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A principle of ‘Least Effort’ to describe the natural movements of animals

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Abstract

This paper presents a general theory for the dynamical properties of natural movements of animals with articulated bodies. The theory assumes only that the animal's choice of movement is in some way optimal, whilst respecting classical laws of physics. This leads to a variational principle governing the movement of animals, represented by a simple equation, the solution of which is life-like motion. Although many ad hoc algorithms exist for animating creatures, the present paper brings animal movement into the realm of mathematical physics by formalising life-like dynamics in an explicit, physically motivated equation with well defined solutions. The variational principle generates graceful movements between chosen beginning and end states without relying on data sets or human intervention to find in-between postures. Importantly, the movements respect the laws of Newtonian dynamics, while also capturing the lazy appearance of the voluntary movements of animals that have evolved to move efficiently. The formalism makes a distinction between passive and active degrees of freedom. The former respect Hamilton's principle of least action, while the latter respect a principle of least effort, which is non-trivial to implement due to the coupling between passive and active degrees of freedom. Both numerical and analytical solutions to the problem are developed here. Central to the numerical solution is the careful counting of the appropriate number of constraints for the number of variables used. Both approaches are demonstrated on some minimal models. The aim of the paper is not to compete with state-of-the-art computer animation, but to establish a



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rigorous approach, with potential applications in sports science, veterinary and human medicine as well as computer-generated animation.

Keywords: classical dynamics, variational principle, animal movement, simulation, analytical mechanics, mathematical modelling

1. Introduction

When we observe the dynamics of an articulated set of objects, it is obvious whether the mechanical system is alive or not. A monkey swinging playfully from a branch is immediately distinguishable from a jointed puppet of a monkey swinging limply from the branch. Even from a distance, when detailed features cannot be discerned, we recognise the movements of a living creature, without necessarily having witnessed the exact same trajectory before. For one thing, the living creature has an internal energy source so that its mechanical energy (kinetic plus potential) may increase, whereas the puppet's motion can only be conservative or dissipative. But the distinction goes beyond that because we would easily distinguish a real animal's movement even from a motorized puppet. Clearly, then, we are instinctively familiar with some features (which one might call 'laws') of the dynamics of *living* mechanical systems that are additional to those formulated by Newton for *all* mechanical systems. Here, we shall develop the dynamical equations of those familiar life-like trajectories.

Many ad hoc algorithms exist for animating living creatures, developed by the gaming and film industries. Some are more successful than others. Their aim is to trick the eye, whereas ours will be to develop a general theory for the dynamical properties of natural movements of animals, with well motivated and physically correct equations of motion.

The simulation of creatures and people with realistic movements is a difficult problem. It involves finding an interpolation between the desired initial and final states that reproduces the animal's graceful gait whilst also respecting the laws of physics. Achieving either of those goals without the other leads to computer-generated creatures in computer games and TV programmes that look unconvincing when they move, appearing either mechanical or off balance [1, 2]. One major impediment to simulating animal movement convincingly is that many animals—particularly bipeds—move along unstable trajectories. So, numerically time-stepping their equations of motion from some chosen initial conditions (i.e. a shooting algorithm) will not lead to the desired end state, unless the initial conditions and the ersatz animal's muscular impulses are chosen with great prescience and precision. Various algorithms have been designed to solve the problem, each with its own strengths and weaknesses and with varying degrees of accuracy [3–11].

Most current computer-generated animation of characters is data-based, relying on large data-sets encoding a repertoire of trajectories taken either from real-world capture of human or animal movement, or from other simulations [3]. Meanwhile, much animation is still done in a completely unphysical way, making animals move unconvincingly, e.g. off balance, or accelerating unnaturally. Such movements are quicker to calculate; the realistic ones are harder to find [7, 8]. While purely physics-based movement solvers are less widely used, those that have been developed [2, 12] perform a similar task to that presented here, but are typically based on complex controllers with learnt behaviour [12], as opposed to the simple physical principles set out below. Furthermore, while physical validity is a necessary condition in selecting the appropriate trajectory, it is not a sufficient condition in order to create life-like motion. A solver may choose a path that respects physics, but not necessarily the path that an animal would choose. For further background on the state of the art in computer animation of animals and humans, see [3, 8–11].

To determine the time-dependence of an animal's muscular movements might seem beyond the realm of mathematical calculation, as the animal, having free will, may choose to move in an infinite variety of ways. Nevertheless, its choices are strongly constrained by the requirement to get itself from the initial to the final state while respecting the laws of physics. Furthermore, our everyday observations of animals in zoos and natural history documentaries demonstrate that, although in principle, without violating physics, an animal could exercise its free will to walk like a robot or to throw itself jerkily from one place to another, they do not. Instead, invariably and predictably, a gibbon swings like a gibbon and a panther walks like a panther and their motions are recognisably graceful and efficient to the point of appearing lazy. It is often remarked of natural animal behaviours that they appear to move 'effortlessly' and this derives from the fact that their motion has been somehow optimized by Darwinian evolution.

Early postulates of human and animal movement included minimization of the mean-square jerk [14, 15] or mean-square torque [16] or rate of change of torque [17] applied to a body part. Rose *et al* [16] state 'Experience has shown that motion that minimizes energy looks natural' but then proceed to minimize mean-square joint torque instead, because it had been suggested to correlate with metabolic energy consumption. The motivation for the mean-square jerk criterion [14, 15] was that it guarantees a graceful result, with minimal jerkiness, and it had some success in reproducing measurements of intentional gentle swaying of a human hand [14] (less so for involuntary movements of monkeys [15]). Here, we aim instead to address more strenuous movements, for which the animal's physical dynamics significantly limit its options.

A general solution to the problem of realistic animal movement is presented in sections 2–4, in the form of a variational principle, whereby the simulated creature's initial and final states (postures and velocities) can be chosen and a physically valid trajectory found both for the creature's passive and active degrees of freedom. In principle, an animal could select any of those physically valid trajectories and we shall assume only that its choice is in some way optimal. The quantity to be optimized will be called 'effort' and we shall discuss some of its necessary properties. By minimizing the animal's effort, we shall develop methods to determine motion that has the apparent ease characteristic of wild animals. Those methods solve the non-trivial problem of simultaneously minimizing the action and the effort of the passive and active degrees of freedom respectively.

By careful consideration of the number of constraints appropriate to the degrees of freedom, it is shown in section 5 how to apply the variational principle in efficient numerical algorithms. By deriving its Euler–Lagrange equations, in sections 8 and 9, the variational principle is also cast into the alternative form of an equivalent set of coupled differential equations, allowing insights and generalisations not provided by machine learning.

The use of the formalism is demonstrated by deriving solutions for some minimal models in sections 11–13. As well as being of potential use to game- and film-makers, the principle leads to calculable predictions of the most efficient or comfortable movements performed by animals, which may be of scientific interest and practical use to zoologists, veterinary practitioners and sports scientists.

2. The formalism

Let us model an animal as an articulated set of rigid and/or elastic objects. The animal therefore has a number of degrees of freedom: the angles of its joints, the lengths of any extendable parts, the deformations of any elastic modes [18], and the position of its centre of mass. A

number D_a of those degrees of freedom are actively determined by the animal using its muscles. The animal controls the state of those active degrees of freedom (e.g. the angle of each joint) as a function of time, thereby performing work. The remaining D_p degrees of freedom are passive, not under direct control of muscles but subject to Newton's laws of motion, influenced indirectly by the movements of the active degrees of freedom. For example, a frog, having leapt off the ground, may control the extension or retraction of its legs (an active degree of freedom) but the x , y and z coordinates of its centre of mass (three passive degrees of freedom) are governed by Newtonian dynamics alone.

As is conventional in analytical mechanics [13], the passive degrees of freedom shall be represented by an equal number D_p of generalized coordinates, denoted q_i , which are functions (to be determined) of time t . We may more compactly denote all of these variables simultaneously as the components of a D_p -dimensional vector, $\vec{q}(t)$. The D_a generalized coordinates for the active degrees of freedom will be denoted α_i , which may be written as components of the vector $\vec{\alpha}(t)$.

It is desirable to allow the initial and final positions to be chosen *a priori* (as opposed to specifying only initial conditions). We therefore seek a variational principle for determining the realistic trajectories, $[\vec{q}(t), \vec{\alpha}(t)]$, that connect the initial and final states.

For the passive degrees of freedom, $\vec{q}(t)$, Hamilton's principle of least action [13] provides the appropriate dynamical rules. Meanwhile, the time-dependence of $\vec{\alpha}(t)$ is chosen by the animal and a variational principle governing that choice will be presented in section 3. For now, let us assume $\vec{\alpha}(t)$ to be fixed functions of time. In the presence of those functions, the freely moving (passive) coordinates follow trajectories $\vec{q}(t)$ that extremize the action [13],

$$S[\vec{q}, \vec{\alpha}] := \int_{t_0}^{t_1} L dt \quad (1)$$

as discovered by Lagrange and Hamilton, where L is the Lagrangian of the system (discussed below). The action is a functional of the functions $\vec{q}(t)$ and $\vec{\alpha}(t)$, but is extremized with respect to $\vec{q}(t)$ only, given fixed end points $\vec{q}(t_0)$ and $\vec{q}(t_1)$ at initial and final times t_0 and t_1 respectively.

The 'Principle of Least Action' (more strictly, stationary action), which determines the physical trajectory $\vec{q}^*(t)$ of the passive variables, can be written

$$\left. \frac{\delta S[\vec{q}, \vec{\alpha}]}{\delta \vec{q}} \right|_{\vec{q}(t)=\vec{q}^*(t)} = \vec{0}, \quad (2)$$

where $\delta/\delta \vec{q}$ is a functional derivative with respect to variations in the trajectory $\vec{q}(t)$. Note, then, that $\vec{q}^*(t)$ is itself implicitly a functional of the active trajectory $\vec{\alpha}(t)$, since the path $\vec{q}^*(t)$ that respects the laws of physics depends on the movements $\vec{\alpha}(t)$ applied by the animal.

The formalism developed here is valid for systems described by an arbitrary Lagrangian, which may be a function of the variables $\vec{q}$, $\vec{\alpha}$, their time derivatives $\dot{\vec{q}}$, $\dot{\vec{\alpha}}$ and any higher derivatives, $\ddot{\vec{q}}$, $\ddot{\vec{\alpha}}$, etc. However, for definiteness, one may think in terms of a simple mechanical system, with potential energy, $U(\vec{q}, \vec{\alpha})$ and kinetic energy, $T(\vec{q}, \dot{\vec{q}}, \vec{\alpha}, \dot{\vec{\alpha}})$, for which the Lagrangian is given [13] by

$$L = T - U. \quad (3)$$

Such a system has a total mechanical energy

$$E = T + U. \quad (4)$$

Here, the potential energy U includes only contributions relating to the mechanical objects constituting the animal's body (such as elastic energy of a tendon or gravitational potential energy). The animal's stored (chemical) energy is not included. Hence, positive work done by

the animal's muscles (via the time-dependence of $\vec{\alpha}$) leads to an increase in the system's total energy.

In general, the Lagrangian-based formalism remains valid even for systems without a well defined energy or Hamiltonian, for which equation (1) remains well defined, while equations (3) and (4) are not required.

3. Proposal

To determine the trajectories of the active variables $\vec{\alpha}(t)$ chosen by an animal, let us return to the common observation that the motion appears 'lazy' or 'effortless'. There are good evolutionary reasons for animals to ration their energy output by moving in a way that requires least 'effort'. Thus, if we can define a functional that quantifies the effort associated with any given movement then, by minimizing it, we would find the manner in which an animal is expected to move. Without loss of generality (i.e. without specifying what aspect of its motion the animal seeks to optimize), let us define effort to be a functional of the animal's trajectory,

$$F[\vec{q}(t), \vec{\alpha}(t)] = \int_{t_0}^{t_1} f dt \quad (5)$$

in terms of an 'effort rate', f which is a function of the positions, $\vec{q}(t)$, $\vec{\alpha}(t)$, velocities, $\dot{\vec{q}}(t)$, $\dot{\vec{\alpha}}(t)$ and arbitrarily many higher time derivatives, but not of t itself, by time-translation invariance.

It is proposed that an animal moves its active coordinates along a trajectory $\vec{\alpha}(t)$ of least effort F , subject to some conditions and constraints to be discussed in section 3.2. Let us first consider the properties that the functional in equation (5) is expected to have.

3.1. Properties of an effort functional

A first guess at the form of the effort functional might be $F = W$, to quantify the total mechanical work performed by the animal (via its muscles applied to its active degrees of freedom) over the course of the trajectory between the specified (fixed) initial and final states,

$$W = \int_{t_0}^{t_1} P dt,$$

where P is the rate at which the animal performs work via its active degrees of freedom (its power output). If we assume a simple Hamiltonian system in which the passive degrees of freedom conserve energy (thus neglecting drag and dynamic friction, which may be a reasonable assumption for trajectories close to those chosen by land-based animals), any change in the total energy E of the system must be due to work done by the active degrees of freedom. And hence, in that conservative case, the animal's power output is found simply by $P = \dot{E}$ (as confirmed in appendix C). On the other hand in the presence of non-conservative forces, the calculation of P is still straightforward (as given in section 7), from the forces and displacements on a given trajectory.

However, the above objective function defining work is not a suitable candidate for the effort functional to be minimized, as becomes obvious if we consider a simple case. Consider an animal required to begin and end its trajectory static at the foot of a hill. It could achieve this by staying still and expending no energy, which is clearly the option that requires least 'effort' according to an intuitive everyday understanding of the term. Alternatively, the animal could walk up the hill and return within the time interval $[t_0, t_1]$. The uphill part of this journey would require energy expenditure, resulting in $P > 0$ as the animal's limbs perform work by moving

a force through a displacement. On the downhill part, its limbs would absorb work from its gravitational potential energy as its limbs are displaced by reaction forces from the ground. Thus its rate of energy expenditure would be negative, $P < 0$, on the downhill part, and the net work done during the whole journey, given by the above functional, would vanish. Indeed, that integral is straightforward to evaluate in the conservative case, where $P = \dot{E}$ leading to $W = E(t_1) - E(t_0)$. So this objective function does not favour the static option over any other choice of trajectory, as the end points (at t_0 and t_1) are fixed.

Everyday experience tells us that walking downhill takes more effort than staying still. So ‘effort’ is clearly not synonymous with ‘work’. Absorbing work from the environment (as happens on a downhill journey) does not allow muscles to convert mechanical energy back into the chemical energy of food, but instead requires further expense from the animal. Thus, our effort functional should be expressed in terms of a utility function that ascribes an expense to both positive and negative values of P and is minimal (and takes a value of zero by definition, without loss of generality) at $P = 0$.

In the simplest conjecture, where the effort rate,

$$f = f(P) \quad (6)$$

is a function of P only, then, by the above observations, it must have the properties

$$\begin{aligned} f(0) &= 0 \\ \text{and } f(x) &> 0 \quad \text{for } x \neq 0. \end{aligned} \quad (7)$$

It would then also be reasonable to assume that the first derivative f' of the function $f(P)$ has the properties

$$\begin{aligned} f'(P) &> 0 \quad \forall \quad P > 0 \\ \text{and } f'(P) &< 0 \quad \forall \quad P < 0, \end{aligned} \quad (8)$$

since a higher rate of work is always harder to perform or to absorb than a low rate. This simplest conjecture, expressed in equation (6), implies that the effort rate does not depend on any time derivatives of P so that, given a choice between trajectories requiring equal durations of equally high-power movement interspersed with equally low-power episodes, the animal has no preference as to the time-ordering of the high- and low-power episodes. It also neglects any preference that an animal may have in expending work via strong joints rather than delicate ones. This may be a reasonable approximation to empirical fact when considering motion of an animal’s largest muscles and joints.

The properties of a simple effort rate function given in equations (6)–(8) are presented for the sake of a concrete example, and will be used again in analysing some toy models in sections 11–13. However, only the most general form of equation (5) will be assumed in developing the formalism below.

3.2. Statement of the problem

To determine the optimal movement $\vec{\alpha}(t)$, we cannot simply minimize the functional in equation (5) with respect to functions $\vec{\alpha}(t)$, because F is also a functional of the arbitrary passive trajectory $\vec{q}(t)$. The animal must choose a movement of least effort only from amongst dynamical paths that are physically possible. Hence, we must evaluate the effort, equation (5) for the ($\vec{\alpha}$ -dependent) physical case $\vec{q}(t) = \vec{q}^*(t)$ defined by equation (2) and then find the trajectory $\vec{\alpha}(t)$ that minimizes it. Thus, in minimizing $F[\vec{q}^*(t), \vec{\alpha}(t)]$ with respect to $\vec{\alpha}(t)$, the variations δF are non-trivial to evaluate, since a variation $\delta \vec{\alpha}(t)$ leads to a corresponding variation of the physical trajectory $\delta \vec{q}^*(t)$.

One further complication arises from the fact that, for an arbitrary active motion $\vec{\alpha}(t)$, the physical path $\vec{q}^*(t)$ that passes through the required initial and final configurations, $\vec{q}(t_0)$ and $\vec{q}(t_1)$, has initial and final velocities, $\dot{\vec{q}}^*(t_0)$ and $\dot{\vec{q}}^*(t_1)$, that cannot be chosen independently and may not be those desired for the case under consideration. This is because, while the initial and final points of the trajectory $\vec{q}(t)$ are fixed in the variation described by equations (1) and (2), the initial and final velocities are not.

Thus, if the method thus far described is used in its present form to calculate how an animal would move with least effort in order to climb from the bottom to the top of a hill, the result would be that the animal performs no work, and achieves the ascent ballistically by possessing a high initial velocity. This unsatisfying answer highlights the fact that the formalism will be useful only if it allows us to specify initial and final velocities as well as positions. Thus, we refine the question under consideration from, ‘What physical trajectory minimizes the effort,’ to, ‘What physical trajectory minimizes the effort for a given initial and final velocity?’.

4. Minimizing the physical effort

Let us now consider how to perform the minimization of effort (equation (5)) subject to the motion remaining physical and having the desired initial and final postures and velocities. This is a constrained minimization—a standard type of problem in mathematics and computer science. Specifically, we have a minimization problem with an uncountable infinity of constraints, arising from the condition that the passive variables q_i are required *at every moment of time* t to respect the equations of motion imposed by equation (2).

Note that the left-hand side of equation (2) represents a generalized force (that includes d’Alembert’s inertial force [13]) *acting on* each generalized coordinate, so that the generalized force *applied by* each generalized coordinate is

$$\vec{A} := -\frac{\delta S[\vec{q}, \vec{\alpha}]}{\delta \vec{q}}. \quad (9)$$

This is required, by physical dynamics, to vanish for passive coordinates, so that equation (2) can be written

$$A_i = 0 \quad \forall t \in [t_0, t_1]; \quad i = 1 \dots D_p \quad (10)$$

(treating q_i and $\dot{q}_i$ as components of the vectors $\vec{q}$ and $\dot{\vec{q}}$).

For the usual case where L is a function only of generalized positions and velocities (no higher time derivatives), equation (9) becomes [13]

$$\vec{A} = \frac{d}{dt} L_{\dot{\vec{q}}} - L_{\vec{q}} \quad (11)$$

so equation (10) yields Lagrange’s equations, where the subscript notation represents partial derivatives,

$$L_{q_i} := \frac{\partial L}{\partial q_i}$$

and

$$L_{\dot{q}_i} := \frac{\partial L}{\partial \dot{q}_i}$$

so the vectorial quantity $L_{\vec{q}}$, with components L_{q_i} , represents a gradient of L in $\vec{q}$ -space.

Now, the method of Lagrange multipliers [19] may be used to minimize $F[\vec{q}(t), \vec{\alpha}(t)]$ subject to the constraints $\vec{q}(t) = \vec{q}^*(t) \forall t \in [t_0, t_1]$ (expressed by equation (2)). Since there is a

continuum (an infinite set) of constraints (because equation (10) must be respected at every value of $t \in [t_0, t_1]$), we require a continuum of Lagrange multipliers given by the function $\vec{\Lambda}(t) \forall t \in [t_0, t_1]$. Thus, the constrained minimization of effort $F[\vec{q}(t), \vec{\alpha}(t)]|_{\vec{q}(t)=\vec{q}^*(t)}$ is equivalent to the unconstrained minimization of *physical effort*

$$\begin{aligned} \Phi[\vec{q}(t), \vec{\alpha}(t)] &:= F[\vec{q}(t), \vec{\alpha}(t)] + \int_{t_0}^{t_1} \vec{\Lambda}(t) \cdot \vec{A} dt \\ &= \int_{t_0}^{t_1} \left\{ f + \vec{\Lambda}(t) \cdot \vec{A} \right\} dt \end{aligned} \quad (12)$$

with respect to all of its arguments. Thus, we have

$$\frac{\delta \Phi}{\delta \{\vec{q}(t), \vec{\alpha}(t)\}} = \vec{0}, \quad (13)$$

with the unknown D_p -component vectorial functions $\vec{\Lambda}(t)$ chosen such that the resulting optimal trajectories respect equation (10). The quantity Φ defined in equation (12), which is closely related to effort, will be termed ‘physical effort’ and the optimization in equation (13) the Principle of Least Physical Effort.

The further constraints on initial and final velocities, discussed in section 3.2, can now be imposed by performing the minimization with respect to variations drawn only from a family of functions $\vec{q}(t), \vec{\alpha}(t)$ with the desired initial and final conditions. Further restrictions on the family of functions may be imposed in order to respect any desirable inequalities e.g. to exclude trajectories with excessive joint torques or angles. The resulting dynamics is guaranteed to be physical (i.e. respecting equation (10)) by appropriate choice of functions $\vec{\Lambda}(t)$. Note that the above derivation of equations (12) and (13) is consistent with Pontryagin’s maximum principle [14, 20].

The optimization in equation (13) can either be performed numerically, using a standard algorithm [21], as discussed in sections 5 and 6, or analytically, as derived in sections 8 and 9. The numerical approach has the practical advantage that initial and final positions and velocities are straightforwardly specified, making it the appropriate basis for software design to perform in-betweening for animation. The analytical approach yields a differential equation of motion and the insights afforded by various exact properties of the dynamics.

5. Reduction to a finite problem for numerics

The unknown $\vec{\Lambda}(t)$ can be expanded in a set of basis functions $\{e_i(t)\}$ (such as Fourier modes) of size N_c and a set of unknown coefficients $\{\vec{\Lambda}_i\}$ thus:

$$\vec{\Lambda}(t) = \sum_{i=1}^{N_c} \vec{\Lambda}_i e_i(t), \quad (14)$$

yielding a representation of $\vec{\Lambda}(t)$ that is expected (for an appropriate ordering of basis functions) to become increasingly accurate as more basis functions are included in the set, and to converge to an exact result in the limit $N_c \rightarrow \infty$ where the set becomes complete.

Hence, the functional Φ to be minimized (equation (12)) is re-cast as

$$\Phi[\vec{q}(t), \vec{\alpha}(t)] = F[\vec{q}(t), \vec{\alpha}(t)] + \sum_{i=1}^{N_c} \vec{\Lambda}_i \cdot \vec{C}_i[\vec{q}(t), \vec{\alpha}(t)], \quad (15)$$

where the functionals $\vec{C}_i[\vec{q}(t), \vec{\alpha}(t)]$ are defined as

$$\vec{C}_i[\vec{q}(t), \vec{\alpha}(t)] := \int_{t_0}^{t_1} e_i(t) \vec{A} dt. \quad (16)$$

Equation (15) is exactly the form of expression one would minimize if required to perform a constrained minimization of F subject to a number N_c of *discrete* vectorial constraints $\vec{C}_i$, each assigned a Lagrange multiplier $\vec{\Lambda}_i$. Hence the problem becomes one of minimizing the original effort functional F in equation (5) while enforcing a number N_c of discrete constraints defined by vanishing of the constraint functions in equation (16). While the procedure exactly respects physical dynamics only in the limit $N_c \rightarrow \infty$, the number of constraints required in practice for consistency and sufficient physical accuracy of a numerical algorithm is discussed below.

When the trajectories are expressed in a suitable expansion, as in section 5.1 below, F and $\vec{C}_i$ become functions of the expansion coefficients and standard algorithms may be used to perform the constrained minimization with respect to those variables. Such optimization algorithms often require derivatives of the object function and constraints with respect to the variables. Those derivatives are given in appendix B.

5.1. Counting the variables and constraints

The problem of minimizing the functional in equation (15) may be further rationalized by expanding the functions $\vec{q}(t)$ and $\vec{\alpha}(t)$ in sets of basis functions, $\{g_i(t)\}$ and $\{h_i(t)\}$ respectively, which are not necessarily the same as each other or as the set $\{e_i(t)\}$ used for the Lagrange multiplier function $\vec{\Lambda}(t)$. Each of these three sets forms a basis for expression of a differentiable function, but each is subject to different boundary conditions, as discussed for each of the three below.

(i) The function $\vec{\Lambda}(t)$ has no restrictions on its initial and final positions and derivatives so its basis $\{e_i(t)\}$ must become complete in the limit $N_c \rightarrow \infty$, with respect to arbitrary boundary conditions.

(ii) As discussed, we wish to be able to specify initial and final positions and velocities of the active coordinates $\vec{\alpha}(t)$. Being active, those coordinates are not constrained to respect a least action principle with fixed end points, as the passive coordinates are. Therefore, we are free to specify those desired boundary conditions, and to choose a basis set $\{h_i(t)\}$ of size N_a that respects them and becomes complete in the limit $N_a \rightarrow \infty$. One such suitable expansion—a recasting of a Fourier expansion—is provided in appendix A, in a form that simplifies the specification of initial and final positions and velocities and the expression of the variational parameters. Thus, the trajectories of the active variables are specified by a number N_a of D_a -component vectorial expansion parameters, in a description which, in the limit $N_a \rightarrow \infty$, is guaranteed to include the trajectory of least effort, but may be truncated to a finite value for an approximate solution.

(iii) The choice of basis set $\{g_i(t)\}$ (of size N_v) for the D_p -dimensional passive coordinates $\vec{q}(t)$ requires some care. Hamilton's principle requires the extremization of equation (1), as specified by equation (2), to be performed with fixed initial and final positions but freely varying velocities, equivalent to applying Dirichlet boundary conditions to Lagrange's equations (equations (10) and (11)). Hence, we must consider an expansion consistent with those boundary conditions. The free variables in that expansion (the expansion coefficients) are fully determined by the laws of physics, as represented by equation (10) or, equivalently, by vanishing of the constraint functionals in equation (16). Thus, if the expansion is truncated to a number N_v of D_p -component vectorial variables (where the exact dynamics is recovered in the

limit $N_v \rightarrow \infty$), then an exactly equal number of discrete D_p -component vectorial constraints, $N_c = N_v$ is required in order to fully determine (and not over-determine) the passive dynamics.

For convenience, an expansion of the same form (e.g. that given in appendix A) as used for the active coordinates may also be used for the passive coordinates if the initial and final velocities $\dot{\vec{q}}(t_0)$ and $\dot{\vec{q}}(t_1)$ (represented by $\dot{x}_0$ and $\dot{x}_1$ in appendix A which were constants when used to describe the active coordinates) are counted among the N_v variables in this case. (In appendix A, we then have $N_v = N + 2$, where N is the number of D_p -dimensional vector-valued expansion coefficients $\vec{b}_k$ used in the summation in equation (A1).)

As noted below equation (13), we may now choose to impose particular initial and final velocities on the system, by fixing the values $\dot{\vec{q}}(t_0)$ and $\dot{\vec{q}}(t_1)$, thus removing $2D_p$ degrees of freedom from the variational problem, but we cannot choose to violate the laws of physics and hence the number N_c of required constraints, discussed above, does not change when this choice is made. Hence, if $N_p = N_v - 2$ vector-valued variables remain in the description of the passive coordinates' trajectory with fixed initial and final positions and velocities, then the number of D_p -dimensional constraints of the form in equation (16) required (and hence, the number of basis functions $e_i(t)$) is

$$N_c = N_p + 2. \quad (17)$$

The imposed choice of initial and final velocities is accommodated by optimizing the effort with respect to the remaining N_p and N_a vector-valued variables only. In general, the animal must exert extra effort in order to satisfy the user's demand for particular boundary velocities.

5.2. Practical considerations

In practice, for a suitable choice of N_a , it is found that standard constrained optimization algorithms are successful and efficient in finding accurate numerical approximations to the trajectories of least physical effort if $N_p \gg N_a$, e.g. $N_p = 10N_a$, so that Newtonian dynamics is respected on all relevant time-scales, including those significantly faster than the active movements of the animal.

Furthermore, it is found that the modified Fourier expansion in appendix A worked well for all of the toy models investigated (discussed in sections 11–13), whereas a Fourier basis is not so effective for the $e_i(t)$ in the constraints (equation (16)), as this sometimes leads to spurious unphysical solutions for which the constraints are satisfied by cancellations between large positive and negative regions of the integrand. Instead, a more stable and efficient choice is found to be a set of Dirac delta functions, $e_i(t) = \delta(t - t_i)$ at a number $N_c = N_p + 2$ of equally-spaced time points $\{t_i\}$ in the interval $[t_0, t_1]$, so that equation (16) reduces to

$$\vec{C}_i [\vec{q}(t), \vec{\alpha}(t)] = \vec{A}(t_i). \quad (18)$$

In all the models investigated, any deviation from the number of constraints in equation (17) was found to result in failure of the optimization or highly unphysical trajectories.

6. A compact notation

To make progress, let us re-cast the problem in terms of a $(D_p + D_a)$ -dimensional vector function of time, $\underline{Q}(t)$ that includes both active and passive generalized coordinates, thus:

$$\underline{Q} := \begin{pmatrix} \vec{q} \\ \vec{\alpha} \end{pmatrix}.$$

That is,

$$Q_i = \begin{cases} q_i & \text{for } 1 \leq i \leq D_p, \\ \alpha_{i-D_p} & \text{for } D_p + 1 \leq i \leq D_p + D_a. \end{cases}$$

We similarly extend the dimensionality of the vector of Lagrange multipliers, but without increasing the number of constraints, by writing

$$\underline{\Lambda}(t) := \begin{pmatrix} \vec{\Lambda}(t) \\ \vec{0} \end{pmatrix}. \quad (19)$$

That is,

$$\Lambda_i = \begin{cases} \Lambda_i & \text{for } 1 \leq i \leq D_p, \\ 0 & \text{for } D_p + 1 \leq i \leq D_p + D_a. \end{cases}$$

Note that $(D_p + D_a)$ -dimensional vectors are written underlined, while the D_p -dimensional vectors relating to passive coordinates and D_a -dimensional vectors relating to active coordinates have an over-arrow. In all cases, the first D_p components of an extended (underlined) vector relate to passive coordinates and the remaining components to active ones.

Now, the definition in equation (9) is extended to

$$\underline{A} := -\frac{\delta S[\underline{Q}(t)]}{\delta \underline{Q}}, \quad (20)$$

which represents the generalized force [13] applied by *all* generalized coordinates (both passive and active ones), but is physically required to vanish only for passive coordinates (equation (10)), as implemented by the truncated vector $\underline{\Lambda}$ of Lagrange multipliers defined in equation (19), with the physical effort in equation (12) recast as

$$\Phi[\underline{Q}(t)] = \int_{t_0}^{t_1} \psi(\underline{Q}, \dot{\underline{Q}}, \ddot{\underline{Q}}, \dots) dt, \quad (21)$$

where

$$\psi = f + \underline{\Lambda} \cdot \underline{A}. \quad (22)$$

And the principle of least physical effort, equation (13), becomes simply

$$\frac{\delta \Phi}{\delta \underline{Q}(t)} = \underline{0}. \quad (23)$$

Thus, the numerical problem in section 5 becomes one of minimizing the functional

$$F[\underline{Q}(t)] = \int_{t_0}^{t_1} f dt \quad (24)$$

with respect to the trajectory $\underline{Q}(t)$ subject to the vanishing of the first D_p components of the N_c constraint functionals

$$\underline{C}_i[\underline{Q}(t)] := \int_{t_0}^{t_1} e_i(t) \underline{A} dt, \quad i = 1 \dots N_c, \quad (25)$$

which are defined as extended vectors in equation (25) for ease of notation, although only their passive components (the first D_p) need to be used or evaluated.

In the equations that follow, we shall use a convention that an inner product (represented by the dot product symbol as in equation (22)) between two matrices or vectors is implemented

by contracting on whichever uncontracted vectorial quantities are written closest to the dot. For example,

$$\left[(T_{\underline{Q}\underline{\dot{Q}}} \cdot \underline{\dot{Q}}) \cdot \underline{\dot{A}} \right]_i = \sum_{j,k} T_{\underline{Q}\underline{\dot{Q}}} Q_k \frac{\partial A_j}{\partial \dot{Q}_i}.$$

7. Power-dependent effort

To make further progress, let us henceforth consider the case represented by equation (6), where the effort rate f is a function $f(P)$ only of the animal's power output $P(t)$. Generalizations to other forms of effort rate follow straightforwardly, such as $f(P, \dot{P})$ or $f(\underline{Q}, \underline{\dot{Q}})$ if, for instance, metabolic cost is found to be dominated by certain joints. See section 14 for further generalization.

The total power expended by the animal's muscles in controlling the time-dependence of the active degrees of freedom is equal to the power input to the mechanical system, given by

$$P = \underline{\dot{Q}} \cdot \underline{A} \quad (26)$$

which is the generalized expression for velocity multiplied by the parallel component of force applied by the animal. Only active degrees of freedom contribute to the power, since the passive components of $\underline{A}$ vanish for physically valid trajectories. For conservative Hamiltonian systems, it is shown in appendix C that equation (26) is equivalent to the time derivative of energy.

Note that the effort

$$F[\underline{Q}(t)] = \int_{t_0}^{t_1} f(\underline{\dot{Q}} \cdot \underline{A}) dt \quad (27)$$

would be absolutely minimized by the solution $\underline{A} = \underline{0} \forall t \in [t_0, t_1]$, whereby *all* coordinates behave passively, contributing zero power and hence zero rate of effort. This solution is valid only if it is consistent with the required initial and final velocities. If those velocities do not match the purely passive dynamics, then the animal must expend some effort.

8. Analytical minimization of the functional

While the variational approach to the problem (involving families of trial functions), described in section 5, is fruitful for numerics, another informative approach is to find the differential equations that formally solve the variational problem. These equations (derived below) could potentially be used to make contact with experimental applications in sports science (optimizing athletes' performance) and veterinary medicine (involving problems in animals' movement) or to determine the effort rate function f employed by humans and animals in the real world.

A functional of the form given in equation (21) has the functional derivative [22]

$$\frac{\delta \Phi}{\delta \underline{Q}(t)} = \psi_{\underline{Q}} - \frac{d}{dt} \psi_{\underline{\dot{Q}}} + \frac{d^2}{dt^2} \psi_{\underline{\ddot{Q}}} - \frac{d^3}{dt^3} \psi_{\underline{Q}^{(3)}} + \dots = \underline{0}, \quad (28)$$

where the final equality implements the principle of least physical effort.

Henceforth assuming a Lagrangian $L(\underline{Q}, \underline{\dot{Q}})$ that depends only on positions and velocities (the typical case) implies $\psi = \psi(\underline{Q}, \underline{\dot{Q}}, \underline{\ddot{Q}})$ depends on no time derivatives of $\underline{Q}$ higher than the second. Hence, substituting equations (22) and (26) into equation (28), implies the trajectory

of least physical effort is given by

$$\begin{aligned} [f'(P)\dot{\underline{Q}} + \underline{\Lambda}] \cdot \underline{A}_{\underline{Q}} - \frac{d}{dt} \left\{ [f'(P)\dot{\underline{Q}} + \underline{\Lambda}] \cdot \underline{A}_{\underline{Q}} + f'(P)\underline{A} \right\} \\ + \frac{d^2}{dt^2} \left\{ [f'(P)\dot{\underline{Q}} + \underline{\Lambda}] \cdot \underline{A}_{\underline{Q}} \right\} = 0, \end{aligned} \quad (29)$$

where the generalized forces (equation (20)) (both active and passive) are given as usual [13] by

$$\underline{A} = \frac{d}{dt} L_{\underline{Q}} - L_{\underline{Q}}. \quad (30)$$

Equation (29), together with equation (10) (i.e. vanishing of only the D_p passive components of the generalized force), fully defines an animal's trajectory for given boundary conditions. Note that the form of equation (29) derives from the fact that the animal is optimizing some aspect of its rate of work. It thus specifies the general dynamics of living creatures that have been somehow optimized by evolution, without needing to know the exact form of the optimized quantity $f(P)$.

9. Conservative Hamiltonian case

For conservative Hamiltonian systems—i.e. when the Legendre transform of the Lagrangian that defines the Hamiltonian [13] exists and in the absence of dissipation in the mechanical system (so that no energy is added or removed other than via the active degrees of freedom)—then equation (26) for the power is equal to the rate of change of mechanical energy, as one would expect and as confirmed in appendix C. Let us henceforth consider such systems.

It may be reasonable to assume that large land-based animals are well represented by such conservative Hamiltonian system, as they conform to standard Newtonian mechanics and are likely to choose to move without significant dissipation, as noted in section 2. In this case, the generalized force in equation (30) evaluates to

$$\underline{A} = U_{\underline{Q}} - T_{\underline{Q}} + \dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}} + \ddot{\underline{Q}} \cdot T_{\underline{Q}\ddot{\underline{Q}}}, \quad (31)$$

in terms of derivative of the potential energy $U(\underline{Q})$ and kinetic energy $T(\underline{Q}, \dot{\underline{Q}})$. Here, the total time derivative of the function $T_{\dot{\underline{Q}}}(\underline{Q}, \dot{\underline{Q}})$ of two variables, has been found using the chain rule. Note that $T_{\underline{Q}\dot{\underline{Q}}}$ is a matrix of second derivatives of T .

The required partial derivatives of the generalized force vector $\underline{A}$ are found from equation (31), yielding

$$\underline{A}_{\underline{Q}} = U_{\underline{Q}\underline{Q}} - T_{\underline{Q}\underline{Q}} + \dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}\underline{Q}} + \ddot{\underline{Q}} \cdot T_{\underline{Q}\ddot{\underline{Q}}\underline{Q}} \quad (32)$$

$$= U_{\underline{Q}\underline{Q}} - T_{\underline{Q}\underline{Q}} + \frac{d}{dt} T_{\dot{\underline{Q}}\underline{Q}} \quad (33)$$

$$\underline{A}_{\dot{\underline{Q}}} = \dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}\dot{\underline{Q}}} \quad (34)$$

$$= \frac{d}{dt} T_{\underline{Q}\dot{\underline{Q}}} \quad (35)$$

$$\underline{A}_{\ddot{\underline{Q}}} = T_{\underline{Q}\ddot{\underline{Q}}} \quad (36)$$

where the evaluation of $\underline{A}_{\dot{Q}}$ has assumed that both $\underline{U}_{\dot{Q}}$ and $\underline{T}_{\dot{Q}\dot{Q}}$ are independent of $\dot{Q}$. Using Eqs 35 and 36, we can simplify equation (29), yielding

$$[f'(P)(\dot{Q} + \underline{\Lambda}) \cdot \underline{A}_{\dot{Q}} - \frac{d}{dt} \left\{ f'(P) \underline{A} - \underline{T}_{\dot{Q}\dot{Q}} \cdot \frac{d}{dt} [f'(P)(\dot{Q} + \underline{\Lambda})] \right\}] = 0. \quad (37)$$

Some useful identities for evaluating the terms in equations (29) and (37) are given in appendix B.

10. A simple utility function

The forms of equations (29) and (37) are informative in themselves, and define a class of trajectories with living dynamics. However, to calculate trajectories of least physical effort explicitly, we require knowledge of the ‘effort rate’ utility function f used by the animal in question. If we continue to assume an effort rate $f(P)$ that depends only on the animal’s total power output P , then the conditions in equations (7) and (8) put strong restrictions on that function, but do not define it uniquely. Its precise form specifies the animal’s relative preference for a brief period of high-power exercise or a more extended period of low-power exercise. Its form could be measured by comparing the predictions of the present formalism with observations of the movements of real animals and/or sports-people. It would be interesting to discover to what extent (if at all) the function differs between species. In the absence of such an experimental study, we may appeal to aesthetics and use the simplest function consistent with equations (7) and (8), which is

$$f(P) = P^2. \quad (38)$$

In reality, although both positive and negative values of P constitute positive effort, it is likely that animals favour negative values of P to positive ones (i.e. it is easier to absorb than to expend a given power), so that an asymmetric function such as $f(P) = P^2 + P^3 + P^4$ would be closer to the truth. But, in the interest of simplicity and to avoid introducing too many unknown polynomial coefficients, we shall apply equation (38) to the toy models below.

One might consider the absolute function, $f(P) = |P|$ as an alternative to equation (38), as in [25], but this is unsuitable as it would lead to highly degenerate families of trajectories and therefore no discrete solutions, for the following reasons. Any putative trajectory in the time interval $[t_0, t_1]$ may be divided into a set of sub-trajectories on sub-intervals during which the animal’s power output P is single-signed (i.e. either all positive or all negative). In any of those sub-intervals, this effort rate function evaluates to $f(P) = P = \dot{E}$ or $f(P) = -P = -\dot{E}$ which is a total time derivative. So, the effort (equation (5)) becomes independent of the trajectory, depending only on the system’s total energy at the discrete set of end-points of the sub-trajectories, defined by the times at which $P = 0$. We shall see that this would be the case in the model presented in the next section.

11. Toy model 1: one degree of freedom

The formalism developed in this paper is now demonstrated in practice, by application to three minimal models. For completeness, the case of a single degree of freedom is demonstrated first and is found to be analytically tractable. But, greater mathematical insight will be gained from the next model, demonstrated in section 12, while the model in section 13 will give a more physical insight and a realistic idea of the method’s usefulness.

The simplest possible case to which the formalism can be applied is a system with a single coordinate: the one-dimensional position α of a free point-mass m , which is somehow actively controlled. (If the single coordinate was chosen to be passive, so that the system had no active degree of freedom, Newtonian physics would be recovered from equation (10) yielding nothing novel.)

This simplest example is not typical of the formalism's intended use, as the agency represented by this active coordinate somehow applies an external force to the system, as opposed to applying momentum-conserving internal forces representing the exertion of muscles within an animal's body. For concreteness, one could consider this to be an over-simplified model of the trajectory chosen by a person instructed to grasp a massive frictionless puck and slide it a short distance horizontally from one point to another nearby, within a specified time, where the mass of the person's arm is neglected or absorbed into the definition of m .

The model is defined by its potential energy, $U = 0$, and kinetic energy $T = \frac{1}{2}m\dot{\alpha}^2$. With no passive coordinate ($D_p = 0$) and only a single active coordinate ($D_a = 1$), each vectorial and tensorial quantity in sections 8 and 9 reduces to a single component and all required quantities are trivially evaluated as follows:

$$\begin{aligned} U_{\underline{Q}} &= T_{\underline{Q}} = U_{\alpha} = T_{\alpha} = 0 \\ P &= \dot{T} + \dot{U} = m\dot{\alpha}\ddot{\alpha} \\ T_{\underline{Q}} &= T_{\alpha} = m\dot{\alpha} \\ T_{\underline{Q}\underline{Q}} &= T_{\dot{\alpha}\dot{\alpha}} = m. \end{aligned}$$

So, from equation (31),

$$\underline{A} = m\ddot{\alpha}.$$

Hence, equation (37) reduces to

$$\frac{d}{dt} \left\{ f'(P) m\ddot{\alpha} - m \frac{d}{dt} (f'(P) \dot{\alpha}) \right\} = 0, \quad (39)$$

and hence

$$\frac{d}{dt} \left\{ \dot{\alpha} \frac{d}{dt} f'(P) \right\} = 0. \quad (40)$$

As discussed in section 10, it is clear that $f(P) = |P|$ would be a pathological choice of effort rate function, as it yields $f'(P) = \pm 1$ for non-zero P , so that equation (40) becomes $0 = 0$, and is thus consistent with any trajectory of non-zero power output. For the effort rate function $f(P) = P^2$ as assumed in equation (38), equation (40) with $P = m\dot{\alpha}\ddot{\alpha}$ integrates to an autonomous equation for $v := \dot{\alpha}$,

$$\frac{d}{dt} (v\dot{v}) = \frac{a}{2v}$$

where a is a constant of integration. Defining $w := v\dot{v}$ yields

$$\frac{dv}{dw} = \frac{2w}{a}$$

which integrates to

$$v - c = w^2/a$$

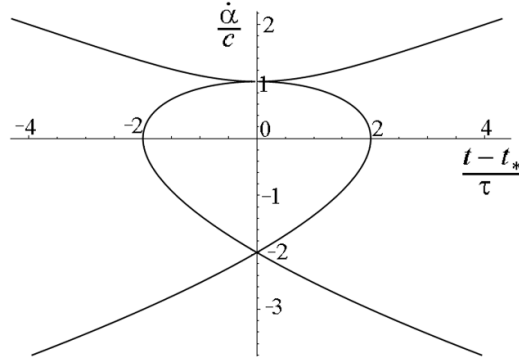


Figure 1. Graph of scaled velocity versus scaled and translated time for Toy Model 1. Note that the velocity scale c can be positive or negative. Of particular interest is the arched section touching the time axis at -2 and 2 , which is the preferred motion for moving a static, frictionless object from one location and placing it, static, in another (assuming the simplest effort rate function).

with c another constant of integration. Hence,

$$\frac{dt}{dv} = \pm \sqrt{\frac{v^2}{a(v-c)}}, \quad (41)$$

where $a(v-c) > 0$, which integrates (with constant of integration t_*) to explicit expressions relating time and velocity:

$$\frac{t-t_*}{\tau} = \pm \left(\frac{v}{c} + 2 \right) \sqrt{\left| \frac{v}{c} - 1 \right|} \quad \text{for } c \neq 0, \quad (42)$$

$$\frac{t-t_*}{k} = \pm v \sqrt{|v|} \quad \text{for } c = 0, \quad (43)$$

where $\tau = (2/3)c\sqrt{|c/a|}$ and $k = 2/(3\sqrt{|a|})$. Equation (42) is plotted in figure 1.

Now, to find α , we may use

$$\alpha = \int \dot{\alpha} dt = \int \dot{\alpha} \frac{dt}{d\dot{\alpha}} d\dot{\alpha} = \int v \frac{dt}{dv} dv,$$

where $\frac{dt}{dv}$ is given by equation (41). Hence, in terms of constant of integration α_0 , we find

$$\frac{\alpha - \alpha_0}{c\tau} = \pm \frac{1}{5} \sqrt{\left| \frac{v}{c} - 1 \right|} \left(3 \frac{v^2}{c^2} + 4 \frac{v}{c} + 8 \right) \quad (44)$$

for $c \neq 0$ and the straightforward limit of that expression in the case $c \rightarrow 0$. Equations (42) and (44) share the same choice of sign and are used to plot $\alpha(t)$ parametrically in figure 2, by varying the parameter v/c . As equation (40) is a fourth-order ordinary differential equation for $\alpha(t)$, its solution in equations (42) and (44) has four constants of integration, $\{t_*, \tau, \alpha_0, c\}$, which, in principle, can be determined by substitution of the four boundary conditions $\{\alpha(t_0), \alpha(t_1), \dot{\alpha}(t_0), \dot{\alpha}(t_1)\}$. In practice, while trivial in some cases, this becomes a highly non-trivial procedure in cases where the initial and final velocities have different signs so that the solution includes a point where $\dot{\alpha} \rightarrow 0$. Then the full solution becomes a concatenation of the different branches in figure 2 with different constants of integration. Exploring the interesting mathematical structure of that problem is left for future work.

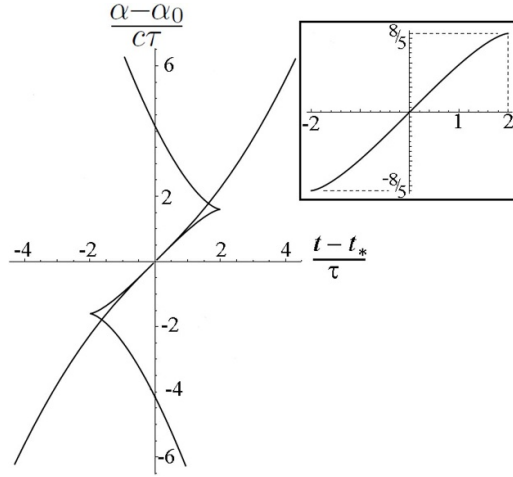


Figure 2. Graph of scaled and translated position versus scaled and translated time for Toy Model 1. By choosing the scales and the time-offset as well as arbitrary beginning and end points on any of the branches, all possible durations $(t_1 - t_0)$, and boundary conditions (initial and final positions and velocities) can be realised. Note that c can be positive or negative so that the time-reverse of each trajectory is also a solution. Inset: The branch of the curve that begins and ends at stationary points $\pm(2, \frac{8}{5})$, showing the least-effort trajectory for moving a static object from one position to another and leaving it static.

12. Toy model 2: two degrees of freedom

The toy model in section 11 was trivial, in that it had no passive degrees of freedom and therefore required no constraint arising from the need to respect Newtonian physics, since an active degree of freedom, being powered, can move along any desired trajectory. We now turn our attention to a toy model that possesses both a passive and an active degree of freedom, so $D_p = D_a = 1$. Let us consider two equal masses, m , moving in one dimension and connected by a Hookeian spring, of spring constant k . We take the position α of one of the masses to be an active coordinate and that of the other, q to be passive. It is non-trivial to solve the problem of moving the active mass between specified initial and final positions and velocities, in such a way as to ensure that the passive mass moves between other specified initial and final positions and velocities, within a specified duration. Nevertheless, there exists an infinite family of such trajectories, from which we require one of minimal effort. As for toy model 1, toy model 2 is also an atypical application of the formalism, because the agency represented by its active coordinate applies an unbalanced external force to the system, and therefore does not represent the application of an animal's internal musculature. For concreteness, one could visualise the model and an idealised representation of a child's toy consisting of bat and ball connected by elastic, where the game is to control the ball after it has been thrown with a given position and velocity, such that both bat and ball arrive at given target positions and velocities.

The model has potential and kinetic energies given, respectively, by

$$U = \frac{1}{2}k(q - \alpha)^2$$

$$T = \frac{1}{2}m(\dot{\alpha}^2 + \dot{q}^2).$$

Hence, in terms of the vector

$$\underline{Q} = \begin{pmatrix} q \\ \alpha \end{pmatrix},$$

we have derivatives

$$U_{\underline{Q}} = k(q - \alpha) \begin{pmatrix} 1 \\ -1 \end{pmatrix}, \quad (45)$$

$$T_{\underline{Q}} = \underline{0}, \quad (46)$$

$$T_{\dot{\underline{Q}}} = m \begin{pmatrix} \dot{q} \\ \dot{\alpha} \end{pmatrix}, \quad (47)$$

$$T_{\underline{Q}\dot{\underline{Q}}} = \underline{0}, \quad (48)$$

$$T_{\dot{\underline{Q}}\dot{\underline{Q}}} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} m, \quad (49)$$

$$\dot{U} = k(q - \alpha)(\dot{q} - \dot{\alpha}), \quad (50)$$

$$\dot{T} = m(\dot{q}\ddot{q} + \dot{\alpha}\ddot{\alpha}). \quad (51)$$

Hence, the generalized force (equation (31)) is

$$\underline{A} = \begin{pmatrix} k(q - \alpha) + m\ddot{q} \\ k(\alpha - q) + m\ddot{\alpha} \end{pmatrix}. \quad (52)$$

So, Lagrange's equation (10), which applies to the passive coordinate's force, $A_1 = 0$ yields

$$\ddot{q} = \frac{k}{m}(\alpha - q), \quad (53)$$

which can be used to simplify the expression for the power, yielding

$$P = \dot{U} + \dot{T} = m\dot{\alpha}(\ddot{q} + \ddot{\alpha}). \quad (54)$$

In making this substitution we are replacing the original function $P(\underline{Q}, \dot{\underline{Q}}, \ddot{\underline{Q}})$, and therefore also the function $f(P)$ to be optimized, by a new function that differs from the original in some parts of the $(\underline{Q}, \dot{\underline{Q}}, \ddot{\underline{Q}})$ phase-space, but is unchanged on the physical subspace defined by the constraint(s) of Lagrange's equation, and will therefore result in the same constrained optimum.

The general non-dissipative equation of motion, equation (37), also requires the derivative

$$\underline{A}_{\underline{Q}} = \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix} k \quad (55)$$

and the Lagrange multiplier vector function (equation (19))

$$\underline{\Lambda}(t) = \begin{pmatrix} \Lambda(t) \\ 0 \end{pmatrix}. \quad (56)$$

Thus, equation (37) becomes

$$\begin{pmatrix} 1 \\ -1 \end{pmatrix} [(\dot{q} - \dot{\alpha})f'(P) + \Lambda] - \frac{d}{dt} \left\{ \begin{pmatrix} 0 \\ (\alpha - q + \frac{m}{k}\ddot{\alpha})f'(P) \end{pmatrix} \right\}$$

$$-\frac{m}{k} \frac{d}{dt} \left[\begin{pmatrix} \dot{q} \\ \dot{\alpha} \end{pmatrix} f'(P) + \begin{pmatrix} \Lambda \\ 0 \end{pmatrix} \right] \Big\} = 0. \quad (57)$$

Summing the components yields

$$\frac{d}{dt} \left\{ \left(\alpha - q + \frac{m}{k} \ddot{\alpha} \right) f'(P) - \frac{m}{k} \frac{d}{dt} [(\dot{q} + \dot{\alpha}) f'(P) + \Lambda] \right\} = 0. \quad (58)$$

The unknown Lagrange multiplier function $\Lambda(t)$ can be eliminated from this ODE using the second component of equation (57), yielding

$$\frac{d}{dt} \left\{ -2\dot{\alpha}\dot{P} + \frac{m}{k} \left[\frac{d^2}{dt^2} (\dot{\alpha}\dot{P}) - \ddot{q}\ddot{P} \right] \right\} = 0 \quad (59)$$

where, again, the simple form of effort rate function in equation (38) has been assumed.

Equations (53), (54) and (59) form a closed set of equations for q , α and P , which could be combined into a single, eighth-order ODE and therefore require eight constants of integration to be set by the eight boundary conditions: the initial and final positions and velocities of the passive and active coordinates. This closed set of equations has been numerically integrated using RK4 (Runge-Kutta fourth-order quadrature [21]) for a particular case, shown in figure 3. We can regard such a quadrature scheme as a ‘shooting method’, because it requires a number (8 in this case) of initial conditions (at time t_0) and yields the resulting trajectory at all subsequent times; it does not allow the user to specify *a priori* the final state at time t_1 . For that, we instead require the variational method presented in section 5.

The solutions found using the RK4 method provide a test case for the variational method. That method, as set out in sections 5 and 6 has been implemented using the computer code available at [23], which calls a standard library function for constrained minimization, and requires only the functions in equation (54) and the first component, A_1 of equation 52 and their derivatives (for use in equations (B11) and (B13)),

$$P_{\underline{Q}} = \underline{0}, \quad (60)$$

$$P_{\underline{\dot{Q}}} = \begin{pmatrix} 0 \\ m(\ddot{q} + \ddot{\alpha}) \end{pmatrix}, \quad (61)$$

$$P_{\underline{\ddot{Q}}} = m\dot{\alpha} \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \quad (62)$$

$$A_{1,\underline{Q}} = (1, -1)k, \quad (63)$$

$$A_{1,\underline{\dot{Q}}} = \underline{0}, \quad (64)$$

$$A_{1,\underline{\ddot{Q}}} = (m, 0). \quad (65)$$

Using 10 free variables b_k to parametrize the active coordinate $\alpha(t)$ and 100 for the passive coordinate, $q(t)$ and, by equation (17), 102 constraints, the algorithm quickly found the path of least physical effort to an accuracy almost indistinguishable from the RK4 solution, as shown in figure 3.

13. Toy model 3: a lazy monkey

To demonstrate the formalism with a more realistic and intuitively instructive example, let us model a monkey hanging from a slippery branch and swinging in a vertical plane. It can exercise some control over its movement by using its abdominal muscles to lift its legs but it cannot directly set the angle at which it hangs relative to the vertical—that is a passive

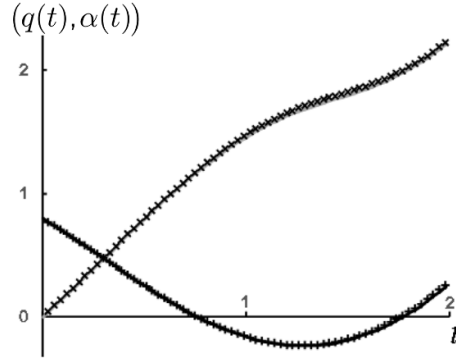


Figure 3. Least-physical-effort trajectory $(q(t), \alpha(t))$ of Toy Model 2 with $m = k = 1$, $t_0 = 0$, $t_1 = 2$, for the case $q(t_0) = 0.8$, $\alpha(t_0) = 0$, $\dot{q}(t_0) = -1$, $\dot{\alpha}(t_0) = 1.5$, $q(t_1) = 0.27788$, $\alpha(t_1) = 2.23866$, $\dot{q}(t_1) = 1.42047$, $\dot{\alpha}(t_1) = 1.31241$. The conditions at t_1 correspond to the further initial conditions (required for RK4 time-stepping) $P(t_0) = 0.04$, $\dot{P}(t_0) = 0$, $\ddot{P}(t_0) = 0$, $C = 0.4$, where C is the constant of integration of equation (59). The RK4 solution is shown with time-step 0.003 for $q(t)$ (+), $\alpha(t)$ (x) and variational solution for $q(t)$ (black line) and $\alpha(t)$ (grey line). The continuous lines are almost completely hidden by the data points.

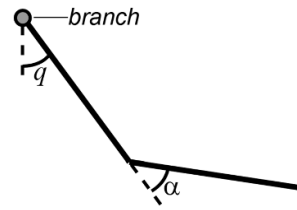


Figure 4. A monkey swinging from a branch, modelled as two articulated uniform rods. The first rod rotates freely about the branch, so that its angle q from vertical is a passive dynamical variable. The second rod is connected to the first by a hinge with angle α (relative to the first rod), which is an active dynamical variable, being controlled by the monkey.

coordinate, governed by the laws of physics and influenced only indirectly by the monkey's active contortions. As shown in figure 4, a minimal model of this animal is given by two rigid rods, connected end-to-end by a hinged joint (representing the monkey's abdomen) with an angle α which is an active coordinate. One of these rods (representing the monkey's arms and upper torso) is connected to a fixed point (representing the branch) by a freely-rotating joint (where the monkey grips the frictionless branch) so that the rod has an angle q relative to the downward vertical. The variable q is a passive coordinate because it is not directly 'motorized' in the monkey's anatomy and must therefore swing freely. This system, executing least-physical-effort dynamics, shall be known as the Lazy Monkey model.

Using this model, we shall conduct an exacting test of the methods developed in this paper: to find the motion of the monkey as it performs a hand-stand on the branch, beginning from an initially static posture hanging vertically beneath the branch. This difficult feat, often performed by Olympic gymnasts at the start of a high-bar routine, is modelled by setting the initial conditions $q(t_0) = \alpha(t_0) = 0$ with $\dot{q}(t_0) = \dot{\alpha}(t_0) = 0$ and final conditions $q(t_1) = \pi$, $\alpha(t_1) = 0$ with $\dot{q}(t_1) = \dot{\alpha}(t_1) = 0$. This is a particularly taxing problem because it requires the mechanical

system to move into an unstable equilibrium. So, an arbitrary shooting method might not find the solution and would not have the ‘lazy’ quality of a real animal’s movement, while standard ‘in-betweening’ (a.k.a. ‘motion-stitching’ or ‘frame-stitching’) methods of animation would lead to noticeably unphysical motion.

In reality, the animal’s physiology would limit its joint angle α to some finite range $[\alpha_{\min}, \alpha_{\max}]$. Solutions can be straightforwardly restricted to respect such a constraint by making a transformation $\alpha \rightarrow x$, such as $\alpha = \alpha_{\min} + (\alpha_{\max} - \alpha_{\min}) \cos^2 x$ and proceeding to solve the equations in terms of (q, x) . But, for simplicity, no such restriction will be made in the present example.

For simplicity, we shall assume the two rods have equal lengths r and masses m . In a gravitational field g , the system’s potential energy is

$$U = \frac{1}{2}mgr\{-3\cos q - \cos(q + \alpha)\} \quad (66)$$

and its kinetic energy (having both translational and rotational contributions from each of the uniform rods) is

$$T = \frac{1}{6}mr^2\{5\dot{q}^2 + 2\dot{q}\dot{\alpha} + \dot{\alpha}^2 + 3\dot{q}(\dot{q} + \dot{\alpha})\cos\alpha\}. \quad (67)$$

Henceforth, let us measure energies in units of $\frac{1}{2}mgr$ and time in units of $\sqrt{r/3g}$ so that the prefactors outside the curly brackets can be dropped from equations (66) and (67) without loss of generality.

The resulting generalized force, from equation (31), is

$$\underline{A} = \begin{pmatrix} A_1 \\ A_2 \end{pmatrix}; \quad (68)$$

$$\begin{aligned} A_1 &= \sin(q + \alpha) + 3\sin q \\ &\quad - 3\dot{\alpha}(2\dot{q} + \dot{\alpha})\sin\alpha + 10\ddot{q} + 2\ddot{\alpha} + 3(2\ddot{q} + \ddot{\alpha})\cos\alpha \\ A_2 &= \sin(q + \alpha) + 3\dot{q}^2\sin\alpha + 2\ddot{q} + \ddot{\alpha} + 3\ddot{q}\cos\alpha. \end{aligned}$$

A neat expression for the power is obtained from equation (26) with substitution of Lagrange’s equation, $A_1 = 0$, (equation (10)), yielding

$$P = \dot{\alpha}A_2. \quad (69)$$

In equations (67)–(69), we have all the necessary expressions for substitution into the differential equation (37) which, together with Lagrange’s equation, $A_1 = 0$, fully determines $q(t)$, $\alpha(t)$ and $\Lambda(t)$. In practice, those equations become untidy and their solution is difficult, so, we shall rely solely on the variational numerics to solve this model.

Using the same computer code [23] as in section 12 to implement the variational method, but now using the above expressions for A_1 and P together with their derivatives, numerical solutions to the difficult hand-stand problem were quickly obtained, given appropriate values of t_0 and t_1 . If the available duration $(t_1 - t_0)$ is too short, no solution to the hand-stand problem is found and it is suspected that no solution exists below some threshold duration. Above that threshold, there may exist one or many solutions (local minima of physical effort), depending on the value of $(t_1 - t_0)$.

A valid least-physical-effort solution, found for $t_1 - t_0 = 60$, is shown in figure 5. The green line in the figure shows the value of $A_1(t)$, which vanishes (to a high precision $\sim 10^{-16}$) at all times, demonstrating that the trajectory is physical, respecting Lagrange’s equation for the passive variable q . A more intuitive conception of the result can be gained by viewing an animation of the motion, available at [24]. In order to appreciate the nature of the problem, it is recommended that readers also view the animations there of unphysical trajectories that

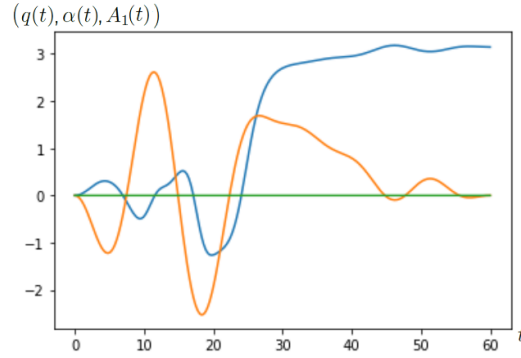


Figure 5. Variational solution of the hand-stand problem for the Lazy Monkey model. Using 12 free variables b_k to parametrize the active coordinate $\alpha(t)$ and 120 for the passive coordinate, $q(t)$ and, by equation (17), 122 constraints, the algorithm quickly found the path of least physical effort, $F \approx 2.41$. Functions of time shown are the passive angle $q(t)$ (blue curve from $(0, 0)$ to $(60, \pi)$), the active angle $\alpha(t)$ (orange curve from $(0, 0)$ to $(60, 0)$) and the violation of physics $A_1(t)$ (horizontal green line). See also animation at [24].

match the boundary conditions and of an arbitrary physical trajectory that respects Newtonian dynamics but does not minimize the physical effort. It is striking that the correct motion—the trajectory of least physical effort—imparts a life-like quality to a simple pair of sticks.

14. Summary and generalization

It is reasonable to assume that, when an animal moves naturally and gracefully, *some* aspect of its motion is optimal. In its most general form (given concisely in equations (20)–(25) and (28)), the present theory proposes nothing more than that, together with the need to respect the laws of classical physics.

Once the animal’s passive and active generalized coordinates are identified, all of the specific physical properties of the system are embodied in the expression of the generalized force $\underline{A}$. And all of the animal’s preferences are encoded in the formula of the effort rate, $f(\underline{Q}, \underline{\dot{Q}}, \underline{\ddot{Q}}, \dots)$. If that effort rate depends only on power, as assumed in section 7, then an expression for $\underline{A}$ is the only input required by the formalism (due to equation (26)).

The standard expressions of $\underline{A}$ for simple Lagrangian and conservative Hamiltonian systems are given in equations (30) and (31) respectively, but the present formalism is not restricted to those cases. For example, we may include a sliding frictional force $\underline{g}(\underline{Q}, \underline{\dot{Q}})$ on the animal, that is non-zero only when the configuration $\underline{Q}$ involves contact of a body part with the ground. The only non-zero components of $\underline{g}$ would be those corresponding to the generalized coordinates acted on by the friction. Other forces, $\underline{A}_{\text{other}}$, including those arising from conservative potentials and d’Alembert’s fictitious force of acceleration, can be formulated in the usual way from equation (30) or (31). Then the total force is simply given by

$$\underline{A} = \underline{A}_{\text{other}} - \underline{g},$$

where the negative sign arises from the definitions of $\underline{A}$ as the force applied *by* the generalized coordinates and $\underline{g}$ as the frictional force *on* those coordinates. The above expression of $\underline{A}$ can then be used to derive the trajectory of least physical effort, either numerically, as described

in section 5 and equations (24) and (25), or analytically in equation (28) or, in the case of a power-dependent effort, equation (29).

For completeness, let us imagine an example of an effort rate $f(\underline{Q}, \dot{\underline{Q}}, \ddot{\underline{Q}}, \dots)$ that does not depend solely on the animal's total power output P . An animal may find it more taxing to expend power via some degrees of freedom than others. Consider, for example, two of the articulated joints controlled by an animal's muscles, characterized by angles $\alpha_1(t)$ and $\alpha_2(t)$. If the animal finds it more difficult (taking greater effort) to expend a given power via the second of these joint (perhaps because it has the smaller muscle), we can model this by assigning different weights to the power outputs due to $\dot{\alpha}_1(t)$ and $\dot{\alpha}_2(t)$, so that $f(\dot{\underline{Q}} \cdot \underline{A})$ in equation (27) is replaced by

$$f(\dot{\underline{Q}} \cdot \underline{W} \cdot \underline{A}),$$

where the weight matrix $\underline{W}$ is diagonal, with different values on the rows associated with α_1 and α_2 and the function f continues to respect the conditions set out in section 3.1.

Furthermore, an animal's choice of trajectory may be significantly influenced by the breaking strengths of its body parts, resulting in an additional term in the effort rate, of the form

$$(\underline{A} \cdot \underline{B} \cdot \underline{A})^n$$

where the exponent n is some positive number and the matrix $\underline{B}$ weights the force components according to the strengths of corresponding body parts.

15. Conclusion

Life-like movement is distinguishable by eye and deserves foundational treatment in physics. The aim of this paper has been to formalise the simple observation that the motion of living creatures is recognisably different from that of passive or robotic systems. This ubiquitous identifiability of biotic movement, often described as graceful or lazy, suggests the presence of underlying dynamical principles. As well as identifying life-like motion as a physical phenomenon, key innovations introduced here are the derivation of a physically motivated variational principle, the treatment of coupled active and passive degrees of freedom and the numerical constraint structure (with the important criterion in equation (17)). The mathematical principles governing life-like motion lead to graceful, efficient trajectories without relying on empirical data or control systems.

By distinguishing between active and passive degrees of freedom, and requiring each to obey an appropriate variational optimization, the dynamics can eventually be cast as a single equation (equation (23)), the solution of which yields trajectories that are both physically valid and qualitatively life-like. Thus, a domain typically addressed by heuristics, empirical data, or learning algorithms is brought within the framework of analytical mechanics. The resulting formalism yields both explicit equations of motion and a practical numerical method for calculating the trajectories of articulated systems that exhibit animal-like dynamics.

The approach developed here is fundamentally different from algorithmic solutions based on controllers [12] or motion capture [3, 6]. While those methods are effective for their specific tasks, they do not address the core question: what fundamentally characterises the dynamics of life-like movement and distinguishes it from the dynamics of inanimate systems? The formalism presented here does so without needing empirical data or tuning to specific morphologies. The minimal models of sections 11–13 serve as proof-of-principle,

illustrating key features of the dynamics, including passive-active coupling, the mathematical practicalities of the minimisation and constraint resolution, and emergent life-like movement.

Li *et al* [25] introduced related ideas—notably their ‘L-score’, which is equivalent to a special case of the effort functional used here with all coordinates active and a utility function $f(x) = |x|$. However, their utility function leads to a lack of uniqueness discussed in sections 10 and 11 above. As with earlier discussions of variational principles, [14–17], their approach treated all variables as active, thus lacking the constraint structure required to enforce Newtonian dynamics, as applied in the present study.

When cast as a numerical variational problem (in section 5), the theory presented here allows a user to specify initial and final states and discover the physically valid trajectory connecting them that minimizes effort (if one exists). This provides a basis for applications in naturalistic animation, where it could be used for theoretically grounded in-betweening or exploratory motion synthesis. For instance, by setting boundary conditions that are far apart in time and space, the method can serve as a sandbox for discovering novel, efficient, or fantastical trajectories—a potentially creative tool for animators and designers and an advantage over machine learning algorithms that would struggle to cope with motions far removed from those on which they were trained. In this case, the problem of finding the physically valid (constraint-respecting) hypersurface in the high-dimensional optimization is a non-trivial one that would benefit from extant algorithmic innovations (such as [7]) in order to find a globally valid path for the effort minimization.

Beyond computational use, the theory has implications for understanding human and animal movement in scientific contexts. When cast in differential form (section 8), the framework could be used in sports science or veterinary medicine to infer how optimal or pathological a given movement pattern is. Importantly, the theory allows us to address questions such as, what is the effort functional being optimised by a given species or individual?

While a simple quadratic power-dependent effort rate was employed in section 10 for illustration, the general form is unconstrained. Empirical studies could treat equation (28), (29) or (37) as differential equations for the unknown effort rate f , given observed trajectories. If the simple power-dependence in equation (6) and section 7 holds, the resulting data would collapse onto a universal curve, $f(P(t))$ versus $P(t)$, specific to the organism. If not, the method still provides a rigorous foundation for interpreting experimental movement data.

In summary, this paper lays the groundwork for a mathematical physics of life-like motion. By distinguishing between what an animal controls and what follows passively, it becomes possible to write down physical laws for animate systems; laws that extend but do not contradict Newton’s. The resulting equations, and the principles behind them, offer a unifying framework for analysing, simulating and understanding naturalistic strategies of motion. More elaborate biomechanical models could be incorporated in future work. However, such complexity is not required to illustrate the core dynamics of the principle of least physical effort.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://doi.org/10.5518/1734>. The computer code associated with this paper is openly available from GitHub [23]. Animations and associated graphs are openly available from the University of Leeds Data Repository [24]. All other data underlying the results are available as part of the article and no additional source data are required.

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Appendix A. A Fourier expansion with appropriate boundary conditions

The vector function $\vec{q}(t)$ or $\vec{\alpha}(t)$ may be expressed in general as a function $\vec{x}(t)$ (or, with an obvious generalization to compact notation, $\underline{x}(t)$ to express the whole trajectory $\underline{Q}(t)$) with specified initial and final values and derivatives

$$\begin{aligned}\vec{x}(t_0) &= \vec{x}_0, \\ \vec{x}(t_1) &= \vec{x}_1, \\ \dot{\vec{x}}(t_0) &= \dot{\vec{x}}_0, \\ \dot{\vec{x}}(t_1) &= \dot{\vec{x}}_1\end{aligned}$$

by defining constants

$$\begin{aligned}\vec{a}_0 &= \frac{\vec{x}_0 + \vec{x}_1}{2} + \frac{\dot{\vec{x}}_1 - \dot{\vec{x}}_0}{\omega}, \\ \vec{a}_1 &= \frac{\vec{x}_0 - \vec{x}_1}{2} + \frac{\dot{\vec{x}}_0 + \dot{\vec{x}}_1}{\omega}, \\ \vec{a}_2 &= 2\dot{\vec{x}}_0/\omega, \\ \vec{a}_3 &= -2\dot{\vec{x}}_1/\omega,\end{aligned}$$

where $\omega = \pi/(t_1 - t_0)$. Then, we may write

$$\begin{aligned}\vec{x}(t) &= \vec{a}_0 + \vec{a}_1 \cos \omega t' + \vec{a}_2 \sin \frac{\omega t'}{2} + \vec{a}_3 \cos \frac{\omega t'}{2} \\ &\quad + (\sin \omega t') \sum_{k=1}^N \vec{b}_k \sin k \omega t'\end{aligned}\tag{A1}$$

in terms of the relative time $t' := t - t_0$ and a set of vectorial expansion coefficients $\vec{b}_k$ (written instead as extended vectors $\underline{b}_k$ if expressing $\underline{Q}(t)$). The formulation in equation (A1) is a recasting of the standard Fourier series that is complete on the interval $[t_0, t_1]$ in the limit $N \rightarrow \infty$. This formulation has the advantage that odd and even parts of the Fourier expansion (sines and cosines) do not need to be treated separately using two distinct sets of coefficients. Notice that the first line of equation (A1) represents a function with the required initial and final values and derivatives, so that the second line is required to express the most arbitrary repeatedly-differentiable function with vanishing boundary values and first derivatives on the interval $[t_0, t_1]$. For this expansion, the partial derivatives of the form required in equations (B11) and (B13) are given by

$$\frac{\partial \underline{x}}{\partial \underline{b}_k} = \underline{I} \sin \omega t' \sin k \omega t' \tag{A2}$$

$$\frac{\partial \dot{\underline{x}}}{\partial \underline{b}_k} = \underline{I} \{ \omega \cos \omega t' \sin k \omega t' + k \omega \sin \omega t' \cos k \omega t' \} \tag{A3}$$

$$\frac{\partial \ddot{\underline{x}}}{\partial \underline{b}_k} = \underline{I} \{ 2k\omega^2 \cos \omega t' \cos k \omega t' - (1 + k^2) \omega^2 \sin \omega t' \sin k \omega t' \}, \tag{A4}$$

where $\underline{I}$ is the identity matrix, denoting the fact that each component of the vector $\underline{x}$ depends only on the same component of the coefficients $\underline{b}_k$.

Appendix B. Some identities

For all Newtonian systems, we may assume the kinetic energy T is purely quadratic in velocities; that is,

$$T(\underline{Q}, \dot{\underline{Q}}) = \dot{\underline{Q}} \cdot \underline{G}(\underline{Q}) \cdot \dot{\underline{Q}} \quad (\text{B1})$$

where the position-dependent symmetric matrix of coefficients $\underline{G}(\underline{Q})$ has components $G_{ij} = G_{ji}$ so that, using Einstein summation convention, equation (B1) is written

$$T(\underline{Q}, \dot{\underline{Q}}) = G_{ij}(\underline{Q}) \dot{Q}_i \dot{Q}_j. \quad (\text{B2})$$

Hence, the product, $\dot{\underline{Q}} \cdot (\dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}})$ evaluates to

$$\begin{aligned} \dot{Q}_n \left(\dot{Q}_m T_{Q_m \dot{Q}_n} \right) &= \dot{Q}_n \dot{Q}_m \frac{\partial^2 T}{\partial Q_m \partial \dot{Q}_n} \\ &= \dot{Q}_n \dot{Q}_m \frac{\partial G_{ij}}{\partial Q_m} \left(\frac{\partial}{\partial \dot{Q}_n} (\dot{Q}_i \dot{Q}_j) \right) \\ &= \dot{Q}_n \dot{Q}_m \frac{\partial G_{ij}}{\partial Q_m} (\delta_{in} \dot{Q}_j + \dot{Q}_i \delta_{jn}) \\ &= \dot{Q}_m \frac{\partial G_{ij}}{\partial Q_m} (\dot{Q}_i \dot{Q}_j + \dot{Q}_i \dot{Q}_j) \\ &= 2 \dot{Q}_m \frac{\partial}{\partial Q_m} (G_{ij} \dot{Q}_i \dot{Q}_j) \\ \Rightarrow \dot{\underline{Q}} \cdot (\dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}}) &\equiv 2 \dot{\underline{Q}} \cdot T_{\underline{Q}} \end{aligned} \quad (\text{B3})$$

where partial derivatives of independent variables, $\partial \dot{Q}_i / \partial \dot{Q}_n = \delta_{in}$ have been expressed in terms of the Kronecker delta.

Similarly,

$$\begin{aligned} \dot{\underline{Q}} \cdot (\ddot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}}) &= \dot{Q}_n \ddot{Q}_m \frac{\partial^2}{\partial \dot{Q}_m \partial \dot{Q}_n} (G_{ij} \dot{Q}_i \dot{Q}_j) \\ &= \dot{Q}_n \ddot{Q}_m G_{ij} (\delta_{in} \delta_{jm} + \delta_{im} \delta_{jn}) \\ &= 2 \ddot{Q}_i G_{ij} \dot{Q}_j \\ &= \ddot{Q}_i \frac{\partial}{\partial \dot{Q}_i} (G_{mn} \dot{Q}_m \dot{Q}_n) \\ \Rightarrow \dot{\underline{Q}} \cdot (\ddot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}}) &\equiv \ddot{\underline{Q}} \cdot T_{\dot{\underline{Q}}} \end{aligned} \quad (\text{B4})$$

And the quadratic velocity dependence may be similarly exploited to obtain the following identities.

$$\dot{\underline{Q}} \cdot (\dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}\dot{\underline{Q}}}) \equiv 2 \dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}}, \quad (\text{B5})$$

$$\dot{\underline{Q}} \cdot (\ddot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}\dot{\underline{Q}}}) \equiv \ddot{\underline{Q}} \cdot T_{\dot{\underline{Q}}\dot{\underline{Q}}}, \quad (\text{B6})$$

$$\dot{\underline{Q}} \cdot (\dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}\dot{\underline{Q}}}) \equiv \dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}}. \quad (\text{B7})$$

Hence, from Equations (32), (34) and (36), we find the following properties of the generalized force vector for the conservative Hamiltonian case:

$$\dot{\underline{Q}} \cdot \underline{A}_{\underline{Q}} \equiv \dot{\underline{Q}} \cdot \left(U_{\underline{Q}\underline{Q}} + T_{\underline{Q}\underline{Q}} \right) + \ddot{\underline{Q}} \cdot T_{\dot{\underline{Q}}\underline{Q}} \equiv \frac{d}{dt} E_{\underline{Q}} \quad (\text{B8})$$

$$\dot{\underline{Q}} \cdot \underline{A}_{\dot{\underline{Q}}} \equiv \dot{\underline{Q}} \cdot T_{\underline{Q}\dot{\underline{Q}}} \quad (\text{B9})$$

$$\dot{\underline{Q}} \cdot \underline{A}_{\ddot{\underline{Q}}} \equiv T_{\dot{\underline{Q}}\ddot{\underline{Q}}} \quad (\text{B10})$$

which may be useful when evaluating equation (29) or, for numerical purposes, when evaluating derivatives of the power-dependent effort (equation (27)),

$$\begin{aligned} \frac{\partial F}{\partial \underline{b}_k} = & \int_{t_0}^{t_1} f'(P) \left\{ P_{\underline{Q}} \cdot \partial \underline{Q} / \partial \underline{b}_k \right. \\ & \left. + P_{\dot{\underline{Q}}} \cdot \partial \dot{\underline{Q}} / \partial \underline{b}_k + P_{\ddot{\underline{Q}}} \cdot \partial \ddot{\underline{Q}} / \partial \underline{b}_k \right\} dt, \end{aligned} \quad (\text{B11})$$

with respect to coefficients $\underline{b}_k$ of the trajectory expansion in appendix A.

Substituting equation (26) into equation (B11) yields

$$\begin{aligned} \frac{\partial F}{\partial \underline{b}_k} = & \int_{t_0}^{t_1} f'(\dot{\underline{Q}} \cdot \underline{A}) \left\{ \dot{\underline{Q}} \cdot \underline{A}_{\underline{Q}} \cdot \partial \underline{Q} / \partial \underline{b}_k \right. \\ & \left. + \left(\underline{A} + \dot{\underline{Q}} \cdot \underline{A}_{\dot{\underline{Q}}} \right) \cdot \partial \dot{\underline{Q}} / \partial \underline{b}_k + \dot{\underline{Q}} \cdot \underline{A}_{\ddot{\underline{Q}}} \cdot \partial \ddot{\underline{Q}} / \partial \underline{b}_k \right\} dt, \end{aligned} \quad (\text{B12})$$

which can be simplified using the above identities. Alternatively, in some cases, direct differentiation of an expression for P may be more straightforward.

Furthermore, derivatives of constraint functions are given by

$$\begin{aligned} \frac{\partial C_i}{\partial \underline{b}_k} = & \int_{t_0}^{t_1} e_i(t) \left\{ \underline{A}_{\underline{Q}} \cdot \partial \underline{Q} / \partial \underline{b}_k + \underline{A}_{\dot{\underline{Q}}} \cdot \partial \dot{\underline{Q}} / \partial \underline{b}_k \right. \\ & \left. + \underline{A}_{\ddot{\underline{Q}}} \cdot \partial \ddot{\underline{Q}} / \partial \underline{b}_k \right\} dt, \end{aligned} \quad (\text{B13})$$

and may be re-written using equations (33), (35) and (36) and integration by parts, to yield

$$\begin{aligned} \frac{\partial C_i}{\partial \underline{b}_k} = & \int_{t_0}^{t_1} \left\{ e_i(t) \left[\left(U_{\underline{Q}\underline{Q}} - T_{\underline{Q}\underline{Q}} \right) \cdot \partial \underline{Q} / \partial \underline{b}_k - T_{\dot{\underline{Q}}\underline{Q}} \cdot \partial \dot{\underline{Q}} / \partial \underline{b}_k \right] \right. \\ & \left. - \dot{e}_i(t) \left[T_{\dot{\underline{Q}}\underline{Q}} \cdot \partial \underline{Q} / \partial \underline{b}_k + T_{\underline{Q}\dot{\underline{Q}}} \cdot \partial \dot{\underline{Q}} / \partial \underline{b}_k \right] \right\} dt \end{aligned} \quad (\text{B14})$$

where boundary terms have been dropped on the assumption that $\partial \underline{Q} / \partial \underline{b}_k$ and $\partial \dot{\underline{Q}} / \partial \underline{b}_k$ vanish at t_0 and t_1 , as for the expansion in appendix A. Alternatively, in some cases, direct differentiation of an expression for $\underline{A}$ may be more straightforward.

Appendix C. Equivalence of power and rate of change of energy for conservative Hamiltonian systems

As noted in section 7, the power input to a system by the generalized force $\underline{A}$ is given (in terms of *all* coordinates, both passive and active) by equation (26),

$$P = \dot{\underline{Q}} \cdot \underline{A}.$$

Let us consider the usual case, where the Lagrangian is a function $L(\underline{Q}, \dot{\underline{Q}})$ of generalized positions and velocities only (and not independently a function also of time t), and where the Legendre transform [13] defining the Hamiltonian,

$$H = \underline{\dot{Q}} \cdot \frac{\partial L}{\partial \underline{\dot{Q}}} - L$$

exists. In this conservative case, the Hamiltonian is equal to the energy $H = E$ [13] and the generalized force is given by equation (30). Hence, we have

$$\begin{aligned} P &= \underline{\dot{Q}} \cdot \left(\frac{d}{dt} \frac{\partial L}{\partial \underline{\dot{Q}}} - \frac{\partial L}{\partial \underline{Q}} \right) \\ &= \frac{d}{dt} \left(\underline{\dot{Q}} \cdot \frac{\partial L}{\partial \underline{\dot{Q}}} \right) - \underline{\ddot{Q}} \cdot \frac{\partial L}{\partial \underline{\dot{Q}}} - \underline{\dot{Q}} \cdot \frac{\partial L}{\partial \underline{Q}} \\ &= \frac{d}{dt} \left(\underline{\dot{Q}} \cdot \frac{\partial L}{\partial \underline{\dot{Q}}} - L \right) = \frac{dH}{dt} \\ &= \dot{E} \end{aligned}$$

as expected for a conservative system, thus providing reassurance that the generalized forces applied by the animal, that supply the work on the mechanical system have been correctly identified in these calculations.

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