



Original investigation

Observations on escape runs in wild European hare as a basis for the mechanical concept of extreme cornering with special inference of a role of the peculiar subclavian muscle

A.N. Kuznetsov^{a,*}, O.S. Luchkina^b, A.A. Panyutina^b, N.V. Kryukova^b^a Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow 119234, Russia^b Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia

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ABSTRACT

Hares are known for their turning performance which is studied here for the first time. The present qualitative analysis of the hare turning technique is based on video recordings of *Lepus europaeus* being chased by borzoi sighthounds. Movements of body parts, especially of the ears, act like natural accelerometers, allowing as to restore directions of ground reaction forces acting upon each limb. It was established that the major centripetal force is produced by the forelimbs, the inside hindlimb mainly brakes the forward movement, and the thrust produced by the outside hindlimb is vertical with a minor centripetal component. The turn starts from landing of the outside forelimb, which makes a specific lateral kick against the ground. It is performed by means of pronation of the scapula, apparently driven by unique, peculiarly expanded *M. subclavius*. Thus, the main action in hare turning is non-parasagittal. Surprisingly, the muscular drive of the second (inside) forelimb appears to be the same. Due to the increase in roll-inclination of the body inside the turn, the respective (left or right) *M. subclavius* produces centripetal ground reaction force in both outside and inside forelimbs. The use of the same muscle in both limbs shows the efficiency of muscular employment in cornering performance of the hare. It was established that the cornering hare combines crabbed (based on yaw) and banked (based on roll) turning techniques – the crabbed turn is used in the first locomotor cycle, then banked turn. The crabbed turn in the first locomotor cycle is performed in two stages: first, during the forelimb support, hindquarters yaw outside, then, during the hindlimb support, forequarters yaw inside. This half-by-half yawing allows to reorient the fore-aft axis of the trunk faster.

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Introduction

Hares are well known for their ability for extremely sharp turns which help them escape terrestrial and aerial predators who are faster than they are. Based on morpho-functional comparison of locomotor apparatus of hares and rabbits with pikas, Gambaryan (1974) concluded that the ancestral locomotive substrate for lagomorphs as a group was a rocky terrain, where extant pikas still live. Indeed, ability to abruptly change the direction of run is vital on rocks which provide discrete and stochastically distributed landing points. However, biomechanics of maneuvering were never studied in any lagomorphs. Studies of turning performance of other animals are scarce too. Special muscular adaptations for cornering are yet to be uncovered. Let us provide a brief summary of the main findings.

To our knowledge, the first experimental study of cornering was performed using three-flash stroboscope on the great jerboa (*Allactaga jaculus*), a small agile biped (Aristov et al., 1980). The major findings were: (1) the sideways swing of the tail helps turn the fore-aft axis of the trunk in the suspension (also called floating) phase of the jump due to the tail inertia and (we suppose) due to interaction with the air of the wide hair fan on the tail tip; (2) the first hindlimb to land (the trailing limb) is usually the inside one, in respect of the turn direction. It is worth mentioning, that, contrary to kangaroos, straight-ahead hopping in most of jerboas is performed by slightly out-of-phase hindlimb action (Fokin, 1978).

A study of great theoretical importance was performed on the cockroach *Blaberus discoidalis* (Jindrich and Full, 1999). There, two events were distinguished in the turn in the horizontal plane: (1) the change of direction of travel, which is the deflection of the velocity vector of the common center of mass of the body due to centripetal (i.e., perpendicular to the velocity vector) horizontal component of the ground reaction force acting on a limb, and (2)

* Corresponding author.

E-mail address: sasakuzn@mail.ru (A.N. Kuznetsov).

reorientation of the fore-aft axis of the body in the same direction caused by torque due to misalignment of the horizontal component of the ground reaction force with the center of mass. Ideally, the direction of travel and fore-aft axis coincide throughout the turn, but to do so, the six legs of hexapods (as well as the four legs of quadrupeds) must act differently. For the forelimbs, it is enough to produce a purely centripetal force in the horizontal plane, but it is not so for the hindlimbs: to minimize divergence of the fore-aft axis from the direction of travel, the inside hindlimb must produce a braking force component, and the outside hindlimb must produce accelerating component. However, in their model, Jindrich and Full (1999) ignored the changes in magnitude of the velocity, because cockroaches performed relatively gentle (big radius) turns. By means of sophisticated photoelastic technique, they measured single-leg horizontal ground reaction forces and found that the outside legs play the primary role in force and torque production for cockroach cornering. Sprawling limbs easily generate lateral thrusts and, in response, medially-directed forces of ground reaction. These forces are involved in the straight-ahead running of cockroach. In fact, change of direction of travel results from reduction of medially-directed components of ground reaction on the inside limbs, and the respective reorientation of the fore-aft axis of the body results from the prevalence of the medially-directed component on the outside forelimb. In respect of force distribution, cornering of sprawlers may be compared to that of a four-wheeled vehicle (Alexander, 2002).

As compared to the sprawling limbs of arthropods, amphibians and reptiles, the parasagittal legs of mammals and birds are much less conductive in producing transverse forces. That is why, these animals need to use, somehow, available parasagittal forces to turn. Parasagittal force of ground reaction can be represented as two Cartesian components, one pointing dorsally, and the other pointing anteriorly or posteriorly. In straight-ahead locomotion over level substrate, the first one is vertical (normal to the substrate), and the second is based on friction or grip, but both of them can be employed in cornering: (1) banked turn implies that the dorsally-directed component becomes centripetal when body rolls, i.e. leans into the curve of the turn, as does the bicyclist; (2) so-called “crabbed turn” implies that the anteriorly-directed component becomes centripetal when the body yaws into the curve of the turn, in advance, in order to change the direction of travel. Wild mice (*Mus musculus*) were shown to use the second technique in right-angle cornering when bounding at 1.3 m/s (Walter, 2003). They do it as follows. At the end of the forelimb contact phase of the stride, when the back is most crouched and, hence, the rotational inertia of the trunk in respect of yawing reaches its minimum, mice rather easily rotate their trunk into the turn, and this motion enables them to use propulsive effort of the limbs centripetally. This yawing starts head-first by centripetal shift of the anterior part of the body during the forelimb contact phase. The stride frequency does not change in cornering mice, but the limb duty factor increases so that duration of the suspension phases of the stride, when the limbs do not control the trajectory of movement, is reduced.

Similar to mouse on the ground, the lesser short-nosed fruit bat *Cynopterus brachyotis* in the air starts the 90° horizontal maneuver as the crabbed turn, by fore-aft body axis reorientation during the wing upstroke (Iriarte-Díaz and Swartz, 2008). Then, during downstroke, the bat rolls into the banked turn to deflect the velocity vector of its center of mass. Note the contradictory usage of the term “heading” by Iriarte-Díaz and Swartz (2008) and by Jindrich and Full (1999). For the bat “heading” meant the fore-aft body axis reorientation, while for the cockroach it meant the deflection of the direction of travel of the common center of mass. So, we will avoid this term.

Very important point in maneuvering is the possible limit of minimization of turning radius, which can serve as a measure for animal's agility. The radius is proportional to the kinetic energy of the common center of mass of the body and inversely proportional to the magnitude of centripetal force ($r = mV^2/F$). The lighter, slower and stronger animals turn more tightly. An animal cannot change its mass, but can slow down; the question remains, what factor constrains its centripetal force. Alexander (2002) developed simple mathematic model for two possibilities: (1) the limitation by muscular strength of an organism and (2) the limitation by friction coefficient of a substrate. For humans, the plot of running speed against turning radius, suggests that at smaller radii the speed is limited by ground friction (grip), while at larger radii it is limited by ability of an athlete to exert forces. This means that at larger radii, although an athlete runs faster than at smaller ones, but his speed is lower, than the friction allows. The same is, apparently, true for horses (Tan and Wilson, 2011).

As opposed to humans and horses, greyhounds keep the maximum speed of straight-ahead sprint when they race round a bend with a radius of ~20 m, which means that they have an extra force ability (Usherwood and Wilson, 2005). In fact, it is implemented in the increased dorsally-directed component of the parasagittal limb force, which is inclined centripetally in the banked cornering. Cheetahs definitely rank over greyhounds in locomotor strength, but GPS and accelerometer data show that hunting in wild is not a sporting race, and they slow down while maneuvering in order to reduce radius of turn and catch an agile prey (Wilson et al., 2013a,b).

Recently, on humans, it was shown that turning is associated with extra energy costs, and so the speed is limited in cornering not only by ground friction and force capacity of an animal, but also by the power constraint (Wilson et al., 2013c). In our opinion, this may account for, otherwise mysterious, significantly higher power output of muscle fibers of the rabbit than of those of the cheetah (West et al., 2013). Indeed, rabbits and even hares are not as fast and as heavy as cheetahs and greyhounds, but they turn tighter and, due to enlarged digestive tract, possess smaller muscular mass relative to the body weight. This may necessitate increased power properties of the striated muscular tissue. Data on the weight of digestive tract are rather scarce indeed and, in most cases, one has to recalculate relative weights from available absolute values. In leporids stomach and intestine comprise together from 10 to 20% of the body weight (Meredith, 2010; Jin et al., 2014), while in felidae and domestic dogs this value is normally below 6% (Crile and Quiring, 1940; Chivers and Hladik, 1980; Bourreau et al., 2004).

With respect to the energetics of turns, one more question should be posed, which was never considered in the literature on animal cornering. What energy conversions can be expected in turning locomotion? When an animal starts cornering, it possesses some amount of kinetic energy of its common center of mass. Now it needs to gain some rotational kinetic energy, either to yaw into the turn if it uses the crabbed technique, or to roll on the inner side if it uses the banked technique. How can the animal convert part of the initial kinetic energy of the center of mass into the rotational kinetic energy and, at the end of cornering, convert it back? This would much decrease the cost of turning, and, at the same time, reduce its radius, since the speed of the center of mass would fall in favor of rotation.

Taking into account all of the above, we performed field video recording of extreme maneuvers of the European hare (*Lepus europaeus*) chased by Russian and chortai borzoi sighthounds. This species is one of the fastest lagomorphs: its straight-ahead running speed is known to reach 20 m/s (Garland, 1983).

Our main intention was the search for adaptive significance of myologic peculiarities of hares in their cornering technique. The most striking peculiarity is found in subclavian muscle, the *M. subclavius*. In most therians, if present, it is hidden under the clavicle,

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