

# Influence of increased rotational inertia on the turning performance of humans

David V. Lee, Rebecca M. Walter, Stephen M. Deban and David R. Carrier\*

*Department of Biology, 201 South Biology Building, University of Utah, Salt Lake City, UT 84112, USA*

\*e-mail: carrier@biology.utah.edu

*Accepted 24 August 2001*

## Summary

The rotational inertia of an animal can be expected to influence directly its ability to execute rapid turning maneuvers. We hypothesized that a ninefold increase in rotational inertia would reduce maximum turning performance to one-ninth of control values. To test this prediction, we increased rotational inertia about the vertical axis of six human subjects and measured their ability to turn during maximum-effort jump turns. We measured the free moment about a vertical (i.e. yaw) axis as the subjects performed maximum-effort jump turns under three conditions: (i) unencumbered, (ii) wearing a backpack with a control weight and (iii) wearing a backpack of the same mass that increased the rotational inertia of the subject to 9.2 times that with the control weight. Rotational inertia measurements allowed us to estimate the angle turned during the take-off period (i.e. from jump initiation until the feet leave the ground) and the angular power and work of the maximum-effort turns. Surprisingly, the angle turned during take-off in the increased inertia trials was 44.7% of that of the control trials, rather than the 10.9% (9.2-fold reduction) expected on the basis of the increase in rotational inertia. When the subjects turned with increased rotational

inertia, the maximum and mean torques exerted were, on average, 142% and 190%, respectively, of the values recorded during the control trials. Maximum torques during increased rotational inertia trials actually approached isometric maxima. In the increased rotational inertia trials, the angular impulse was 252% of that of the control trials and the take-off period was 130% of that of the control trials. By exerting larger torques over longer take-off periods, the subjects were able partially to compensate for the excess rotational inertia. In contrast to the observed changes in torque, maximum and mean angular power were highest in the unencumbered trials and lowest in the increased inertia trials. On the basis of a decreased ability to generate vertical force when turning and of our estimates of angular power, we speculate that the greater than expected turning performance was due (i) to adjustments in the pattern of muscle recruitment and (ii) to a reduction in the velocity of muscle shortening that resulted in increased muscle forces.

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

---

## Introduction

Rotational inertia ( $I$ ) is the resistance a body offers to torques that act to spin it about an axis. It is the sum of differential elements of mass ( $m$ ) multiplied by the square of their perpendicular distances ( $r$ ) from the axis of rotation: ( $I = \sum m_i r_i^2$ ). Because the perpendicular distance of a mass element from the axis of rotation has a large effect on the rotational inertia of a body (Kreighbaum and Barthels, 1985; Halliday et al., 1993), the size and shape of the body of an animal can be expected to have a profound effect on its turning agility. Although organismal biologists have focused considerable attention on the many ways in which body size and shape influence animal locomotion, only a few studies have considered the impact of rotational inertia on turning performance (Thollesson and Norberg, 1991; Evans and Thomas, 1992; Eilam, 1994; Van Den Berg and Rayner, 1995; Jindrich and Full, 1999). Given the apparent

importance of turning agility in predator/prey contests (Boswell, 1981; Willock and Pearson, 1992), the influence of rotational inertia on locomotor performance warrants further investigation.

We became interested in the effect of rotational inertia on turning performance because we were curious about the extent to which body configuration influenced the agility of theropod dinosaurs (Carrier et al., 2001). The results from that study led us to suspect that the relationship between rotational inertia and turning performance is not as simple as one might initially expect. Elevation of rotational inertia in human subjects decreased turning performance, but the effect appeared to be less than would be predicted from the change in rotational inertia. Here, we quantify the effect of an elevation of rotational inertia on the turning performance of human subjects.

### Materials and methods

To determine the effects of rotational inertia on turning performance, we elevated the rotational inertia of human subjects approximately 9.2-fold above natural values and had the subjects execute maximum-effort turns during vertical leaps from a force plate (i.e. 'jump turns'). The degree to which rotational inertia was elevated (9.2-fold) for the experiment was chosen to provide data that were complementary to a parallel study that addresses the possible impact of rotational inertia on the turning performance of theropod dinosaurs (Carrier et al., 2001). Force plate recordings allowed us to measure the mean and maximum torques, the period of torque application, the total angular impulse, the maximum and mean angular power and the angular work during the turn. At first glance, jump turns might appear to be an unusual type of behavior. In nature, however, 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, to which was attached a 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). The shoulder straps and waist belt of the backpack anchored the apparatus securely to the trunk of the subjects, such that the turning of the subject and the apparatus were tightly coupled. 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.

Ideally, there is no horizontal translation in a simple jump turn, so nearly all the rotation is due to a force couple exerted on the ground by the feet. The resulting ground reaction torque is termed the free moment. Free moments generated by the subjects during maximal jump turns were measured as a force couple by the horizontal sensors of a Kistler 9281B SN force plate. Forces applied to the force plate were sampled at 200 Hz with a BioPac Systems, Inc. (MP 100) analog-to-digital converter and stored on a Macintosh computer. Force outputs from the horizontal sensors were summed to yield the net horizontal force. The appropriate fraction of net horizontal force (determined by the proximity of the center of pressure to the sensors) was subtracted from the outputs of two parallel sensors to remove translational components, yielding equal and opposite forces with parallel lines of action (a force couple). One of these forces was then multiplied by the distance between the sensors to yield a moment. This procedure was carried out for both components of the horizontal force, and their moments were summed to give the free moment (Holden and Cavanagh, 1991).

Each subject performed six maximum-effort jump turns under three conditions for a total of 18 turns: turning

unencumbered (U), turning with the control weight (W) and turning with the increased rotational inertia (I). To control for the effects of fatigue, the 18 turns were conducted in two recording sessions in the order U, W, I, I, U, W, W, I, U in the first session; the order was reversed in the second session: U, I, W, W, U, I, I, W, U. The subjects began each jump with their feet at shoulder width, and their arms were kept at their sides in a relaxed position throughout the jump. Reported values of torque, impulse, power, etc. represent the means of the six jumps for each subject and the average of the means of all six subjects. To test for significant differences between the three experimental conditions, we used a repeated-measures analysis of variance (ANOVA) with Tukey–Kramer multiple-comparisons test, accepted at  $\alpha < 0.05$ . Comparisons between jump-turns and non-turning vertical jumps were made with Student's *t*-test, accepted at  $\alpha < 0.05$ .

To determine empirically the rotational inertia of the subjects under the three test conditions [unencumbered ( $I_U$ ), control weight ( $I_W$ ) and elevated inertia ( $I_I$ )] subjects performed slow, 360° stepping turns on the force plate (Kistler 9281B SN). Rotational inertia was calculated for each subject by double-integrating the time variation of the free moment,  $\tau(t)$ , applied during the stepping turn and dividing by the angle turned ( $2\pi$  rad):

$$I = \int \tau(t) dt^2 / 2\pi,$$

Constants of integration are zero because initial angle and initial angular velocity are zero. Reported values represent the mean and standard deviation (S.D.) of six turns under each condition for each subject. Because the subjects performed these 360° turns while standing in an erect posture, the reported values closely approximate their rotational inertia from the end of take-off through the flight phase of a jump turn. During the take-off phase of a jump turn, however, humans first crouch down, flexing at the ankles, knees and hips, and then leap upwards as they begin to spin about a vertical axis. Because rotational inertia is influenced by the crouched posture, it was necessary to approximate the average rotational inertia during the take-off phase of the jump turn to calculate angular power and work. To estimate the time-averaged rotational inertia during the take-off phase of the jump turn, we averaged the rotational inertia values measured in six 360° stepping turns in a standing posture and six 360° stepping turns in a crouched posture that matched the posture of each subject at the start of the jump turn.

Angular velocity at each instant during the take-off phase of a jump turn was determined by dividing the integral of the ground reaction torque by the estimated time-averaged rotational inertia. For each jump turn, angular power was calculated as the product of the time-varying ground reaction torque and angular velocity during the take-off period. For measurement of translational power and work with force plates, see Cavagna (1985). Angular power was then integrated to yield the total angular work during take-off. The angle turned during the take-off period of a jump turn was determined by double-integrating the ground reaction torque

Table 1. Subject mass and rotational inertia during standing and crouching

Subject	Mass (kg)	Standing			Crouching	
		$I_U$ (kg m <sup>2</sup> )	$I_W$ (kg m <sup>2</sup> )	$I_I$ (kg m <sup>2</sup> )*	$I_U$ (kg m <sup>2</sup> )	$I_W$ (kg m <sup>2</sup> )
A	79.1	1.28±0.02	1.69±0.03	16.12±0.15 (954%)	2.47±0.16	3.22±0.20
B	75.9	1.16±0.01	1.71±0.04	16.52±0.12 (966%)	2.73±0.17	3.73±0.19
C	63.6	0.91±0.03	1.45±0.04	12.50±0.10 (862%)	1.60±0.18	2.74±0.28
D	79.5	1.37±0.02	1.98±0.01	16.47±0.06 (832%)	2.57±0.13	3.62±0.12
E	61.4	0.83±0.03	1.50±0.02	12.79±0.03 (853%)	1.66±0.10	2.58±0.11
F	77.4	1.15±0.02	1.55±0.04	16.47±0.10 (1062%)	2.35±0.11	3.27±0.23
Mean	72.8	1.12	1.65	15.15 (921%)	2.23	3.19
S.E.M.		0.085	0.079	0.794	0.197	0.188

Means and standard deviations from six trials are given for each subject.

Measurements were unencumbered ( $I_U$ ), weight-controlled ( $I_W$ ) or increased inertia ( $I_I$ ).

\*Values in parentheses indicate the increase in rotational inertia as a percentage of weight-controlled values.

and dividing by the estimated time-averaged rotational inertia.

To determine the extent to which increased rotational inertia influenced the ability of the subjects to apply vertical forces to the ground and the extent to which the act of turning affected the application of vertical force, each subject executed control trials in which they attempted to jump as high as possible without turning. For each condition (unencumbered, weight-controlled and increased inertia), each subject performed six maximum-effort vertical jumps from the force plate. To control for the effects of fatigue, these trials were conducted in the same alternating sequence described above for the jump turns.

Jump turn performance improved with experience. Hence, subjects were required to practice until their performance became repeatable.

#### Manipulation of rotational inertia

We measured the rotational inertia about a vertical axis in erect, standing subjects (Table 1). This posture closely approximates the posture at the end of take-off and during the flight phase of a jump turn. Hence, the standing values reported in Table 1 were similar to rotational inertia at the end of take-off and during the flight phase of a jump turn. The mean rotational inertia of the unencumbered subjects was 1.12 kg m<sup>2</sup>. Carrying the control weight increased the rotational inertia of the subjects to 147% to a mean of 1.65 kg m<sup>2</sup>. The manipulation to increase rotational inertia resulted in a mean 9.2-fold (921%) increase above the rotational inertia of the weight-controlled trials.

Rotational inertia was also measured in a crouched posture resembling that of jump initiation. Mean values were 2.23 kg m<sup>2</sup> and 3.19 kg m<sup>2</sup> for unencumbered and weight-controlled stepping turns, respectively (Table 1). Hence, crouching approximately doubled standing values of rotational inertia for these two conditions. The means of standing and crouched rotational inertia values provided estimates of time-averaged rotational inertia during the take-off period.

To provide an indication of the maximum isometric torque

that our subjects could apply about a vertical axis, four of the six subjects stood in a crouched posture on the force plate and attempted to twist as hard as possible while they were held stationary by resistance applied to the pack they were wearing.

## Results

### Maximum-effort jump turns

Examples of ground reaction torques recorded by the force plate during maximum-effort jump turns are shown in Fig. 1. The pattern of torque application was similar in the weight-controlled and increased rotational inertia trials. The amplitude of torque rose gradually initially, increased rapidly to a peak midway through take-off and then decreased at a roughly constant rate. A reversal in the direction of the torque was often observed at the end of take-off in both the unencumbered and weight-controlled trials, but not in the increased rotational inertia trials.

The maximum torque produced by the subjects was not significantly different between the unencumbered and weight-controlled trials, but increased to 142% ( $P < 0.001$ ) in the increased rotational inertia trials (Table 2). Similarly, mean torque during the take-off period (i.e. from jump initiation until the feet leave the ground) did not change between unencumbered and weight-controlled trials, but increased to 190% ( $P < 0.001$ ) from the control to the increased rotational inertia trials (Table 2). Hence, both the maximum torque and the mean torque applied to the force plate during the take-off period increased significantly when the rotational inertia of the subjects was increased 9.2-fold.

From stationary trials, the mean maximum isometric torque of the four subjects was  $92.50 \pm 7.99$  N m (mean  $\pm$  S.E.M.,  $N=4$ ). In comparison, when these same subjects turned with the increased rotational inertia, the average of their maximum torques was  $82.42 \pm 5.37$  N m (mean  $\pm$  S.E.M.,  $N=4$ ) and the average of their mean torques was  $42.25 \pm 3.07$  N m (mean  $\pm$  S.E.M.,  $N=4$ ).

The angular impulse of the increased inertia trials was 252%

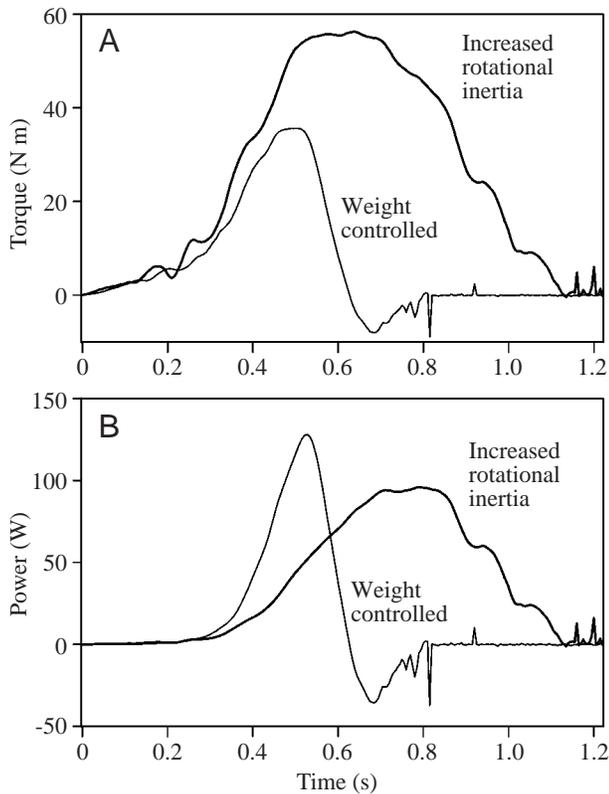


Fig. 1. Sample recordings of the ground reaction torque (A) and angular power (B) applied during maximum-effort jump turns by subject 'B'. The thick lines denote the recording obtained when the subject turned with his rotational inertia elevated 9.7-fold (Table 1) above that of the weight-controlled jump (shown by the thin line). Note that subject B did more angular work (i.e. area under the angular power curves) in the increased rotational inertia trials than in the control trials (Table 5).

of that of the impulse of the weight-controlled trials ( $P < 0.001$ ) (Table 3). The greater angular impulse in the increased rotational inertia trials was a function of both the greater torque applied and an increased period of torque application when

inertia was elevated (Table 3). The take-off period in the increased rotational inertia trials was 130% of that of the weight-controlled trials ( $P < 0.01$ ).

The angle turned during the take-off period was much greater than predicted when the subjects turned with increased rotational inertia (Table 4). The estimated angle turned during take-off averaged  $95^\circ$  when the subjects turned with the control weight. Given this value, the 9.2-fold increase in rotational inertia would be expected to reduce the angle to approximately  $10^\circ$ . Instead, we observed an average of  $42^\circ$  of rotation during take-off when the subjects turned with the increased rotational inertia.

#### Comparison with maximum-effort vertical jumps

The mean vertical force in the take-off period was the same for unencumbered and weight-controlled trials in both maximum-effort vertical jumps and maximum-effort jump turns (Fig. 2A). The mean vertical force was lower, however, when the subjects jumped with increased rotational inertia. In the vertical jumps, the mean vertical force applied to the force plate when the subjects jumped with increased rotational inertia was only 74% of the mean vertical force applied during the control trials ( $P < 0.001$ ). Similarly, in jump turns, the mean vertical force when the subjects turned with increased rotational inertia was only 52% of that for the control trials ( $P < 0.001$ ). Moreover, when the subjects jumped with increased rotational inertia, there was a difference in mean vertical force between vertical jump and jump turn trials. Specifically, the mean vertical force in jump turns was 31% of that of subjects simply jumping vertically ( $P = 0.0011$ ).

The vertical impulse, or area under the force/time curve, during maximum-effort vertical jumps and maximal-effort jump turns showed a pattern very similar to that of the average vertical force described above (Fig. 2B). The vertical impulse did not differ between the unencumbered and weight-controlled trials. Increased rotational inertia did result in a decrease in vertical impulse compared with the weight-controlled trials for both vertical jumps ( $P < 0.001$ ) and jump turns ( $P < 0.001$ ). In addition, vertical impulse was

Table 2. Maximum and mean torques exerted during the take-off phase of maximum-effort jump turns

Subject	Maximum torque (N m)			Mean torque (N m)		
	U	W	I*	U	W	I*
A	47.79±8.60	42.79±4.19	73.40±11.00 (172%)	20.47±4.90	19.09±1.67	45.43±8.11 (238%)
B	52.51±2.13	53.16±5.68	69.49±5.34 (131%)	21.57±2.20	18.80±4.26	35.67±3.55 (190%)
C	60.33±7.91	62.65±5.46	77.85±6.76 (124%)	17.67±3.11	19.38±5.24	41.14±4.43 (212%)
D	70.83±9.53	61.73±2.91	89.54±8.62 (145%)	28.03±6.54	26.30±1.47	41.69±5.88 (158%)
E	46.75±2.67	42.49±5.41	65.49±5.39 (154%)	19.12±2.94	20.53±1.44	41.23±5.95 (201%)
F	63.25±9.02	67.58±5.90	92.79±11.15 (137%)	24.43±2.77	30.31±3.26	50.49±8.53 (167%)
Mean	56.91	55.07	78.09 (142%)	21.88	22.40	42.61 (190%)
S.E.M.	3.88	4.36	4.48	1.54	1.95	2.02

\*Values in parentheses indicate the increase in maximum and mean torques as a percentage of weight-controlled values. Measurements were unencumbered (U), weight-controlled (W) or increased rotational inertia (I).

Table 3. Duration of torque application and angular impulse during the take-off phase of maximum-effort jump turns

Subject	Period (s)			Angular impulse (N m s)		
	U	W	I*	U	W	I*
A	0.493±0.064	0.647±0.091	0.797±0.142 (123%)	9.84±1.25	12.26±1.22	35.60±5.34 (290%)
B	0.467±0.061	0.648±0.105	0.971±0.122 (150%)	9.96±0.69	11.87±1.62	34.38±3.31 (290%)
C	0.562±0.113	0.678±0.127	0.752±0.069 (111%)	9.86±0.95	12.66±1.74	30.93±4.04 (244%)
D	0.491±0.054	0.536±0.051	0.722±0.174 (134%)	13.49±1.62	14.08±1.47	30.92±3.75 (219%)
E	0.535±0.044	0.547±0.032	0.747±0.098 (136%)	10.14±1.08	11.20±0.73	30.45±3.18 (272%)
F	0.468±0.029	0.491±0.032	0.632±0.071 (129%)	11.46±1.57	14.81±1.22	31.51±2.84 (213%)
Mean	0.503	0.591	0.770 (130%)	10.79	12.81	32.30 (252%)
S.E.M.	0.016	0.031	0.046	0.59	0.56	0.88

\*Values in parentheses indicate the increase in period and angular impulse as a percentage of weight-controlled values. Measurements were unencumbered (U), weight-controlled (W) or increased rotational inertia (I).

lower in the increased rotational inertia trials when subjects attempted to turn rather than simply jumping vertically ( $P=0.0010$ ).

Angular power and work

Angular power production followed a slightly delayed time course relative to torque application (Fig. 1B), with the delay

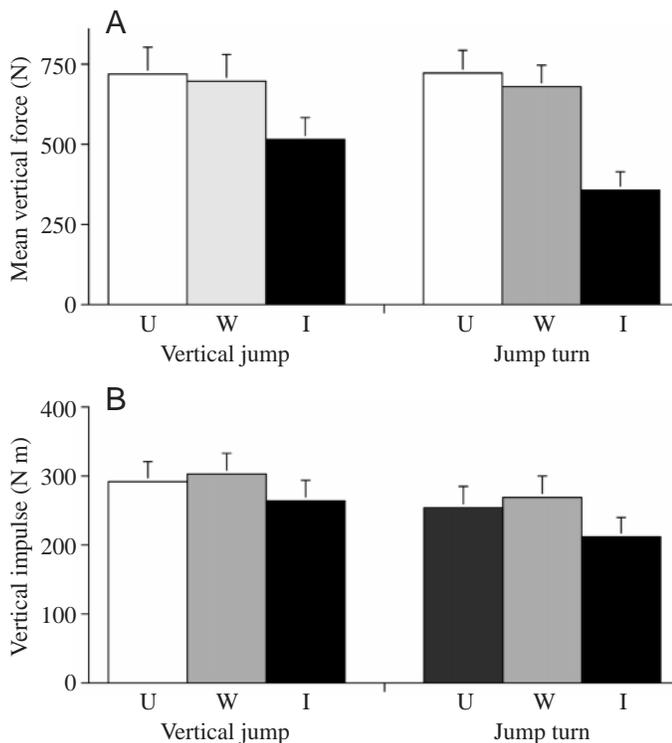


Fig. 2. Mean vertical force (A) and the vertical impulse (B) applied to the force plate by the six subjects during maximal-effort vertical jumps and maximal-effort jump turns. In the vertical jump trials, the subjects did not attempt to turn. In the jump turns trials, the subjects attempted to turn as far as possible as they jumped. In each case, the three columns represent jumping unencumbered (U), jumping with the control weight (W) and jumping with the increased rotational inertia (I). Values are means ± s.d.

being greater in the increased rotational inertia trials than in the weight-controlled trials. The greatest angular power was observed during the unencumbered trials. Both maximum and mean angular power were highest in the unencumbered trials and lowest in the increased inertia trials (Table 5). Maximum angular power in the increased inertia trials was 41 % of that of the weight-controlled trials ( $P<0.05$ ). Mean angular power in the increased inertia trials was 29 % of that of the weight-controlled trials, but this difference was not statistically significant ( $P>0.05$ ). In contrast, the angular work produced by the six subjects during maximum-effort jump turns did not vary significantly in the three test conditions (Table 5). Angular work was highly variable among the different subjects. Some subjects produced greater work in the weight-controlled trials than in the increased inertia trials, whereas other subjects showed the opposite pattern. Note that the example shown in Fig. 1B is from one of the subjects that did more angular work in the increased inertia trials than in the control trials.

Discussion

First principles predict a simple relationship between the rotational inertia and the turning performance of a subject. A doubling of rotational inertia would be expected to cut turning performance by half. In this experiment, we increased the rotational inertia of our human subjects 9.2-fold above that of the weight-controlled trials and would, therefore, have expected turning performance to be reduced 9.2-fold. What we observed, however, was a substantial increase in torque production (Table 2) and a reduction in the angle turned during take-off to 44.7 % of that of weight-controlled values (Table 4) rather than the expected 10.9 %. On average, maximum and mean torques were 142 % and 190 % of those of control trials, respectively, when rotational inertia was elevated. Larger torques combined with an increase in the period of torque application to 130 % resulted in an increase in angular impulse to 252 % when the subjects turned with increased rotational inertia. This larger angular impulse compensated partially for the excess rotational inertia; hence, mean angular velocity during take-off in the increased inertia trials was reduced to

Table 4. Angle turned during take-off of maximum-effort jump turns

Subject	Rotation (degrees)		
	U	W	I*
A	84.3±10.0	101.1±17.9	48.5±11.3 (47.9%)
B	88.7±15.4	93.4±7.6	52.7±10.3 (56.4%)
C	129.3±15.7	104.9±11.8	53.9±14.7 (51.4%)
D	98.1±7.6	78.5±7.3	28.0±4.6 (35.6%)
E	129.9±13.7	89.1±8.1	44.1±9.3 (49.5%)
F	103.1±17.9	100.3±17.4	26.8±8.3 (26.7%)
Mean	105.6	94.6	42.3 (44.7%)
S.E.M.	8.1	4.0	4.9

\*Values in parentheses indicate the decrease in angle turned as a percentage of weight-controlled values.

Measurements were unencumbered (U), weight-controlled (W) or increased rotational inertia (I).

34.5% of that of weight-controlled values, rather than to 10.9%. We suspect that there are at least two factors that contribute to the greater torque production when the subjects turned with increased rotational inertia: (i) adjustments in the pattern of muscle recruitment and (ii) a reduction in muscle shortening velocity that resulted in increased muscle forces.

To distinguish the effects of (i) increased rotational inertia and (ii) turning on the generation of vertical force and vertical impulse, we ran control trials in which the subjects performed maximum-effort vertical jumps. Although the control weight did not influence the abilities of the subjects to apply vertical force, the vertical jump trials demonstrated that increased rotational inertia reduced both the vertical force and the vertical impulse (Fig. 2). Specifically, there was a 26% reduction in mean vertical force from the control to the increased rotational inertia jumps. We suspect that the decrease in vertical jump performance observed in the increased rotational inertia trials resulted from an impaired ability to flex and extend the trunk rapidly at the hip joints because of the increased rotational inertia. In other words, because the elevated inertia apparatus also increased the rotational inertia of the trunk about the pitch axis, the subjects could not rapidly

flex and extend at the hips. The act of turning also decreased the vertical force applied to the ground. When the subjects performed maximum-effort jump turns with increased inertia, the mean vertical force was only 69% of the vertical force generated during vertical jumps with increased inertia (Fig. 2). The explanation for reduced vertical force during jump turns is unclear, but appears to be due to a functional conflict within individual muscles that produce both vertical and angular work. This possibility is discussed below.

Recruitment of muscles that produce both rotational torque and vertical force could change depending on the task. There is good reason to suspect that there is a trade-off in muscle recruitment for maximum angular impulse *versus* maximum vertical impulse produced in a jump turn. Some of the same muscles that produce hip rotation, and hence torque production, also extend the hip joint and, therefore, produce vertical forces. Torque production requires an active lateral rotation of the hip joint on the outside of the turn and/or an active medial rotation of the hip joint on the inside of the turn. The human body has a greater ability to produce lateral hip rotation than medial hip rotation (Williams et al., 1989), and the impression of the subjects in this study, from their sense of muscle fatigue, was that the lateral rotators of the outside hip contributed more to the turns than did the medial rotators of the inside hip. During the impulse of a maximum-effort jump turn, we would expect the lateral rotators of the hip and lower leg to be maximally active in the outside leg but inactive at the same time in the inside leg. At least two of these muscles, the gluteus maximus and biceps femoris, not only contribute to lateral rotation of the leg, but also are instrumental in hip extension and vertical force production (Williams et al., 1989). Hence, if maximum torque production requires that some of the hip extensors in the inside leg be turned off, vertical force and vertical impulse may be compromised in maximum-effort jump turns. A comparison of the average vertical force and vertical impulse in the jump turns *versus* the simple vertical jumps (Fig. 2) supports this suggestion.

Another factor that could account for the larger torques produced when the subjects turned with increased rotational inertia is the force/velocity relationship of muscle contraction (Hill, 1938). If the muscles responsible for torque production

Table 5. Maximum angular power, mean angular power and angular work during the take-off phase of maximum-effort jump turns

Subject	Maximum angular power (W)			Mean angular power (W)			Angular work (J)		
	U	W	I	U	W	I	U	W	I
A	153.35±45.30	148.93±25.19	113.59±34.05	56.97±17.81	44.83±7.55	48.63±14.58	27.02±6.25	31.32±6.10	41.22±12.27
B	182.90±18.99	161.89±23.37	91.42±17.66	55.00±8.18	42.94±13.84	37.09±5.63	26.63±3.36	26.46±6.76	36.44±7.08
C	313.41±64.26	248.19±62.16	123.67±22.98	77.93±12.79	71.15±24.99	49.71±9.43	41.20±7.86	39.67±10.17	39.18±10.07
D	321.13±83.37	183.72±33.59	115.56±23.79	103.48±26.24	68.03±9.92	42.63±8.43	48.12±11.59	36.33±7.25	29.78±6.71
E	238.30±43.49	140.97±33.03	119.62±16.61	84.42±17.17	59.23±10.83	47.86±11.17	42.88±8.87	31.02±3.60	36.43±8.60
F	244.52±79.75	239.32±40.40	103.60±28.18	88.35±22.34	93.94±17.35	45.15±15.68	39.42±10.63	46.63±7.69	27.26±10.00
Mean	242.27	187.17	111.24	77.69	63.35	45.18	37.54	35.24	35.05
S.E.M.	27.53	18.88	4.83	7.68	7.73	1.93	3.59	2.95	2.22

shortened more slowly in the increased inertia trials than in the weight-controlled trials, the force/velocity relationship predicts that they could generate more force. One might expect that the greater rotational inertia would result in a reduced rate of muscle shortening during maximal-effort turns, and our observations suggest that this was the case. In the increased rotational inertia trials, the period of torque application increased to 130% of that of control trials (Table 3) and the angle turned during take-off decreased to 44.7% of that of control values (Table 4). These values indicate that the average velocity of muscle shortening during the increased rotational inertia trials decreased to 34.5% of the control value. Depending on the percentage of maximum shortening velocity at which the muscles were operating during the control trials, a reduction to 34.5% of control values in shortening velocity could easily result in an increase in muscle force production that would account for the increase in mean torque to 190% of the control values.

Our estimates of angular power and recordings of maximum isometric torque provide clues as to where on the force/velocity relationship the muscles responsible for angular work operate during maximum-effort jump turns. Values of both maximum and mean angular power were highest during the unencumbered trials and lowest during the increased inertia trials (Table 5). In addition, our attempts to measure the maximum isometric torque of the subjects gave values that were only slightly larger than the peak torque values observed during the maximum-effort jump turns with increased rotational inertia. Because skeletal muscle produces peak power when it shortens at intermediate velocities (roughly 30% of maximal shortening velocity,  $V_{\max}$ ) (McMahon, 1984), these observations led us to speculate that the muscles responsible for angular work may shorten at velocities that provide close to peak power when unencumbered humans perform maximum-effort jump turns. First, the observation that maximum isometric torques were approximately 200% of the mean torques observed during the increased inertia trials suggests that the average shortening velocities of the increased inertia trials were a small fraction (i.e. 10–20%) of the maximum velocities of shortening of the muscles (refer to a representative force/velocity curve) (e.g. McMahon, 1984). Second, mean power in increased inertia trials was only 58% of mean power in unencumbered trials (Table 5). This suggests that the average shortening velocities were greater in the unencumbered than in the increased inertia trials and implies an average shortening velocity during the unencumbered trials of somewhere in the range 20–40% of  $V_{\max}$ . Hence, the observations of this study do not exclude the possibility that the muscles responsible for rotational work shorten at a velocity that provides close to peak power when unencumbered humans attempt maximum-effort jump turns.

Irrespective of whether humans can approach peak muscle power when performing rapid turning maneuvers, it is clear that the elevation of the rotational inertia of a subject did influence the contractile performance of the muscles producing the maximum-effort turns. The turning muscles did not exert maximum force in unencumbered and weight-controlled trials,

nor did they exert maximum power in increased inertia trials. Furthermore, turning performance was clearly compromised by an upper limit on torque magnitude in the increased rotational inertia trials.

In conclusion, our initial hypothesis that turning performance is related in a simple way to the rotational inertia of the body can be viewed as naive. There are many examples in which physical principles, by themselves, have been shown to be poor predictors of locomotor performance. 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) and cases in which the metabolic cost of carrying loads have been shown to be less than the increase in mechanical work would predict (Maloij et al., 1986; Kram, 1996; Baudinette and Biewener, 1998). These are instances in which our incomplete understanding of the physiology of muscle contraction and the mechanics of musculoskeletal systems has been shown to limit severely the predictive power of physical first principles. In this study, the greater torques exerted on the ground and longer take-off periods when subjects turned with elevated rotational inertia provide another illustration of the complex interface between physical principles and muscle physiology.

We thank C. Farmer, J. Otterstrom and J. Sorensen for assistance in the collection of the data. K. Autumn and an anonymous reviewer provide comments that were instrumental in the initiation of this study. This investigation was supported by The National Science Foundation: IBN-9807534.

## References

- Baudinette, R. V. and Biewener, A. A.** (1998). Young wallabies get a free ride. *Nature* **395**, 653–654.
- Boswell, J.** (1981). *NOVA: Animal Olympians*. Stamford, CT: Vestron Video.
- Carrier, D. R., Walter, R. M. and Lee, D. V.** (2001). Influence of rotational inertia on turning performance of theropod dinosaurs: clues from humans with increased rotational inertia. *J. Exp. Biol.* **204**, 3917–3926.
- Cavagna, G. A.** (1985). Force platforms as ergometers. *J. Appl. Physiol.* **39**, 174–179.
- Cavagna, G. A., Saibene, F. P. and Margaria, R.** (1964). Mechanical work in running. *J. Appl. Physiol.* **19**, 249–256.
- Eilam, D.** (1994). Influence of body morphology on turning behaviors in carnivores. *J. Motor Behav.* **26**, 3–12.
- Evans, M. R. and Thomas, A. L. R.** (1992). The aerodynamic and mechanical effects of elongated tails in the scarlet-tufted malachite sunbird: measuring the cost of a handicap. *Anim. Behav.* **43**, 337–347.
- Halliday, D., Resnick, R. and Walker, J.** (1993). *Fundamentals of Physics*. New York: John Wiley & Sons, Inc.
- Heglund, N. C., Fedak, M. A., Taylor, C. R. and Cavagna, G. A.** (1982). Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 57–66.
- Hill, A. V.** (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. B* **126**, 136–195.
- Holden, J. P. and Cavanagh, P. R.** (1991). The free moment of ground reaction in distance running and its changes with pronation. *J. Biomech.* **24**, 887–897.
- Jindrich, D. L. and Full, R. J.** (1999). Many-legged maneuverability: dynamics of turning in hexapods. *J. Exp. Biol.* **202**, 1603–1623.
- Kram, R.** (1996). Inexpensive load carrying by rhinoceros beetles. *J. Exp. Biol.* **199**, 609–612.

3934 D. V. Lee and others

- Kreighbaum, E. and Barthels, K. M.** (1985). *Biomechanics*. Minneapolis: Burgess Publishing Company.
- Maloiy, G. M. O., Heglund, N. C., Prager, L. M., Cavagna, G. A. and Taylor, C. R.** (1986). Energetic cost of carrying loads: have African women discovered an economic way? *Nature* **319**, 668–669.
- McMahon, T. A.** (1984). *Muscles, Reflexes and Locomotion*. Princeton, NJ: Princeton University Press.
- Taylor, C. R.** (1994). Relating mechanics and energetics during exercise. *Adv. Vet. Sci. Comp. Med.* **38A**, 181–215.
- Thollesson, M. and Norberg, U. M.** (1991). Moments of inertia of bat wings and body. *J. Exp. Biol.* **158**, 19–35.
- Van Den Berg, C. and Rayner, J. M. V.** (1995). The moment of inertia of bird wings and the inertial power requirement for flapping flight. *J. Exp. Biol.* **198**, 1655–1664.
- Williams, P. L., Warwick, R., Dyson, M. and Bannister, L. H.** (1989). *Gray's Anatomy*. 37th Edition. Edinburgh: Churchill-Livingstone.
- Willock, C. and Pearson, J.** (1992). *Predators of the Wild*, vol. 6. Burbank, CA: Warner House Video.