

Propulsive impulse as a covarying performance measure in the comparison of the kinematics of swimming and jumping in frogs

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Summary

Animals have to modulate their locomotor behavior according to changes in external circumstances. The locomotor requirements are expected to be most extreme for species that move through different physical environments, such as water *versus* land.

In this study, we examine the use of the propulsive impulse as a covariate in the comparison of the kinematics of locomotion of a semi-aquatic frog *Rana esculenta*, across land and through water. We focused on the propulsive phase because it is functionally the most significant phase of the locomotor cycle in both jumping and swimming, and it is also the most comparable.

The frog alters the joint angles of its legs in order

to adjust its performance (i.e. impulse) within both locomotor modes. The kinematics and this modulation of the propulsive phase differ between the two modes; however, we found that the impulse ranges of swimming and jumping do not fully overlap. Possible explanations for this include larger lateral forces during swimming, a reduced force transmission due to a lower external load during swimming and reduced muscle recruitment due to differences in coordination patterns.

Key words: locomotion, Anura, frog, *Rana esculenta*, kinematics, swimming, jumping.

Introduction

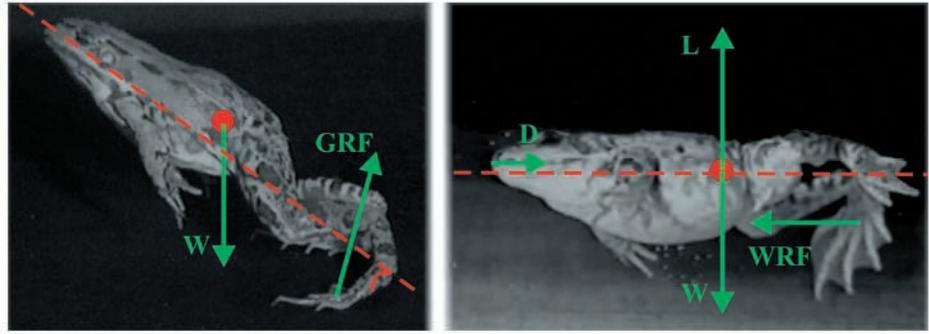
Animal locomotion is far from stereotyped. Animals have to modulate their locomotor behavior according to changes in external circumstances, such as direction, speed or incline (Biewener and Corning, 2001; Irschick and Jayne, 1998). The locomotor requirements are expected to be most extreme for species that move through different physical environments, such as water *versus* land (Biewener and Gillis, 1999). In spite of the striking differences between aquatic and terrestrial environments with respect to several physical properties (Denny, 1993; Vogel, 1994), many animals use their limbs to move about successfully both in water and on land. These semi-aquatic animals occupy a precarious evolutionary position, having to function in both aquatic and terrestrial environments (Fish and Baudinette, 1999). If two tasks require mutually incompatible morphologies of physiologies, it becomes impossible to simultaneously optimize performance in these two tasks: natural selection is expected to result in some intermediate phenotype that provides reasonable performance at both tasks but optimal performance in neither (Shine et al., 2003).

Most anurans use their hind limbs to generate propulsive forces during both jumping and swimming. The same apparatus, the legs, is used to perform the same task, but in two different media. During both locomotor modes, a forceful extension of the legs results in an acceleration of the center

of mass. Since this is essentially the same task, the kinematics of the leg segments are expected to be identical for both locomotor modes. After all, the kinematics represent the dynamic equilibrium between the internal and external forces.

Previous studies on anurans (Kamel et al., 1996; Olson and Marsh, 1998; Gillis and Biewener, 2000) have mainly focused on hind limb muscle function, and have suggested slightly different functional roles for some muscles, depending upon the external environment. However, if the goal of the movement is the same for both locomotor modes (see earlier), but the circumstances are different, muscle recruitment is bound to be different. This theory seems to be confirmed by a study on kinematics of swimming and hopping frogs (Peters et al., 1996), where no differences were found. However, Peters et al. (1996) decided to compare the joint angles at comparable moments in a locomotor cycle, which in turn were determined by limb configuration (essentially the joint angles as well). By determining the different phases in this way, however, the data could be biased. In the present study we have focused on the propulsive phase (the kick), because it is functionally the most significant phase of the locomotor cycle in both jumping and swimming (Nauwelaerts et al., 2001) and it is the only phase that can be independently determined, i.e. from the velocity profile of the center of mass.

Fig. 1. The theoretical sense and orientation of the external forces for jumping and swimming frogs, indicated by green arrows. W, weight; GRF, ground reaction force; L, lift; WRF, water reaction force; D, drag. The red broken line shows the direction of motion. During jumping, the external forces exerted on the frog are at an angle to the direction of motion, whereas in swimming, the external forces are either parallel to or perpendicular to the direction of motion.



The major challenge when comparing aquatic and terrestrial locomotion is to determine which swimming sequence should be compared with which jumping sequence. This is important because it is known that movement patterns change *within* a locomotor mode. Previous studies on kinematics (Peters et al., 1996) and on muscle function (Kamel et al., 1996; Olson and Marsh, 1998; Gillis and Biewener, 2000) compared average sequences, which ignores any intersequential variation. In many studies on terrestrial locomotion, the usual covariate used to assess the within-mode variability is locomotor speed. The drastic difference in the physical properties of the two media, however, rules out the use of velocity in the comparison of terrestrial and aquatic locomotion. We therefore propose to add a covariate to the analysis, assuming that a similar value represents the same ‘effort’ for both locomotor modes. We suggest that a relevant covariate has to control for (1) differences in the physical properties of the medium and (2) for differences in the *direction* and *magnitude* of the resultant force of all external forces (Fig. 1). Both selection criteria may have significant mechanical consequences on the locomotor behavior. On land, some of the vertical ground reaction forces counteract the gravitational forces and result in a vertical acceleration. These parallel forces dominate and work in the vertical plane, while during jumping the direction of the movement of the body is at an angle to the horizontal plane. In contrast, in water, the effective weight of an animal is reduced by buoyancy, whereas fluid-dynamic forces are drastically increased (Martinez et al., 1998). Drag is the resultant force in the orientation of the locomotion, and therefore works for horizontal swimming in the horizontal plane. During aquatic locomotion, the resultant external forces are therefore oriented parallel to the direction of motion.

In this study, we evaluate the use of propulsive impulse as a covarying performance measure that fulfils the two selection criteria above. Impulse is the change in momentum of a body, and equals the integral of the resultant force acting on this body over the equivalent time interval:

$$\int_{t_1}^{t_2} F_{\text{result}} dt = mv_2 - mv_1 \quad (1)$$

where F_{result} is the resultant force, m the mass and v_1 and v_2

the instantaneous velocity at start t_1 and end t_2 , respectively, of the chosen time interval. This resultant force is the difference between the propulsive forces F_{prop} and the resistive forces, acting against locomotion F_{resist} , gravity on land and drag in water. Hence, the propulsive impulse is given by:

$$\int_{t_1}^{t_2} F_{\text{prop}} dt = mv_2 - mv_1 + \int_{t_1}^{t_2} F_{\text{resist}} dt \quad (2)$$

This equation can be solved based on kinematic data only, and will be used for both swimming and jumping in order to obtain the propulsive impulses as a covariate, an independent performance measure.

The purpose of this study is to compare the kinematics of swimming and jumping in a semi-aquatic frog within the full range of their locomotor behaviour. Our working hypothesis is that motor control will strive to achieve similar kinematics for both modes. To make a valid comparison, we will calculate and evaluate the use of propulsive impulse as a covariate. We expect the propulsive impulse to be a measure of the ‘effort’ an animal has to undertake in order to make this movement. Since a full range of impulses was obtained for both modes, we also expect the ranges of the impulses for both locomotor modes to overlap.

Materials and methods

Animals

Five frogs *Rana esculenta* L. (10.8–20.8 g, mean 16.4 g) were caught in the wild at Groot Schietveld (Brecht, Belgium). The animals were housed in a glass terrarium and fed a diet of crickets. Temperature within the holding room was kept at 18°C, and a photoperiod of 12 h:12 h light:dark was maintained during the holding period. The experimental room was kept at a temperature of 20–22°C.

Data recording

Jumping

Frogs jumping from an AMTI force plate were simultaneously recorded, laterally using a high-speed Redlake Motionscope (Redlake MASD, Inc., San Diego, CA, USA) and dorsally using a NAC-1000 (NAC Image Technology, Inc., Tokyo, Japan), both at a frame rate of 500 Hz. The two

Table 1. Number of analyzed sequences, range of differences in speed between start and end of the propulsive phase and mean speed for each individual

Individual	Swimming			Jumping		
	N	Speed (m s ⁻¹)		N	Speed (m s ⁻¹)	
		Range	Mean		Range	Mean
1	6	0.24–0.78	0.40	6	1.23–1.92	1.64
2	5	0.39–0.86	0.66	6	0.70–1.96	1.42
3	7	0.32–0.75	0.49	6	0.94–1.69	1.38
4	5	0.36–0.75	0.49	6	0.92–1.90	1.38
5	5	0.51–0.70	0.60	6	1.03–2.04	1.44

N = number of sequences analysed.

views were synchronized. Care was taken to include maximal jumps. For practical reasons, this set-up did not allow small jumps, so additional (smaller) jumps were recorded using the Redlake Motionscope system only, with a mirror placed at an angle of 45° next to the take-off position. The area was lit using a Tri-lite light (3×650 W; Cool Light Co., Inc., Hollywood, CA, USA). In both experiments, the surface of the take-off position was covered with fine sandpaper to prevent the feet slipping.

The following criteria were used to select the sequences. (1) The whole propulsion phase was visible; (2) both hind limbs extended simultaneously; (3) in the mirror experiments, jumps were straight and parallel to the mirror. For each animal, 20 sequences had to pass the selection criteria before concluding the experiment. These 20 sequences were then screened on their ground reaction force output, and six sequences for each animal (see Table 1) were chosen for further analysis in order to obtain as large a performance range as possible.

Swimming

Swimming sequences were recorded at 250 Hz using a Redlake Motionscope system. The frogs were transferred to a swimming tank consisting of two open tanks (0.5 m × 0.5 m × 0.4 m) connected by a glass tunnel (0.15 m × 0.10 m × 1 m long). The tanks were filled above the level of the tunnel so that the frogs were compelled to swim completely submerged when crossing from one tank to the other. A mirror placed beneath the swimming tunnel allowed both ventral and lateral images to be recorded using a single camera. The water in the swimming tank was kept at a temperature of 21°C for the duration of the experiment.

To ensure that the full velocity range was obtained, frogs were stimulated by touch to swim at maximal speed. The selection of sequences retained for further analysis was based upon the following three criteria: (1) constant swimming depth, (2) displacement parallel to, but not touching, the tunnel walls, and (3) symmetrical hind limb movements.

Again, 20 sequences for each individual were selected. 5–7 sequences for each animal (see Table 1) were chosen for further analysis, based upon the velocity range.

Data analysis

Kinematics

For each sequence, the snout tip, cloaca, hip, knee, ankle and midfoot were digitized, frame by frame, using an APAS (Ariel Performance Analyzing System; Ariel Dynamics, Inc., Trabuco Canyon, CA, USA). We decided to compare the kick, which is the only phase of the cycle that is undoubtedly homologous in the two environments. The kick is defined in this study as the phase in which the snout tip accelerates. We calculated the three-dimensional (3-D) joint angles of the hip, knee and ankle for the entire swimming and jumping trials, but our further analysis was restricted to the data relating to the kick phase. Time was set to zero when velocity reached its maximum.

To compare the posture of the different segments, the coordinates of the digitized markers were transformed from a global coordinate system to a new relative coordinate system that moves (and rotates) with the animal. The origin of this local coordinate system was situated at the coordinates of the cloaca, with the X-axis through the trunk of the frog (on the axis snout–cloaca) and therefore in the direction of the locomotion. The Y-axis was placed parallel to the perpendicular axis on the X-axis through the hip. The Z-axis was defined as the cross product of the X- and Y-axes. The projections of the joint angles in the XY (the coronal plane), the XZ (the sagittal plane) and the YZ plane (the transverse plane) were calculated from these new coordinates (Fig. 2). In this way, we looked not only at the 3-D joint angles, but also at their orientation in reference to the trunk. By ‘immobilizing’ the body in a new coordinate system we were able to compare the leg movements more accurately. As a result of using this method to calculate the projection angles, however, it was impossible to determine the hip angle in the YZ plane, as the hip and trunk segments determine the X- and Y-axis of the local coordinate system.

Impulse

The propulsive impulse was calculated as the sum of the mass multiplied by the velocity change of the snout, and the impulse of the external force acting against motion.

In terrestrial locomotion, the mass is simply the mass of the

frog itself and gravity is the only external force that has to be taken into account. The impulse of gravity was calculated as mass \times gravitational acceleration (9.81 m s^{-2}) \times duration of the kick Δt . For each sequence of the jumping data, the propulsive impulse was calculated as the sum of the velocity impulse and the impulse of the gravitational force:

$$\int_{t_1}^{t_2} F_{\text{prop}} dt = mv_2 - mv_1 + mg\Delta t \cos 50^\circ, \quad (3)$$

where m is mass, g is gravitational acceleration and Δt is duration of the leg extension. $\cos 50^\circ$ was used to account for the fact that frogs on average jump at an angle of 40° and thus correction was needed to obtain the external impulse in the direction of movement. To evaluate the reliability of this kinematically based method, we compared our calculations with impulse calculations based on the integration of ground reaction force recordings, calculated by integrating the resultant force that was filtered using a fourth order Butterworth filter with a cut-off frequency of 30 Hz.

Calculating the propulsive impulse for the swimming sequences is more complex. When a body moves through a fluid, it pushes the fluid out of the way. If the body is

accelerated, the surrounding fluid must also be accelerated. The body behaves as if it were heavier, by an amount called the hydrodynamic mass (or added mass) of the fluid. Therefore, a correction must be made for the mass utilising the added mass factor 0.2 (Nauwelaerts et al., 2001), which is the added mass coefficient (AMC) taken for an ellipsoid body with the dimensions of a frog's trunk (Daniel, 1984). Drag on the body is the resistive force that must be taken into account during swimming. The propulsive impulse during swimming was therefore calculated as:

$$\int_{t_1}^{t_2} F_{\text{prop}} dt = m(1 + \text{AMC})(v_2 - v_1) + \frac{1}{2} \left[C_d \rho A \left(\frac{v_{\text{min}}^2 + v_{\text{max}}^2}{2} \right) \Delta t \right], \quad (4)$$

where C_d is drag coefficient (0.14), ρ is density of the medium (1000 kg m^{-3}), A is area (snout-vent length)², $(v_{\text{min}}^2 + v_{\text{max}}^2)/2$ is mean squared velocity, and Δt is duration. $C_d = 0.14 \pm 0.02$ (mean \pm S.E.M. from 26 sequences) was calculated from the deceleration of the body during the glide phase. The C_d can be calculated in this manner because drag is the only external force during the glide phase, and the velocity of the center of mass is known (Bilo and Nachtigall, 1980; Stelle et al., 2000).

Statistical analysis

To evaluate the method of calculating the impulse from the digitization data, impulse values were compared in pairs with those obtained by integrating the ground reaction force. The two methods were compared and then statistically substantiated using a Method Validation Tool Kit (<http://www.westgard.com/mvtools.html>), using a paired data calculator. The resulting value for the observed bias was tested for significance using a Student t -test (Westgard, 1995).

The 3-D and projection angle profiles (angles against time) were tested for differences between the two locomotor modes, examining not only average differences in profiles *sensus strictus*, but also differences in angle profiles with respect to changes in impulse, using a linear mixed model (ANCOVA) in SAS version 10.0 for Microsoft Windows. This model compared the profiles after adjustments (1) for individual differences, and (2) for correlations of the angles within a sequence (a first order autoregressive covariance-structure). A general Satterthwaite method was used for correcting the degrees of freedom.

Significant interactions (1) between mode, time and impulse were interpreted as differences in the linear changes in impulse

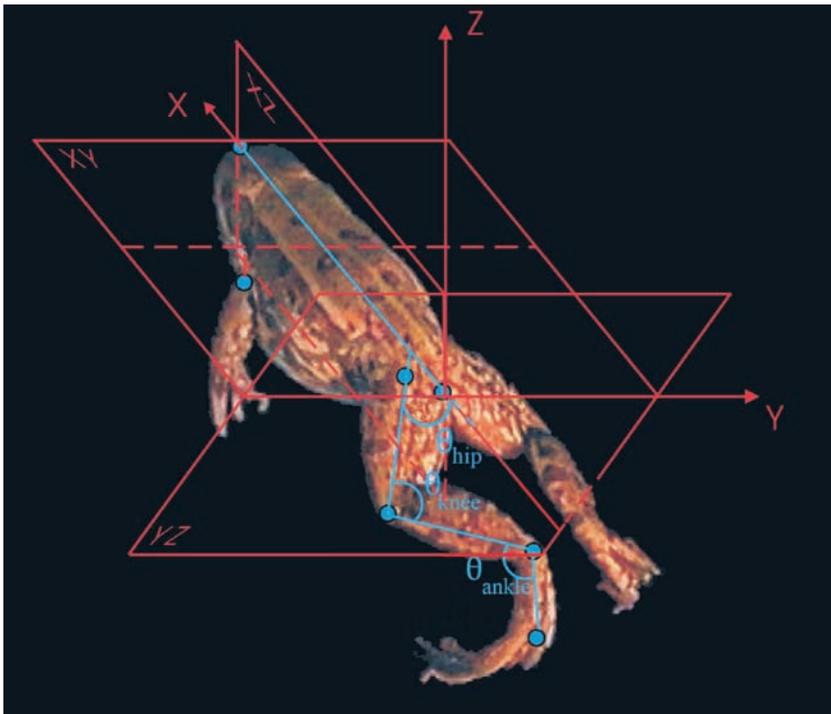


Fig. 2. 3-D joint angles (θ_{Hip} , θ_{Ankle} , θ_{Knee}) and the local coordinate system in a jumping frog. To compare the posture of the different segments, the coordinates of the digitized markers were transformed from a global coordinate system to a new relative coordinate system that moves (and rotates) with the animal. See text for a description. The 3-D projection angles in the XY (the coronal plane), the XZ (the sagittal plane) and the YZ plane (the transverse plane) were calculated from these new coordinates. The red lines represent the local coordinate system XYZ, which is also called the relative coordinate system, while the blue lines indicate the body segments defined by the digitalization points (the blue circles).

modulation, and (2) between mode, time² and impulse as differences in how the shape of the profiles were affected by impulse. A second analysis, within one locomotor mode, was performed using the same linear model to enable us to describe the profiles (angle vs time and angle vs time²) and changes in these profiles that lead to a different impulse for each mode.

Results

Method validation

There was no significant difference between the two methods of calculating the propulsive impulse for jumping. The calculated bias of the test method (impulses from digitization data), the value of systematic error, was -0.0014 , but did not differ significantly from zero ($t=-1.2389$, $P=0.23$). Random error (S.D.differ) between the methods, due to imprecisions of both methods and matrix effects, was 0.0053.

Impulses

Although a large range of impulses was obtained for both locomotor modes, the impulses of the propulsion force were greater in jumping (between 0.018 and 0.053 kg m s⁻¹) than in swimming (between 0.005 and 0.026 kg m s⁻¹). Despite a large overlap in duration, there is little overlap in the impulse-duration graph for the two modes (impulse overlap range = 0.018–0.026 kg m s⁻¹) (Fig. 3).

Kinematics

Mean joint angles within modes

All 3-D joint angles have a significant, linear change with time (see columns T, Table 2), even after Bonferroni correction in both locomotor modes. The angle patterns are shown in Fig. 4, where 3-D angle is plotted against time (time set to zero at maximal velocity). The effect of impulse is shown along the Y-axis.

The projection angles show that most movement occurs in the XY plane (the coronal plane) and the YZ plane (transverse plane).

Mean joint angles between modes

The traditional method for comparing kinematic profiles is to compare the average profile from different situations. Here, the mean slopes of the hip and knee 3-D angle-time profiles differ significantly (see column T×Mode of Table 2A) between the two modes, which indicates a difference in angle velocity or a difference in timing of the extension during the propulsive phase. These dissimilarities are for the knee and ankle due to differences in the slope of the angle-time curves in the XY plane, i.e. the coronal plane through the trunk. However, these significant differences disappear after Bonferroni correction.

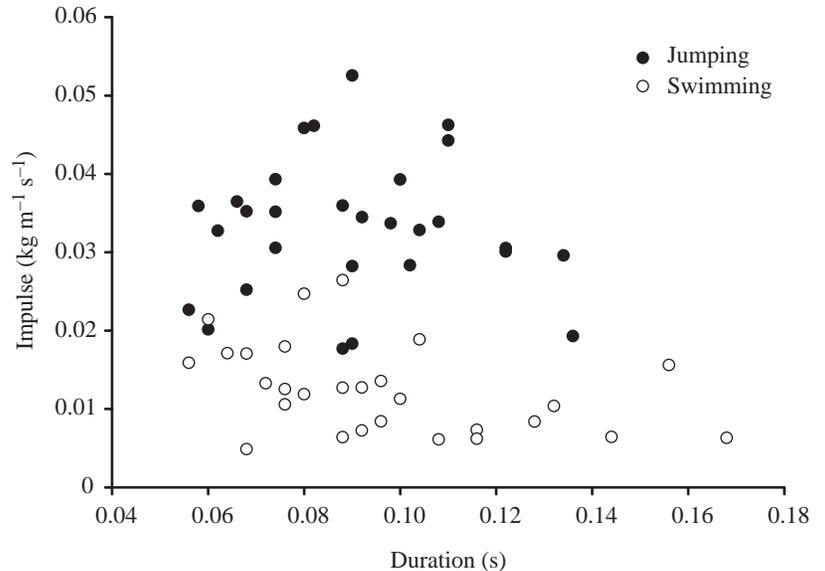


Fig. 3. Differences in impulse between swimming and jumping. There is no relationship between the impulse of the propulsion force and the duration of the propulsive phase within a locomotor mode. The range of the duration of the propulsive phase is greater in swimming, but there is a considerable overlap in the duration of both modes. The impulse gained during jumping is greater, and there is a small overlap area with swimming impulse.

The shape of the angle-time curve (column T²×Mode) only differs for the hip XY angle: during swimming this angle changes linearly over time, while during jumping a significant curvature is found.

This means that the conventional method of comparing the kinematics, that is without taking into account the variation within a locomotor mode, does not yield any differences between the kinematics of jumping and swimming in *R. esculenta*.

Influence of impulse on the kinematic profiles

The intersequential variation is considerable (see Fig. 5). When impulse is added to the analysis, most of the intersequential variation can be explained. The 3-D knee and 3-D ankle angle profiles change significantly with impulse, and this change differs between swimming and jumping. For the knee joint, during jumping, the kinematic profiles change with impulse in the XY and YZ plane, whereas during swimming the change with impulse also occurs in the XY and XZ plane. For the ankle, a trend with impulse is obtained in the XY and XZ plane in both modes, but this modulation differs in the XY plane. In the hip joint, modulation of the 3-D angle differs due to a linear and parabolic change during swimming, and a slight parabolic change during jumping. The difference mainly occurs in the XY plane.

Joint angle profiles between modes with respect to impulse

Most angles change with impulse (see columns T×L of Table 2), which means that to look solely at the average

Table 2. Probabilities of the interactions of the fixed effects of the ANCOVA

(A) Differences between modes

Angle	$T \times \text{Mode}^a$	$T^2 \times \text{Mode}^b$	$T \times L \times \text{Mode}^c$	$T^2 \times L \times \text{Mode}^d$
Hip				
3-D	0.004	0.11	<0.0001	<0.0001
XY	0.22	<0.0001	0.0009	0.05
XZ	0.69	0.46	0.41	0.69
Knee				
3-D	0.007	0.76	<0.0001	<0.0001
XY	0.01	0.63	<0.0001	0.0007
XZ	0.59	0.45	0.16	0.69
YZ	0.92	0.41	0.003	0.02
Ankle				
3-D	0.06	0.66	0.0006	0.015
XY	0.045	0.81	0.01	0.10
XZ	0.67	0.16	0.14	0.71
YZ	0.96	0.67	0.03	0.11

(B) Angle profiles

Angle	Jumping				Swimming			
	T^e	T^{2f}	$T \times L^g$	$T^2 \times L^h$	T^e	T^{2f}	$T \times L^g$	$T^2 \times L^h$
Hip								
3-D	<0.0001	0.44	0.27	0.053	<0.0001	0.11	<0.0001	<0.0001
XY	<0.0001	0.002	<0.0001	<0.0001	<0.0001	0.17	<0.0001	<0.0001
XZ	0.30	0.81	0.94	0.53	0.08	0.22	0.09	0.84
Knee								
3-D	<0.0001	0.40	<0.0001	<0.0001	<0.0001	0.17	<0.0001	<0.0001
XY	<0.0001	0.54	<0.0001	<0.0001	<0.0001	0.09	<0.0001	<0.0001
XZ	0.20	0.24	0.75	0.55	0.15	0.49	0.001	0.28
YZ	0.02	0.77	0.0002	0.0005	<0.0001	0.0017	0.20	0.93
Ankle								
3-D	<0.0001	0.03	<0.0001	<0.0001	<0.0001	0.0007	<0.0001	<0.0001
XY	<0.0001	0.10	<0.0001	<0.0001	<0.0001	0.0002	<0.0001	<0.0001
XZ	0.46	0.15	<0.0001	<0.0001	0.57	0.78	<0.0001	0.0004
YZ	0.02	0.36	0.005	0.004	<0.0001	0.0003	0.53	0.85

Values in bold are significant.

(A) Differences between the two locomotor modes: ^aincrease in angle in time (T), ^bquadratic change in time (T^2), ^clinear profile change with impulse ($T \times L$) and ^dquadratic profile change with impulse ($T^2 \times L$).

(B) Angle profiles within the locomotor mode (swimming and jumping). ^eA significant P -value in the T column means that the joint angle increases significantly over time. ^fIn the T^2 column, a significant value shows a significant quadratic profile in the angle-time relationship. When impulse (L) is added to the equation, a significant P -value then points to a significant change of linear ^g($T \times L$) or quadratic ^h($T^2 \times L$) profile with impulse.

profiles is to overlook a significant source of variation within a locomotor mode. Therefore, for the remaining angles, profiles of different modes should be compared with respect to the impulse. The unexpected finding that the impulse ranges only display a partial overlap means that the overlapping range is based on a limited data set. For the hip, this comparison results in a larger angle (15°) of the hip at the beginning of the propulsion phase of jumping. This means the hip is more flexed at the start position, probably due to the weight of the trunk on the legs, because this difference in

angle is the greatest in the XY plane. Although the knee is extended more and flexed less in the XY plane during swimming, this effect is compensated for by the fact that the knee does not move in the YZ plane during swimming, whereas during jumping, the knee displays considerable movement (60°). This results in a slightly more flexed knee during swimming, but a less extended knee at the end of the propulsive phase, producing the same range of movement for both locomotor modes in 3-D. The ankle flexes more during swimming (15°), because the ankle XY projection angle is

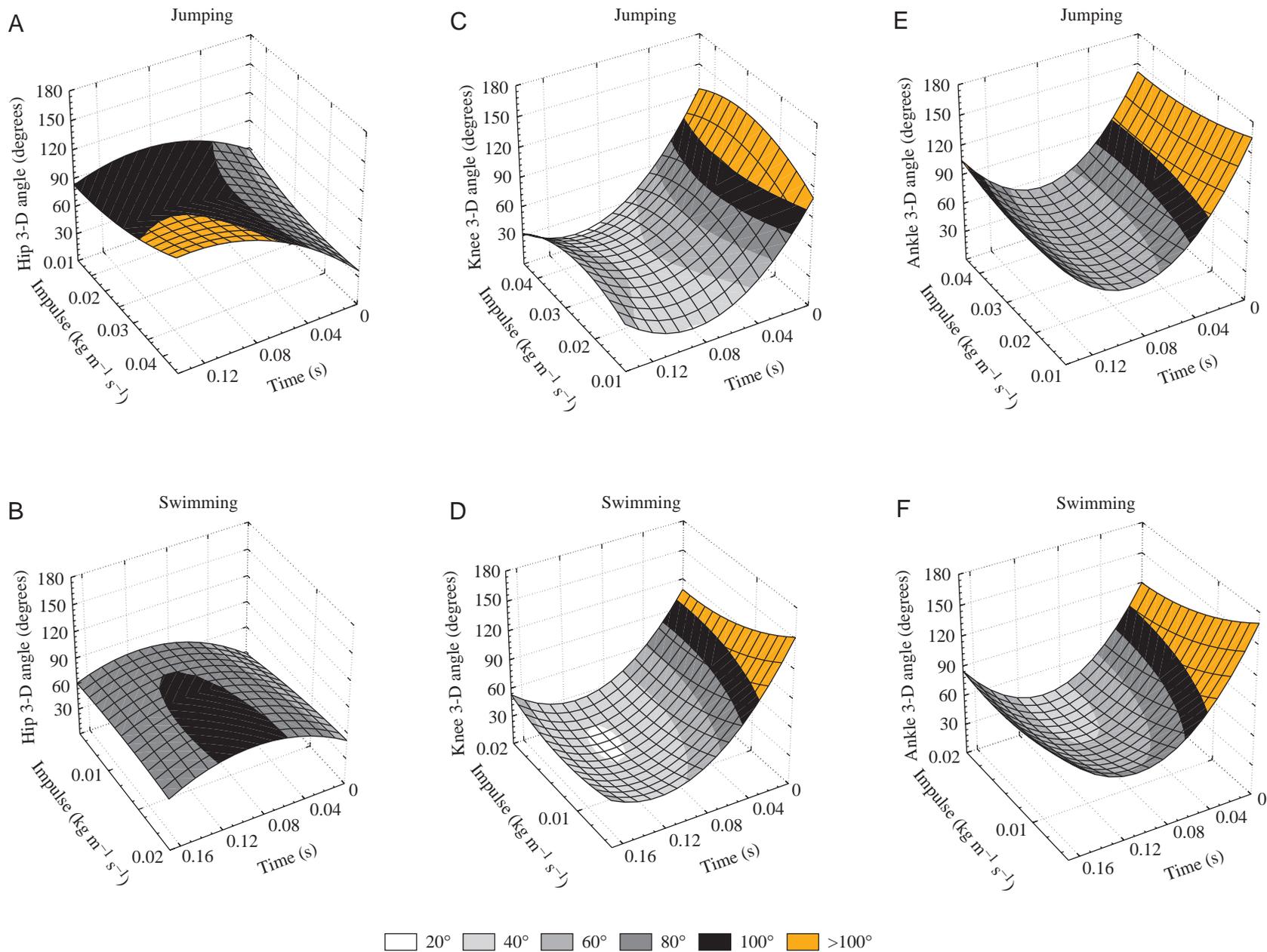


Fig. 4. Surface plots of 3-D hip (A,B), knee (C,D), ankle (E,F) joint angle profiles against impulse during the propulsive phase in both jumping (A,C,E) and swimming (B,D,F). The angle axis is scaled between zero (fully flexed) and 180° (fully extended). Time is set to

zero at the end of the propulsive phase, when maximal velocity is reached. An interactive effect with impulse becomes visible when the colour scheme does not follow the axes of the plot. The key indicates the colour codes for the angles (in degrees) on the Z-axis.

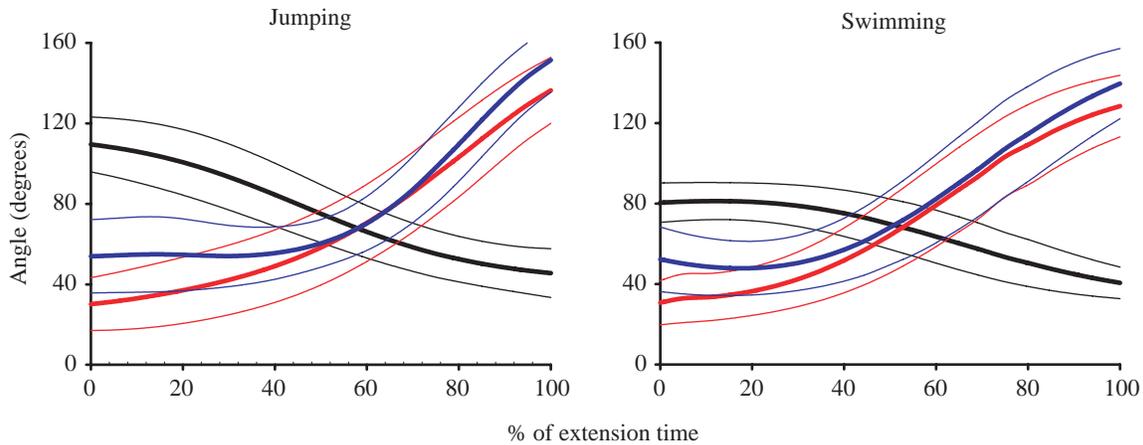


Fig. 5. Mean kinematic profiles of hip (black), knee (red) and ankle (blue) joints during jumping and swimming. The thick lines represent the mean profile, the thin lines indicate \pm s.d. The total time of each propulsive phase is set at 100%.

smaller at the start and extends more slowly during swimming and because the ankle extends more during jumping in the YZ plane.

Discussion

Similar to previous studies of the kinematics of swimming and jumping in frogs (Peters et al., 1996), our mean profiles do not differ. A major issue in such a comparison of means, however, is that factors other than the difference in medium can induce considerable variation, as illustrated in Fig. 5 (s.d. is large). As shown, significant differences between locomotor modes can be overlooked if this variation is ignored.

In locomotion, it is known that the performance level, for example locomotor speed or jumping distance, is an important source of variation. Kinematic characteristics change with speed and a convenient solution is to add speed as a covariate in the kinematic analyses (e.g. Hoyt et al., 2000; Vanhooydonck et al., 2002). Swimming at a certain speed is not similar to performing at the same speed on land, however, because (1) the two media, i.e. water and air, differ drastically in their physical properties, and (2) the musculoskeletal system has to act against different substrates, namely viscous water *versus* solid ground.

Jumping distance and swimming speed can be considered the overall collective result of a more basic performance measure, namely the forces transmitted by the feet to the substrate. These forces are necessary in order to accelerate the body, and in case of swimming, to accelerate the added mass. These forces are also required to overcome resistive forces (gravity and drag) during the propulsive kick in both locomotor modes. Therefore, the use of the propulsive impulse as a covarying performance measure potentially permits a sound comparison of swimming and jumping. This converts the kinematic analysis into the comparison of two 3-D surface plots per joint, one for each medium (see Fig. 4).

For the sequences that result in a similar propulsive impulse, the kinematics of swimming and jumping differ

significantly. As for the 3-D angles, these differences remain small, but the configuration with respect to the animal's body differs. It seems that moving from land to water coincides with a rotation in the hip joint, turning the knee more outwards and resulting in different foot positions. However, this comparison was only based on a limited data set. The initial expectations were that the performance ranges for swimming and jumping would largely overlap, because an effort was made to obtain the full range of performances for both locomotor modes (see Materials and methods). However, the performance overlap is surprisingly small (see Fig. 3) and the impulses for jumping are considerably higher than for swimming.

One possible explanation for this difference in impulse is that our kinematically based estimations of the propulsive impulse are unreliable for either or both locomotor modes. For jumping, however, the kinematic method yielded similar results to those obtained *via* integration of the ground reaction forces (i.e. the more conventional method). This gave support to the kinematic method and the obligatory method of analyzing the swimming bouts. There are two potential sources of error in this model: the drag coefficient and the added mass coefficient (see equation 4). The drag coefficient was obtained from the deceleration of the body during the glide phase. It is possible this causes an underestimation of the C_d because during the propulsive phase, the body is not in such a streamlined posture. However, in order to obtain swimming impulses within the range of the impulses of the jumping trials, a 14-fold increase of the C_d is required, which would correspond to the drag coefficient of a square cylinder normal to the flow. Such a large drag coefficient is impossible for a frog's body. The second potential source of error is the added mass coefficient, which might also be underestimated. Again, to make the impulses overlap would require a unrealistically high value and greatly exceed the values previously used (Daniel, 1984; Gal and Blake, 1988; Nauwelaerts et al., 2001). Moreover, the chosen drag coefficient and added mass coefficient have already been successfully used to mimic the

displacement profiles of swimming frogs (Nauwelaerts et al., 2001). Therefore, we can assume that the difference in propulsive impulse is real and not caused by an unrealistic model for the swimming bouts.

Thus, the *calculated* impulse ranges differ. This leaves us with three possible explanations. First, the present kinematically based impulse calculations are equivalent to the time integral of the force components in the direction of the observed displacement only. Force components perpendicular to the direction of motion, but cancelling each other, might be transmitted to the substrate. These forces do originate from muscular action but do not result in a change in momentum, nor are they used to overcome resistive forces. They therefore do not show up in the impulse estimations. In symmetrical jumping, for instance, lateral forces exerted by left and right foot (if present) cancel each other. From this point of view, maximal swimming and maximal jumping might yield comparable efforts at the muscular level, but these efforts might be translated into largely differing *propulsive* impulses because of larger non-propulsive force components being transmitted to water during swimming. If true, this reduced transmission efficiency can presumably be linked to the fact that frogs are secondary swimmers, primarily adapted to a terrestrial, saltatory motion (Wake, 1997). It is remarkable that fully aquatic frogs like *Xenopus* have entirely different leg configurations, presumably to circumvent this problem, but inhibiting their jumping ability (Trueb, 1996). The kinematic shift observed in *Rana esculenta* brings the legs into a more *Xenopus*-like configuration, but this might not be sufficient to equalize the impulse ranges for this semi-aquatic frog.

Alternatively, it should be considered that comparable efforts at the muscular level result in an overall decreased force transmission to the substrate during swimming, which logically ends in lower impulses. Such conditions can occur when muscles have to act against lower external loads: contraction will proceed more rapidly but, as a consequence of the force-velocity relationship, less forcefully. The external load

acting on the muscle system of the legs derives from two sources: the inertial load (due to the change in momentum) and the load resulting from the resistive forces. If, for the sake of argument, we assume that for the fastest swimming kick and the longest jump both the muscular effort and activation are maximized, we can compare the external loads for a frog of about 0.02 kg by making use of the formulae presented in Equations 3 and 4. It appears that both the average inertial load and the average resistive load are about twice as high for jumping (inertial: 0.42 N *versus* 0.21 N; resistive: 0.12 N *versus* 0.07 N), which gives support to this alternative explanation based on the force-velocity relationship of muscular contraction. However, if this holds true, contraction velocities or joint extension velocities should be higher for the swimming sequences. This is not confirmed by Gillis and Biewener (2000), who found no strain rate differences between swimming and jumping for the muscles examined, nor by the data in the present study. When we compare the velocity patterns of the maximal jumping and the maximal swimming trial for each frog, joint velocities were found to be significantly higher for the *jumping* sequences (paired *t*-test; $P < 0.05$).

Finally, we consider the possibility that estimates of the propulsive impulses are a good measure of the effort made by the frog's leg muscles, but that some of the muscles become less activated, even when performance is maximized. This would be analogous to a terrestrial animal attempting to move on a slippery surface, such as ice. To optimize movement, recruitment is reduced so as not to exceed static friction. This is possible when maximized contraction, optimal for jumping, would cause less coordinated, ineffective movement patterns during swimming, resulting in an even more feeble performance than with reduced recruitment. This seems plausible given the difference in external load and taking into account that frogs are primarily adapted to terrestrial locomotion (Wake, 1997).

When we look at Fig. 6, coordination does differ between

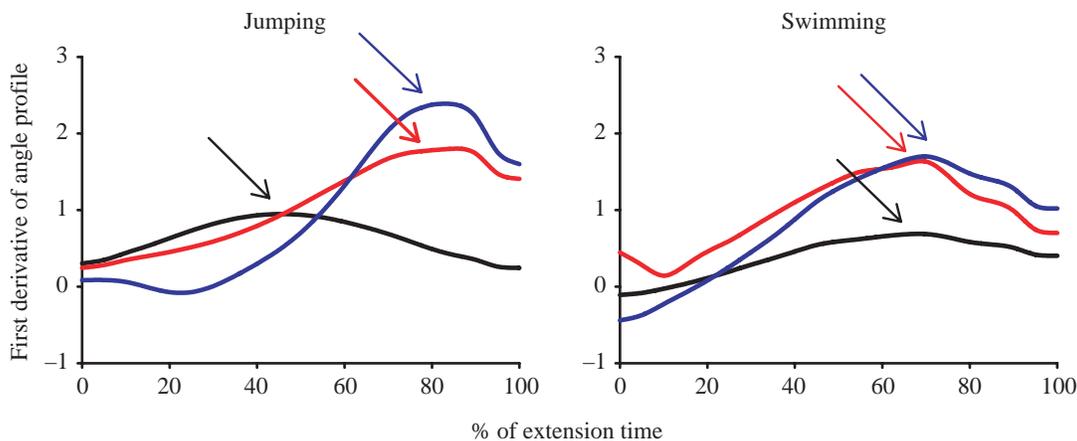


Fig. 6. The first derivatives of the kinematic profiles show that the coordination between the two locomotor modes differs slightly. The colour codes are the same as for Fig. 5. The hip action is earlier in the movement during jumping. Although a proximo-distal succession of the joints is optimal during jumping, the timing of the knee and ankle action is similar. During swimming, all joints are synchronously active.

the locomotor modes. During swimming, all joints are active at the same moment, at approximately 70% of the total propulsive phase, whereas during jumping the hip extends first (halfway the propulsive phase), followed by a synchronous action of knee and hip. To prolong the acceleration phase during jumping, a proximo–distal succession of the joint actions is favourable, causing the maximal velocity to be reached as late as possible during push-off (van Ingen Schenau, 1989). However, a synchronous extension of all joints, as during swimming, enables a higher maximal velocity to be reached (Alexander, 1989). It is plausible that for swimming, attaining a higher velocity is more important than the timing of this velocity peak. Interestingly, the coordination pattern found for *R. esculenta* differs from the one described by Gillis and Blob (2001) for *Bufo marinus*, a more terrestrial species. In these toads, limb extension begins at the knee during swimming. In contrast, during jumping the hip precedes extension at more distal joints, which is similar to *R. esculenta*'s coordination. When the coordination of the two locomotor modes is different, muscle activation patterns are also expected to differ. Gillis and Biewener (2000) found lower EMG intensities for the m. plantaris (primarily an ankle extensor), and a shorter EMG burst duration for the m. cruralis (primarily a knee extensor) during swimming in *Bufo marinus*. From our data, it appears that the knee and ankle are fairly conservative joints. Despite differences in starting angle, they have a similar movement range in both locomotor modes. If we assume that EMG patterns are similar in *Rana esculenta*, this finding may point at an active modulation. Yet, it must be taken into account that the EMG data of Gillis and Biewener (2000) refer to averages over a performance range, and it is not specified whether maximal performance is included. Assuming, however, that the reported lower and shorter EMG-activations also occur at maximal performance, a smaller plantaris and cruralis muscle might suffice for swimming. Again, a comparison with a fully aquatic frog like *Xenopus* might be very helpful.

In conclusion, the kinematically based impulse calculations are a promising tool in the comparison of drastically different locomotor modes, but do not tell the full story. The unexpected finding of the largely non-overlapping impulse ranges in swimming and jumping raises new questions. The formulated hypotheses are not mutually exclusive and the discussed phenomena might act together. Although we agree that the kinematically based method is a simplification of reality, we argue that this alone could not explain the observed discrepancy. Without disregard for other explanations, we believe that the concept of non-propulsive impulses being much larger in swimming than in jumping is the most plausible. One step towards the solution would be to map all the external forces involved in both locomotor modes. In a terrestrial environment, the external forces consist of the gravitational forces and the ground reaction forces, which should be measured for both feet separately. Determining the external forces in an aquatic system is far more complex and requires a special setup, i.e. studying the flow induced by the frog's movements. It would also be

interesting to investigate whether the same EMG patterns and strain rate profiles as described for *B. marinus* (Gillis and Biewener, 2000) occur in a semi-aquatic frog such as *R. esculenta*. Since the coordination patterns are different, the possibility exists that we cannot simply use Gillis and Biewener's results to interpret our data. There remain a few problems with the use of the propulsive impulse as a covariate in the comparison between aquatic and terrestrial sequences. It is not easy to determine a comparable level of effort when examining two locomotor modes in such different physical environments. A measure for power input, the active metabolic rate (Fish and Baudinette, 1999), or the metabolic cost of transport, could be better estimates for the 'effort' exerted during the propulsive phase. However, measuring instantaneous oxygen consumption in frogs is not straightforward. These are all challenges for future research.

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