9.2-fold, to match our estimate for theropods the size of humans, and measured the ability of the subjects to turn. To determine the effect of the increased rotational inertia on maximum turning capability, five subjects jumped vertically while attempting to rotate as far as possible about their vertical axis. This test resulted in a decrease in the average angle turned to 20 % of the control value. We also tested the ability of nine subjects to run as rapidly as possible through a tight slalom course of six 90 ° turns. When the subjects ran with the 9.2-fold greater rotational inertia, the average velocity through the course decreased to 77 % of the control velocity. When the subjects ran the same course but were constrained as to where they placed their feet, the average velocity through the course decreased to 65 % of the control velocity. These results are consistent with the hypothesis that rotational inertia may have limited the turning performance of theropods. They also indicate that the effect of rotational inertia on turning performance is dependent on the type of turning behavior. Characters such as retroverted pubes, reduced tail length, decreased body size, pneumatic vertebrae and the absence of teeth reduced rotational inertia in derived theropods and probably, therefore, improved their turning agility. To reduce rotational inertia, theropods may have run with an arched back and tail, an **S**-curved neck and forelimbs held backwards against the body.

Key words: agility, manoeuvrability, moment of inertia, locomotion, human, theropod dinosaur.

## Introduction

For an animal to turn sharply, it must change the direction of travel of its center of mass to a new heading and it must rotate its body to face the new heading. The ability of individuals to do this rapidly often influences the outcome of predator/prey and intraspecific competitions (Boswell, 1981; Willock and Pearson, 1992). Although there are a number of important studies of the mechanics of turning (Howland, 1974; Andrews et al., 1977; Thollesson and Norberg, 1991; Van Den Berg and Rayner, 1995; Jindrich and Full, 1999), relatively little is known about how animals produce sharp turns; nor do we fully understand the anatomical and physiological characters that influence turning performance. One character that can be expected to influence turning performance is the rotational inertia (i.e. moment of inertia) of a body. The rotational inertia ($I$) of a body is the sum of differential elements of mass ($m$) multiplied by the square of their perpendicular distances ($r$) from the axis of rotation: ($I=\Sigma m_i r_i^2$). The perpendicular distance of a mass element from the axis of rotation, referred to here as the 'radius of gyration', has a profound effect on the rotational inertia of a body (Kreighbaum and Barthels, 1985; Halliday et al., 1993).

Because theropod dinosaurs were habitual bipeds that are thought to have run with a horizontal trunk and tail posture, the radius of gyration about a vertical turning axis through their hind limbs would have been quite large. Hence, the rotational inertia of theropods would have been large and may have limited their ability to rotate quickly to face a new heading while turning. Although it is not possible to test directly what limited the turning agility of theropods, it may be possible to gain insight into whether their large rotational inertia could have influenced turning performance.

First principles of physics suggest that the turning agility of theropod dinosaurs would have been negatively influenced by their large rotational inertia. Nevertheless, there are many examples in which first principles alone provide inadequate, and sometimes misleading, explanations of biological systems. Consider, for example, the unexpected relationship between the mechanical work and the energetics of terrestrial locomotion (Cavagna et al., 1964; Heglund et al., 1982; Taylor,

1994) or cases in which the metabolic costs of carrying loads have been shown to be smaller than the increase in mechanical work would predict (Maloiy et al., 1986; Kram, 1996; Baudinette and Biewener, 1998). Furthermore, in this case, the mechanisms that animals use to turn sharply are poorly understood. Hence, it seemed entirely possible to us that terrestrial animals may have evolved turning mechanisms and behaviors that minimize the influence of rotational inertia, or that something other than rotational inertia could be the primary limit on turning performance (e.g. sensory perception, postural stability, translational accelerations associated with the change in heading of the center of mass or limits on substratum friction).

Before advancing the hypothesis that rotational inertia may have influenced the turning performance of bipedal dinosaurs, we felt that we must first determine whether high values of rotational inertia influence the turning performance of extant bipeds. To this end, we increased the rotational inertia of human subjects to a value appropriate for theropod dinosaurs and measured the ability of subjects to turn. Clearly, humans are not ideal models of theropod dinosaurs. Humans do, however, share with theropods a parasagittal limb posture and a bipedal striding gait. Humans also fall within the size range of theropods. Hence, the experiments of this study were an attempt to estimate the effect of rotational inertia on the turning performance of animals the size and shape of theropod dinosaurs. The hypothesis that rotational inertia influenced the turning performance of theropods would be rejected if theropod values of rotational inertia had little or no impact on the turning performance of human subjects.

Our experiments demonstrated that the turning performance of humans does decrease when their rotational inertia is elevated to theropod values and that certain types of turning behavior are affected by rotational inertia more than are others. On the basis of these findings, we suggest that the turning performance of basal theropods was likely to have been impaired by their large rotational inertia and that many theropods may have been restricted to habitats consisting of relatively simple terrain. We discuss a number of characters in derived theropods that reduced rotational inertia and may have improved turning performance. We also discuss possible postural adjustments that might have reduced rotational inertia and consider the likely effects of rotational inertia in the lineages of theropods that became gigantic.

## Materials and methods
### Modeling of theropod rotational inertia

We based our estimate of theropod rotational inertia on a small plastic model of *Allosaurus* from the Carnegie Institute Collection. This genus includes several large carnosaurs that are well known from the fossil record, and it serves as a good representative of the basal theropod configuration for anatomical characters that would have influenced rotational inertia (e.g. long tail, lots of big teeth). Although adult *Allosaurus* were large animals, they began life as small hatchlings and passed through the size range of adult humans at some point in their ontogeny. Hence, a comparison of humans with similar-sized allosaurids is appropriate. To correct for the low density of the lungs, we assumed a lung volume of 8 % of body volume (Alexander, 1989) and removed this volume from the thoracic region of the model. The final model weighed 119.7 g, had a density of 1360 kg m$^{-3}$ and was configured in a standing posture.

We measured the rotational inertia of the model by letting it oscillate as a pendulum from a dorso-ventral axis midway along the length of its tail (Nigg and Herzog, 1999). The rotational inertia about the turning axis (i.e. a vertical axis through one hindlimb) was calculated using the parallel axis theorem: $I=I_{cm}+md^2$ (Halliday et al., 1993), where $I$ is rotational inertia, $I_{cm}$ is rotational inertia about the center of mass and $d$ is the distance between the center of mass and the axis of rotation. We then corrected for the high density of the model and assumed that rotational inertia scales as the 5/3 power of body mass (i.e. geometric similarity) (Walter et al., 2001) to estimate the rotational inertia of juvenile *Allosaurus* of the same size as our human subjects. The Carnegie Institute model on which we based our estimate of rotational inertia is relatively stocky in the trunk and hips compared with many modern reconstructions that indicate a narrower mediolateral dimension. The relative stockiness of the model would, therefore, lead to an underestimate of the true rotational inertia of *Allosaurus* of any given body mass. Hence, our estimate of the rotational inertia of human-sized juvenile *Allosaurus* is conservative.

Our estimate of the rotational inertia of humans is based on the mean value (1.24±0.10 kg m$^2$) from four subjects of similar body size (78.0±1.7 kg) (means ± S.E.M.) measured by Lee et al. (2001). Using this value, we assumed that rotational inertia scales as the 5/3 power of body mass (i.e. geometric similarity) to estimate the rotational inertia of humans of different body size.

### Turning performance trials

Three types of turn were studied: turns executed during vertical leaps (termed jump turns) (Lee et al., 2001), sharp running turns and sharp running turns in which foot placement was restricted. The biological relevance of running turns is obvious, but the relevance of jump turns may be less clear. In nature, animals are commonly observed to execute jump turns during intraspecific display and combat, during protection of resources and offspring and during many predator/prey contests (Boswell, 1981; Willock and Pearson, 1992).

To increase rotational inertia, our human subjects wore a tight-fitting backpack with an attached horizontally oriented wooden frame. Together, the frame and pack had a mass of 8.4 kg. The frame allowed weights to be added at a distance of 1.2 m in front of and behind the center of mass of the subject. This apparatus allowed us to increase the rotational inertia of the subjects 9.2-fold by the addition of approximately 18 % of body mass (9 % in front and 9 % at the back) (Lee et al., 2001). The shoulder straps and waist belt of the backpack anchored

the apparatus securely to the trunk of the subjects, such that turning of the subject and apparatus were tightly coupled. The frame did not lag behind the torso of the subject by more than 3 or 4°. This was determined by asking the subjects to resist turning as we applied a moment to the frame. We controlled for the effect of the added mass in separate trials in which subjects carried the same weight in a backpack that held the weight close to the subject's body.

To determine the effect of increased rotational inertia on the ability to turn about a vertical axis, five subjects performed maximum-effort jump turns in which they attempted to turn as far as possible as they jumped vertically. The angle turned was judged to be the change in the orientation of the subject's torso at the instant of landing, as judged by three observers. To aid the observers in their assessment of the angle turned by the subjects, a compass grid marking 45° intervals was taped to the floor from which the subjects jumped.

Performance of running turns was tested under two conditions. In the first test, nine subjects ran a tight slalom course of six 90° turns. The poles marking the turns were spaced close to each other (2 m) to make the time to complete the course as dependent as possible on the time required to execute the turns rather than the time required to run the total distance. In the second test, eight subjects ran the same slalom course, but in this case they were required to restrict their foot placements to 20 cement stepping stones (diameter 30 cm) placed along the course (Fig. 1). The stepping stones restricted foot placement to three steps per turn. This test was conducted to simulate the real-world condition in which variable and complex terrain often requires that animals restrict their foot placements to some subset of the available substratum.

There was improved performance in both the jump turns and the slalom course with training. This training effect was particularly apparent in the slalom runs with the increased rotational inertia. Hence, subjects were required to practice until their performance became repeatable. For the experiments, each subject attempted each test (weight control and increased inertia trials) three times, with a 15 min rest between attempts. The statistics presented below are based on the best individual trial from each subject.

### Modeling of the effect of head mass reduction

A factor that might have significantly reduced rotational

inertia in derived theropods was the great reduction in size and mass of the head that occurred in several theropod lineages (Barsbold and Osmolska, 1990; Barshold et al., 1990; Chiappe, 1995). To address the extent to which changes in mass of the head would influence the rotational inertia of theropods, we used Sereno's (1999) reconstruction of *Allosaurus fragilis*. We assumed geometric similarity and based our calculations on a trunk, neck and head length of 1.20 m. We used an elliptical cross-sectional shape in which body depth was twice body width. The pre-caudal body (minus the limbs) was divided into 38 sections of equal length. The rotational inertia of each section around a turning axis at mid-pelvis was calculated and summed to yield the total rotational inertia of the pre-caudal body. We then reduced the mass of the 12 sections that represented the head by 10, 25 and 50° and recalculated pre-caudal body mass and rotational inertia.

## Results

### *Modeling of theropod rotational inertia*

The rotational inertia of the *Allosaurus* model about a turning axis through the hind limbs was $2.26 \times 10^{-4}$ kg m$^2$. We used this value of rotational inertia to extrapolate to theropods the size of humans by assuming that rotational inertia scales to the 5/3 power of body mass. For a 90 kg juvenile *Allosaurus*, these measurements and calculations yielded a rotational inertia of 15.02 kg m$^2$ (Fig. 2). In a running human, the rotational axis will be aligned with the support limb and will pass through the hip joint. Our measurements indicate that the rotational inertia of a 90 kg human is approximately 1.56 kg m$^2$ during running. Thus, our estimated value of rotational inertia for a 90 kg juvenile *Allosaurus* is 9.6 times greater than that expected for a running human.
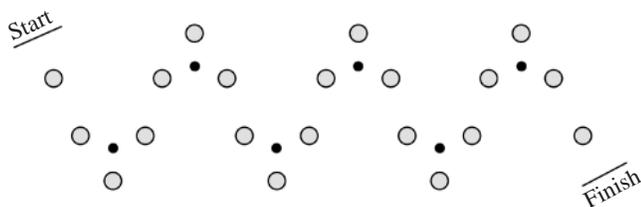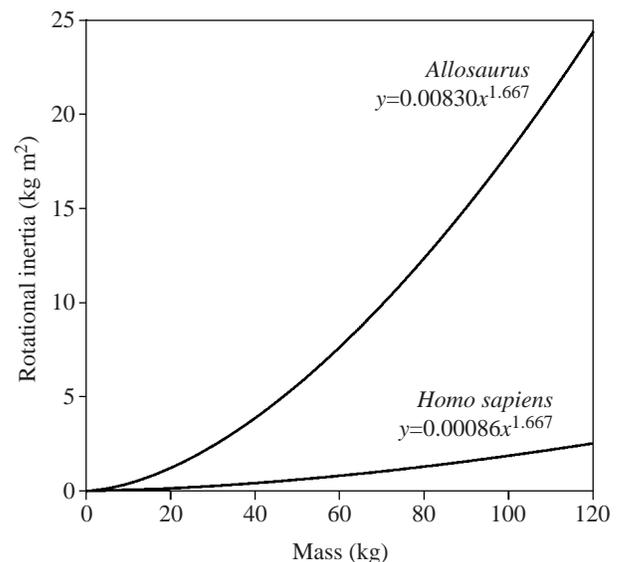


Fig. 1. Layout of the stepping-stone slalom course. The filled circles represent the location of the slalom poles, which were spaced 2 m apart. The larger gray circles represent the location of the cement stepping-stones.



Fig. 2. Estimated rotational inertia *versus* body mass for carnosaur theropods based on a model of *Allosaurus* and of *Homo sapiens*.

*Humans turning with theropod values of rotational inertia*

Direct measurements of rotational inertia of the subjects used in this study showed that the experimental elevation of rotational inertia resulted in a 9.2-fold increase over the rotational inertia of the subjects when they turned with the control weight (Lee et al., 2001). This increase is 4% less than our estimate of the difference in rotational inertia between humans and theropods with the body configuration of *Allosaurus*.

The average angle turned during maximum-effort jump turns was significantly less in the increased rotational inertia trials than in the weighted control trials (Fig. 3A). The average angle turned by the five subjects in the increased inertia trials was only 20% of the average angle turned in the weighted control trials (*P*<0.0001). Elevation of rotational inertia also resulted in a reduction in performance in the running turn trials, but to a lesser extent then in the jump turns. When nine subjects ran with the 9.2-fold greater rotational inertia, the average velocity through the course decreased to 77% of the velocity in the control trials (*P*=0.0005) (Fig. 3B). Similarly, when eight subjects ran the same slalom course, but foot placement was restricted to three stepping stones per turn, the average velocity through the course decreased to 65% of the velocity in the control trials (*P*<0.00001) (Fig. 3C).

*Modeling of the effect of head mass reduction*

To determine the extent to which small changes in head mass would influence the rotational inertia of non-avian theropods, we modeled changes in rotational inertia that would occur as a result of reductions in the head mass of *Allosaurus fragilis*. Decreases in the mass of the head by 10, 25 and 50% reduced pre-caudal body mass by only 2.4, 3.2 and 6.6%, but decreased rotational inertia by 9.1, 14.0 and 28.1%, respectively (Fig. 4).

## Discussion

*Rotational inertia of theropod dinosaurs*

Extrapolation of our measure of the rotational inertia of the model indicates that a 90 kg juvenile *Allosaurus* would have a rotational inertia of approximately 15 kg m$^2$ (Fig. 2). For perspective, compare this value with measured values from humans. The rotational inertia of an adult human is approximately 1 kg m$^2$ about a vertical axis through the center of the body (Donskoi, 1975). This value doubles to 2 kg m$^2$ if the individual holds their arms horizontally out to the side. If the rotational axis is through the hips from side to side, such that the individual somersaults forwards, rotational inertia climbs to 14 kg m$^2$. If the individual then extends both arms above their head, rotational inertia reaches 19 kg m$^2$. In a
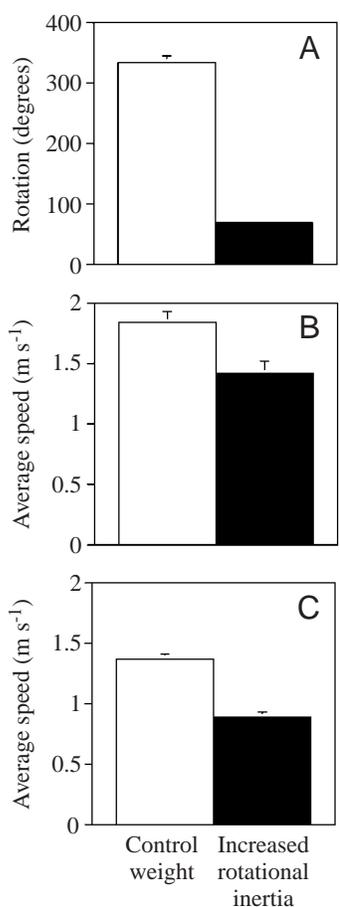


Fig. 3. (A) The angle turned in maximum-effort jump turns when turning with the control weight (open column) and when subjects turned with their rotational inertia increased by 9.2-fold (filled column) (*N*=5; *P*<0.0001, paired *t*-test). (B) The average running velocity in a slalom course of six 90° turns with the control weight (open column) and when the subjects ran with their rotational inertia increased by 9.2-fold (filled column) (*N*=9; *P*=0.0005, paired *t*-test). (C) The average running velocity in a slalom course of six 90° turns in which foot placement was restricted to three stepping-stones per turn (Fig. 1) when the subjects ran with the control weight (open column) and when the subjects ran with 9.2-fold increased rotational inertia (filled column) (*N*=8; *P*<0.00001, paired *t*-test). Values are means + S.E.M.
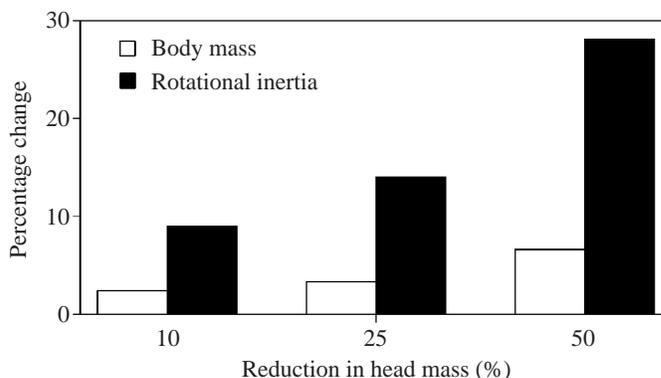


Fig. 4. The percentage decrease in mass (open columns) and rotational inertia (filled columns) of the pre-caudal trunk, neck and head of *Allosaurus fragilis* that results from reductions in the mass of the head. Small changes in distal mass have large effects on rotational inertia.

running human, the rotational axis will be aligned with the support limb and will pass through the hip joint. In this case, our estimates indicate that the rotational inertia of a 90 kg running human is approximately $1.56\,kg\,m^2$ (Fig. 2). Thus, although our estimated value of rotational inertia for a 90 kg juvenile *Allosaurus* is 9.6 times greater than that expected for a running human, it is well below the rotational inertia of a human diver somersaulting in an extended layout position. Common experience tells us that rotational inertia is not a limiting factor for rapid turning in running humans, but a 9.6-fold greater rotational inertia may have posed problems for theropods.

### Turning performance of humans with theropod values of rotational inertia

The turning performance of the human subjects was negatively influenced by the 9.2-fold increase in rotational inertia. When the subjects executed maximum-effort jump turns with the elevated rotational inertia, the average angle turned decreased to 20 % of the angle turned in the control trials (Fig. 3A). Similarly, when the subjects performed with elevated rotational inertia, the average running velocity through a slalom course of six tight turns decreased to 77 % of the control velocity (Fig. 3B). When the subjects ran the same slalom course, but foot placement was restricted to three stepping stones per turn, the average velocity decreased to 65 % of the control velocity (Fig. 3C). These observations suggest two conclusions: (i) that the extent to which increased rotational inertia influences turning performance is dependent on the type of turning behavior and (ii) that the high rotational inertia of theropod dinosaurs would probably have limited their turning performance in many situations.

The large difference in the extent to which elevated rotational inertia reduced maximum performance in jump *versus* running turns warrants further attention. The decrease to 77 % of the control value in the slalom test was substantially less than the decrease to 20 % of the control value in the test of maximum performance in jump turning. We suspect that this difference is due to several factors. First, a significant proportion of the time to complete the slalom course was not related to turning, but represented the time required to run the distance (14 m) of the course. Second, the layout of the slalom course allowed subjects to execute the required 90 ° turns over a series of running steps. Thus, although the course involved sharp turns, subjects produced the necessary rotation of the body over a relatively long period. Third, the subjects may also have used translational ground forces that are required for forward deceleration of the body to generate the torque necessary to complete the turns in the slalom course.

Nevertheless, our results suggest that rotational inertia influences the mechanics and performance of running turns and jump turns differently. Performance in behaviors that involve only angular reorientation of the body (i.e. jump turns) appears to be most affected by changes in rotational inertia. Examples of behaviors in which jump turns are important include mothers attempting to defend their young from predators (Willock and Pearson, 1992), successful predators attempting to defend their kill from other predators (Willock and Pearson, 1992) and members of the same species fighting (Boswell, 1981). Although, performance in the test of sharp running turns was less affected, we believe a decrease in 77 % of the average velocity observed in the control trials represents an effect that would be important in intraspecific or predator/prey competitions. When mammalian and avian predators attempt to run down prey, sharp turning is almost always involved (Boswell, 1981). Hence, the results of both the jump turn trials and the running turn trials lead us to suggest that the turning performance of basal theropods may have been relatively constrained compared with that of Recent birds and mammals.

The results of the stepping-stone slalom test indicate that the effect of rotational inertia on turning performance is more pronounced when foot placement is restricted (Fig. 3C). This test was conducted to simulate the real-world situation of having to make frequent, rapid turning maneuvers when running in complex terrain. Most terrestrial environments include obstacles that require turning and limit foot placement. Even savannas and meadows have irregularities and holes that limit foot placement. Hence, the result of this test suggests that the high rotational inertia of basal theropod dinosaurs would have made rapid movement in rough terrain relatively hazardous. The difficulty of moving rapidly through rough terrain would have been most pronounced in larger theropods (see below) and may have restricted many species of theropod to habitats of relatively low topographic and vegetative complexity.

Certainly, theropods would have dealt with their large rotational inertia with greater skill than our human subjects did. However, the results of our manipulations suggest that rotational inertia may have constrained the turning performance of basal theropods. Individual theropods with characters that reduced rotational inertia would have had greater agility and may have had a selective advantage in predator/prey and intraspecific competitions. Hence, if turning agility were important to theropods, we would expect characters that reduced rotational inertia to be present in derived lineages of theropods.

### Can a big tail improve turning performance?

One criticism of our thesis is that the large tail of non-avian theropods may actually have improved turning performance by inducing counter-rotation of the trunk. Conservation of angular momentum dictates that, for an unsupported body (e.g. suspended in the air during a step or jump), the swing of an appendage, such as a tail, must be met by an opposing swing of some other part of the body. For example, if the rotational inertia of the tail and body were the same, swinging the tail 45 ° counterclockwise would cause the trunk to rotate 45 ° clockwise. Although this effect was probably used, in some circumstances, by theropods to rotate their trunk to face a new direction, it is a mechanism that produces no net rotation of the body and may pose substantial problems in many circumstances.

Consider the problems for a running biped. If both the tail and trunk were rotated 45° to one side or the other (i.e. a 90° bend in the body), the center of mass of the animal would no longer be positioned over the hind limbs. The animal would, therefore, have to catch itself from falling sideways and, at the same time, it would be faced with the problem of returning its tail to the caudal position. Now, however, the tail would have to rotate 90° rather than the initial 45°. Depending on caudal joint mobility, this return rotation of the tail could be done with a reverse lateral swing or a vertically arching swing. In either case, for the animal to maintain its balance and its new heading, the torque exerted on the trunk by the return rotation of the tail would have to be met with ground forces that stabilized the trunk against further rotations.

We will never know how non-avian theropods utilized tail movements in turning maneuvers, but observations on extant species with large tails should be helpful. When basilisk lizards (*Basiliscus basiliscus*) execute rapid 90° running turns, they sometimes use the angular momentum of their long tails to produce body rotations of up to 45° (D. R. Carrier, unpublished observations). To produce the desired rotation of the body, they rapidly swing the tail laterally during a brief period of little or no limb support. The recovery swing of the tail always occurs during periods of simultaneous fore- and hindlimb support and often involves some degree of vertical excursion. Although basilisk lizards are renowned for their bipedal running, they are unable to complete 90° running turns without adopting a quadrupedal gait (Khan and Carrier, 2000). Hence, because the tail of theropods acted as a gravitational counterweight to the body, vertical recovery swings of the tail, such as those used by basilisk lizards, would probably have disrupted dynamic balance. Thus, we believe tail-swinging would have been of limited utility to bipedal theropods during the execution of sudden and sustained turns.

### Evolution of improved turning agility

Basal dinosaurs were characterized by bipedal posture, long bodies and tails, stout forelimbs, straight necks and big heads with a full complement of large teeth (Benton, 1990; Sereno, 1991). From this starting point, theropods evolved a suite of characters that reduced rotational inertia (Fig. 5). (i) Retroverted pubic bones are characteristic of both maniraptoran theropods and ornithischians (Weishampel and Witmer, 1990; Norell and Makovicky, 1997). This pelvic architecture positioned the viscera of these dinosaurs more directly beneath the pelvic girdle, closer to the axis of rotation. (ii) Theropods were characterized by pneumatization of the cervical and, in some groups, dorsal vertebrae (Britt et al., 1998).

Although the function of pneumatization is not known, hollow vertebrae would have lightened the axial skeleton in the neck and thoracic region. (iii) The hands of many theropods were lightened by having only two or three fingers and, in some of the largest theropods, the forearms were greatly reduced in length and mass (Molnar et al., 1990; Bakker et al., 1992). (iv) The size and mass of the head were significantly reduced in several lineages (Barshold and Osmolska, 1990; Barshold et al., 1990; Chiappe, 1995). (v) Teeth, the densest organs in the body, were lost independently in several lineages of theropod, e.g. ornithomimosaurs (Barsbold and Osmolska, 1990) and oviraptorosaurs (Barshold, 1990), and in at least three lineages of Aves, e.g. *Confuciusornis* (Hou et al., 1995) *Gobipteryx* and Neornithes (Chiappe, 1995). Although these characters may have evolved in response to selection that was unrelated to locomotion, they would each have reduced rotational inertia and, therefore, may have improved turning agility.

One might suspect that reductions in head size and the loss of teeth would have had little or no impact on turning performance. However, because rotational inertia is a function of the square of the radius of gyration, small changes in head mass have large effects on rotational inertia. Our modeling of *Allosaurus fragilis* indicates that decreases in the mass of the head would have resulted in small reductions in pre-caudal body mass, but large decreases in rotational inertia (Fig. 4). Hence, the dramatic reductions in head size and the loss of teeth that occurred independently in Ornithomimosauria,
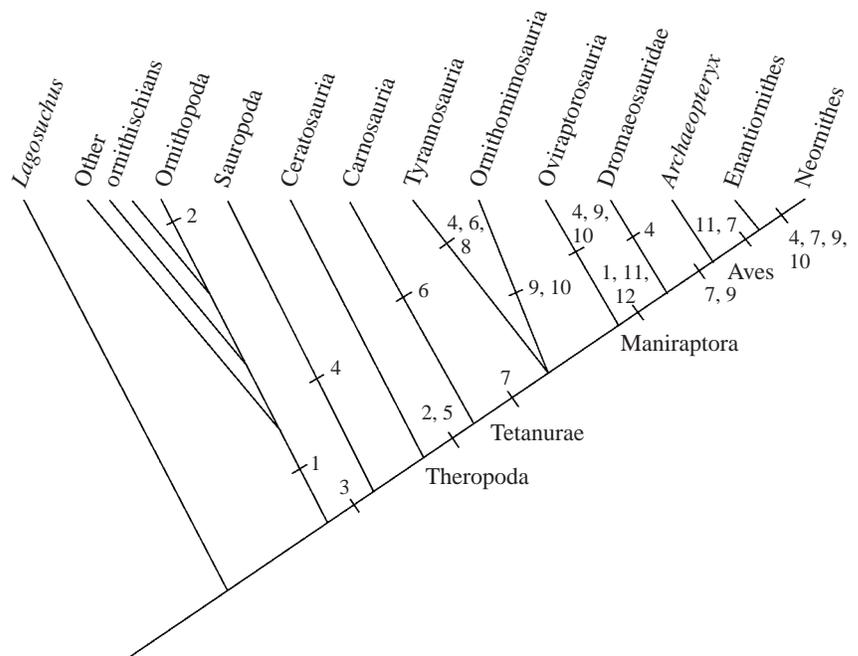


Fig. 5. Phylogeny of dinosaurs (Gauthier, 1986; Sereno, 1999; Holtz, 2000) showing the distribution of characters that are likely to have decreased rotational inertia. 1, pubes retroverted; 2, S-shaped neck; 3, cervical vertebrae pneumatized; 4, dorsal vertebrae pneumatized; 5, manus tridactyl; 6, forelimb reduced; 7, tail shortened; 8, manus didactyl; 9, head size reduced; 10, teeth lost; 11, body size reduced; 12, tail reduced, but more robust proximally. The functional significance of the characters is discussed in the text.

Oviraptosauria and Aves significantly decreased the rotational inertia of these lineages and may have improved their turning agility. The heads of ornithomimids were particularly reduced (Barsbold and Osmolska, 1990) and appear to have represented only 20–30 % of the head mass of equivalent-sized basal theropods. Rotational inertia would also have been reduced by the associated decreases in the mass of the neck in these lineages.

The gradual reduction in tail length in maniraptoran theropods is another derived condition that would have reduced rotational inertia. The gravitational moment (i.e. *mgr*, where *g* is the acceleration due to gravity) of the tails of theropods is generally thought to have functioned as a counterbalance to the gravitational moment of trunk, forelimbs, neck and head. The tails of Maniraptora were shorter, but stouter at the base, than the tails of non-maniraptoran theropods (Gatesy, 1990; Gatesy, 1995; Gatesy and Dial, 1996; Farlow et al., 2000). Because rotational inertia is a function of the square of the radius of gyration, moving the mass of the tail closer to the pelvis would have reduced rotational inertia. Consider a tail composed of a massless moment arm and a point mass at the end of the arm, and give the tail a gravitational moment (i.e. *mgr*) of 4 units. This moment could be produced with a moment arm of 1 unit and a mass of 4 units or with a moment arm of 4 units and a mass of 1 unit. The latter solution would be a tail four times lighter, but one that had a fourfold greater rotational inertia. This example raises the possibility that there may be a tradeoff in the design of counterbalance tails between the need to minimize rotational inertia and the need to minimize mass and gravitational moment. Nevertheless, it is clear that the trend towards shorter and more proximal stout tails in Maniraptora would have reduced rotational inertia.

The great reduction of the tail that occurred within Aves would have had a similar effect. The maximum aerodynamic forces that flying animals can generate are generally much smaller than the forces that terrestrial animals routinely apply to the ground (Earls, 2000). This is particularly true at low flying speeds. It may therefore be harder for slow-flying animals to turn sharply. This suggestion is supported by experimental manipulations of rotational inertia in sunbirds (Evans and Thomas, 1992). Thus, the extreme reduction of the tail that occurred early in the evolution of Aves and the independent loss of teeth in several lineages of Aves probably increased turning agility during flight.

In summary, derived theropods possessed a suite of characters that reduced their rotational inertia below that of basal theropods. As stated above, many or all of these characters may have evolved for reasons other than selection for turning agility. Nevertheless, we know of no derived characters, other than instances of increases in body size, that would have increased rotational inertia. Hence, our analysis illustrates a repeated trend among theropod lineages of a reduction in rotational inertia.

### Running posture that reduces rotational inertia

The view that theropods ran with their trunk and tail held parallel to the ground (Sereno, 1999) is widely accepted, but appears to be based on limited supporting evidence. Evidence that has been suggested to support this hypothesis includes the S-curved posture of the neck (Ostrom, 1969; Newman, 1970), prominent interspinous ligament scars on the neural spines of dorsal vertebrae (Ostrom, 1969; Newman, 1970) and the absence of tail marks in preserved trackways (Newman, 1970). The argument that the S-curved neck posture implies a horizontal trunk posture is based on the assumption that such a neck posture would not bestow an advantage if the trunk were steeply angled relative to the horizontal, as in traditional reconstructions. As we explain below, an S-curved neck would decrease both the gravitational moment and the rotational inertia of the pre-sacral body irrespective of trunk posture.

There are also reasons to question the logic that relates a rigid trunk to a horizontal trunk posture. Prominent ligaments between the neural spines of the dorsal vertebrae indicate that large torques were imposed on the axial skeleton. This suggests some horizontal inclination of the trunk during running, but not necessarily an inclination of 0 ° to the horizontal. Furthermore, the largest torques on the axial skeleton of bipedal theropods were likely to have resulted from non-locomotor activities such as prey handling and intraspecific combat. Finally, the absence of tail marks in preserved trackways indicates that the tail was carried off the substratum, but not necessarily that it was held parallel to the substratum. Hence, the extent to which the horizontal running posture of theropods is ingrained in modern literature and popular science appears to be more a product of an analogy with extant terrestrial birds than with considerations of the available evidence.

A horizontal trunk and tail posture may have been appropriate if a theropod was about to capture an escaping prey, but it also maximizes both the gravitational moment and rotational inertia of the trunk and tail. We suggest that theropods rarely walked or ran with a horizontal posture (Fig. 6A). If the gravitational moment of the trunk and tail could have been reduced during walking and running, less force would have been required from the epaxial musculature to maintain posture, bestowing an energetic savings. Furthermore, as explained above, a reduction in rotational inertia might improve turning performance. To reduce gravitational moment and rotational inertia, both the trunk and tail of theropods may have been carried at an angle, rather than parallel, to the ground (Fig. 6B). Carrying the trunk and tail at 45 ° to the horizontal would have reduced rotational inertia to approximately half that of the horizontal posture. A similar jack-knifed posture is adopted by many species of lizard when they run bipedally (Alexander, 1995). Furthermore, the articulated tails of theropods are frequently preserved in a dorsally arched posture; for example, *Sinosauropteryx prima* (Chen et al., 1998), *Allosaurus* specimen no. 11541 from Dinosaur National Monument, USA, *Compsognathus longipes* (Ostrom, 1978) and the Solnhofer specimen of *Archaeopteryx* (Wellnhofer, 1993). Certainly, the breadth of the neural spines of the caudal vertebrae does not restrict significant dorsal arching of the tail. These observations suggest that the
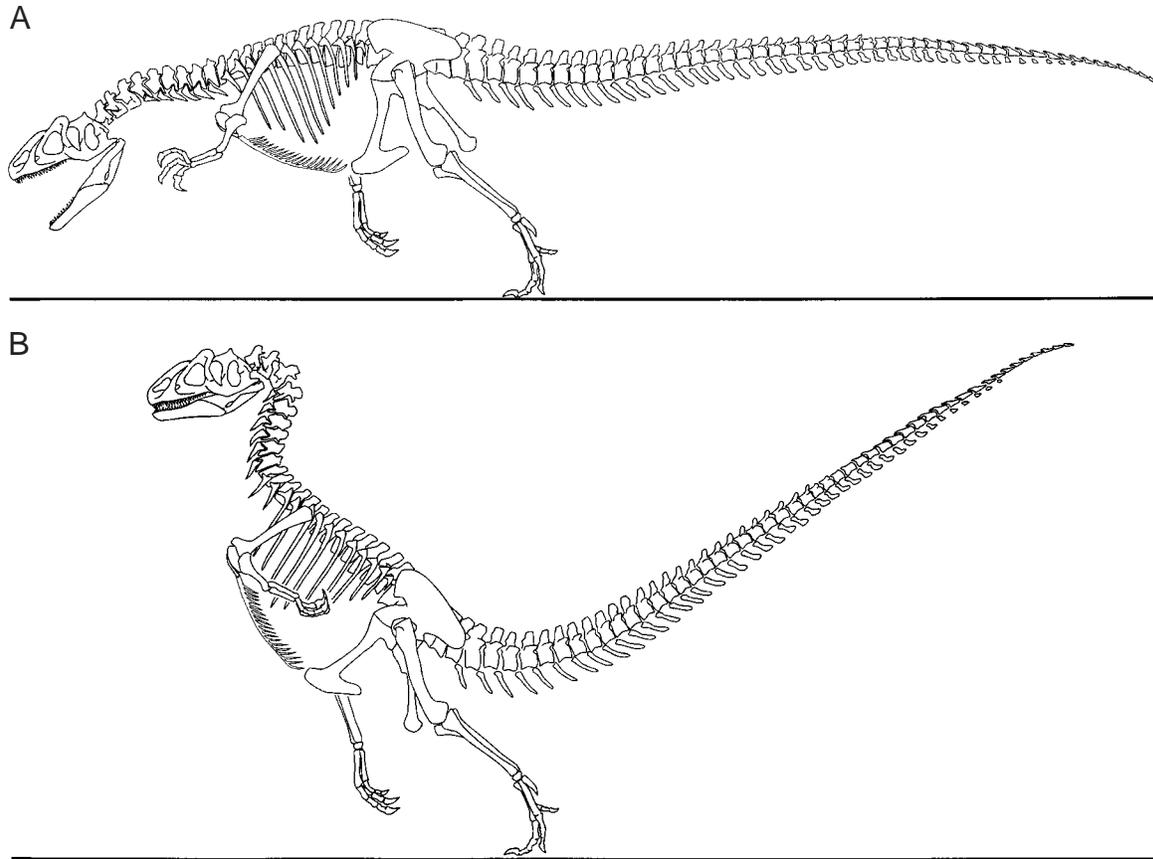
Fig. 6. Hypothesized running postures of a juvenile *Allosaurus*. (A) A horizontal posture of trunk and tail may have been appropriate for prey capture but would have unnecessarily increased the rotational inertia during running. (B) To increase turning performance, theropod dinosaurs may have run with their trunk and tail arched in a jack-knife posture, their neck may have been sharply arched backwards to hold the head closer to the hindlimbs and they may have held their arms backwards along the sides of the body. The angle of the jack-knife posture would not have to have been as dramatic as illustrated in B to reduce rotational inertia significantly.

vertebral articulations of theropods allowed a jack-knife posture.

Direct osteological evidence for elevated trunk posture during running comes from the structure of the acetabulum in allosaurids (Molnar and Farlow, 1990), *Sinraptor dongi* (Currie and Zhao, 1993), *Torvosaurus* (Galton and Jensen, 1979) and dromaeosaurs (Norell and Makovicky, 1997). In these theropods, and possibly others, the most robust aspect of the joint surface is located not on the dorsal surface of the acetabulum, as would be expected if the long axis of the ilium were held horizontal during running, but more cranially and extends onto the pubic peduncle. In humans, the dorsal surface of the acetabulum represents the broadest aspect of the joint. During constant-speed running in humans, the largest ground forces occur at midstance and are oriented vertically through the acetabulum (Winter, 1990). Thus, in humans, the most robust region of the acetabulum also appears to experience the greatest locomotor forces during running. On the basis of similar reasoning, Molnar and Farlow (1990) argue that the configuration of the acetabulum of non-avian theropods suggests that their pelvic girdle and trunk were oriented at a substantial angle to the horizontal during locomotion.

Because the S-curved necks of many theropods (Ostrom, 1969; Newman, 1970; Madsen, 1976) positioned the head and neck closer to the hips, it would have reduced both the gravitational moment and the rotational inertia of the pre-sacral body during running (Fig. 6). Finally, it is likely that theropods held their arms and hands backwards against the body when they ran, which is a posture adopted by many lizards when they run bipedally (Alexander, 1995). Hence, a posture in which the trunk and tail were angled up, the head held back and the arms extended backwards (Fig. 6B) would have been appropriate for situations in which high maneuverability was important, such as escape, most aspects of pursuit and when moving quickly through difficult terrain. Nevertheless, the horizontal trunk and tail posture of modern reconstructions would have provided high stability because of the lower center of mass and high rotational inertia and may, therefore, have been used when maneuverability was relatively unimportant.

### Effect of body size on angular acceleration

Rotational inertia would have had a much greater influence on the turning performance of large than of small theropods. Because rotational inertia is the product of mass and the square

of the radius of gyration, rotational inertia scales to the 5/3 power of body mass in geometrically similar animals. In contrast, the force that a muscle can generate is a function of the cross-sectional area of the muscle and, therefore, scales to the 2/3 power of body mass. From these relationships, we can determine how angular acceleration scales with body size. The angular acceleration ($\alpha$) of a body is a function of the torque ($\tau$) applied to the body divided by its rotational inertia, $I$ ($\alpha = \tau/I$). Torque equals muscle force ($F_m$) multiplied by the moment arm over which the force acts ($\tau = F_m r$) and, therefore, scales to mass to the 2/3 power multiplied by mass to the 1/3 power, or mass to the power 1. Thus, in geometrically similar animals, angular acceleration scales to body mass ($m$) to the −2/3 power (i.e. $\alpha = m^1/m^{-5/3}$). Thus, turning would obviously have been much more difficult for large than for small theropods. The trend of reduced body size in maniraptoran theropods and in early Aves (Sereno, 1999) may have significantly improved their turning agility.

The results from the stepping-stone slalom test (Fig. 3C) combined with the scaling relationship of angular acceleration lead us to suggest that theropods of moderate to large body size (greater than 70 kg) would have been restricted to relatively simple terrain. Among Recent mammals, presumably for reasons of musculoskeletal strength (Alexander, 1979; Biewener, 1989; Vogel, 1988), the largest species are restricted to simple topography. Elephants and rhinoceroses, for example, are not found in boulder fields or on steep slopes. The risk of injury from falls in large animals has been evaluated to address the question of how fast large theropods, such as *Tyrannosaurus*, could have run (Farlow et al., 1995; Alexander, 1996; Farlow et al., 2000). These authors found that large theropods would indeed risk injury if they were to fall while traveling at moderate speeds. To this argument we would like to add the suggestion that the large rotational inertia of basal theropods would have increased the probability of missteps and falls in rough terrain. Hence, theropod communities in broken or mountainous terrain may have had a lower average body size than do Recent mammalian communities in similar terrain.

The negative relationship between angular acceleration and body size may help explain the convergent evolution observed in several lineages of gigantic theropods (Bakker et al., 1992). Theropods evolved the body size of *Tyrannosaurus rex* five times. Four of these groups exhibited convergent reduction of forelimb length and mass and of torso length. These trends were particularly apparent in the giant allosaurid *Epanterias*, in the largest acrocanthosaurs, and in *Tyrannosaurus*. Furthermore, both the acrocanthosaurs and *Tyrannosaurus* also exhibited extensive pneumatization of the braincase. These observations are consistent with our hypothesis that turning agility was highly constrained in the largest bipedal dinosaurs.

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