Symmetry in Running

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Symmetry plays a key role in simplifying the control of legged robots and in giving them the ability to run and balance. The symmetries studied describe motion of the body and legs in terms of even and odd functions of time. A legged system running with these symmetries travels with a fixed forward speed and a stable upright posture. The symmetries used for controlling legged robots may help in elucidating the legged behavior of animals. Measurements of running in the cat and human show that the feet and body sometimes move as predicted by the even and odd symmetry functions.

RUNNING IS A SERIES OF BOUNCING and ballistic motions that accelerate the body within each stride. The bouncing motions are the vertical rebound of the body when the legs push on the ground, and the ballistic motions occur between bounces, when the body is airborne (*1*). For a legged system to run at fixed speed with a stable upright posture, however, the net acceleration of the body over an entire stride must be zero. This requires that the torques and horizontal forces exerted on the body by the legs must integrate to zero over each stride and that the vertical forces must integrate to the body's weight times the duration of the stride. This is true for every form of running animal and for legged robots as well.

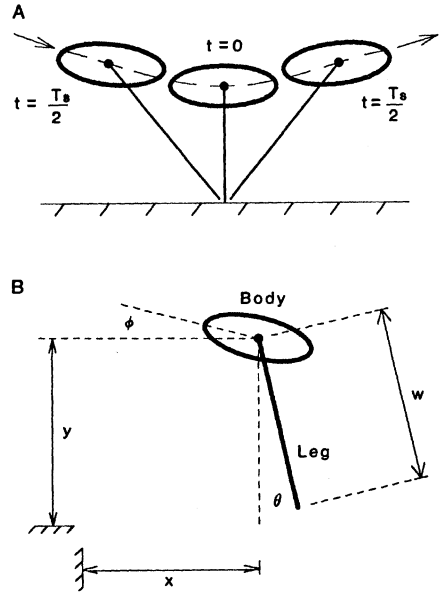

Fig. 1. (A) Symmetric motion used by one-legged system in running. The left-most figure shows the configuration just before the foot touches the ground; the center figure shows the configuration halfway through the stance phase, when the leg is maximally compressed and vertical ($t = 0$, $\theta = 0$, $\phi = 0$); and the right-most figure shows the configuration just after the foot loses contact with the ground. The symmetry of this motion follows from the mechanics of the legged system (*2*). T_s is the duration of the stance phase. (B) Definition of symbols used in symmetry equations for one-legged system. The actuator variables are defined so that positive hip torque, τ, which acts between the body and the leg, accelerates the body in the positive ϕ direction; positive leg thrust, f, which acts along the major axis of the leg, pushes the body away from the ground.

Although there are many patterns of body and leg motion that can satisfy these requirements, a particularly simple solution arises when they have even and odd symmetry during each stance phase (Eqs. 1 to 3):

$$\text{Body symmetry:}\quad \begin{aligned} x(t) &= -x(-t) \\ y(t) &= y(-t) \\ \phi(t) &= -\phi(-t) \end{aligned} \qquad (1)$$

$$\text{Leg symmetry:}\quad \begin{aligned} \theta(t) &= -\theta(-t) \\ w(t) &= w(-t) \end{aligned} \qquad (2)$$

$$\text{Actuator symmetry:}\quad \begin{aligned} f(t) &= f(-t) \\ \tau(t) &= -\tau(-t) \end{aligned} \qquad (3)$$

The variables used in these symmetry equations are defined in Fig. 1. For simplicity, t and x are defined so that $t = 0$ halfway through the stance phase and $x(0) = 0$. These symmetry equations specify that forward body position, body pitch angle, and leg angle are each odd functions of time throughout the stance phase, while body elevation and axial leg length are even functions of time. They also specify that the actuators operate with even and odd symmetry. These symmetries are significant because they result in accelerations of the body that are odd functions of time throughout a stride—odd functions integrate to zero over symmetric limits, leaving the forward running speed, body elevation, and body pitch angle unchanged from one stride to the next (*2, 3*).

The value of symmetry became clear when studying control of robots that ran by hopping on one leg. The goal of that study was to explore active balance in legged locomotion, with particular attention to the dynamic aspects of the problem. Using machines with one leg permitted focus on the problem of balance while avoiding the complicated task of coordinating several legs. By means of control techniques based on symmetry, one-legged machines ran with a stable steady-state gait, traveled along simple paths, and maintained their balance when disturbed (*4, 5*). An extension of the one-leg control algorithm was used in other experiments to control a four-legged machine that runs with a trotting gait and a biped that can run or hop. These experiments showed that the symmetry techniques used to control machines with one leg could also be used to control machines with several legs (*2, 6, 7*).

The importance of symmetry in the control of legged robots raises the question of what role symmetry may play in the behavior of running animals. Hildebrand began studying symmetry in animal locomotion about 20 years ago. He observed that the left half of a horse often uses the same pattern of footfalls as the right half, but 180° out of phase (*8–12*). He devised an elegant characterization of the symmetric walking and running gaits for a variety of quadrupeds using just two parameters: the phase angle between the front and rear legs, and

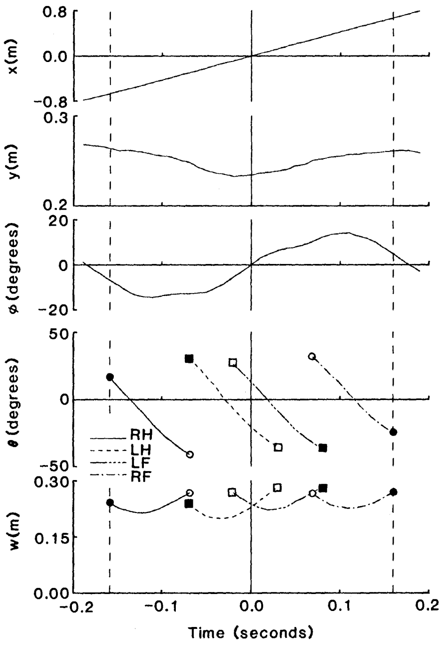

Fig. 2. Body and leg motion of the galloping cat. Data are shown for one stride of a cat running on a treadmill with a rotary gallop. According to symmetry theory, forward body position, x, body pitch angle, ϕ, and leg angle, θ, should each have odd symmetry, while body height, y, and leg length, w, should have even symmetry. Symmetry in behavior of the legs is found when they are considered in reciprocating pairs, that is, when $\theta_{RH}(t) = -\theta_{RF}(-t)$ and $w_{RH}(t) = w_{RF}(-t)$ (*2*). Symbols in the bottom two curves indicate pairs of points that should have symmetric positions with respect to the origin (for odd symmetry) or the y axis (for even symmetry). Data for each leg are shown only when its foot touches the support surface. Dashed vertical lines indicate the beginning and end of the stance phase. Solid vertical line indicates the symmetry point, when $t = 0$.

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the dutycycle of the legs. By mapping each observation of symmetric behavior into a point in phase-dutycycle space, Hildebrand was able systematically to classify gaits for more than 150 quadruped genera.

Rather than look at relations between the footfalls of the left and right legs, as Hildebrand did, I examined the trajectories of the feet with respect to the body and the trajectory of the body through space, all measured in the sagittal plane. The data included a human running on a cinder track and a cat trotting and galloping on a treadmill. Measurements from digitized film provided three parameters of the body's motion [forward position, vertical position, and pitch angle (x, y, ϕ)] and two parameters of each leg's motion [angle with respect to the vertical and length (θ, w)]. In addition to information about the timing of footfalls, these measurements provided information about where on the ground the feet were placed with respect to the body and how the body itself moved (*13*). Several strides of each gait conformed qualitatively to the even and odd symmetry functions. Some data showed a remarkable degree of symmetry when steady-state conditions were precisely maintained. Data for one such stride of the galloping cat are plotted in Fig. 2. They are in good agreement with the even and odd symmetries predicted by the symmetry equations (*14*).

These running symmetries can be visualized graphically. The symmetry equations imply that, if we reverse both the direction of forward travel and the direction of time [$-x(-t)$], then the pattern of forward body movement and of footfalls should not be affected [$x(t) = -x(-t)$]. This invariance is illustrated in Fig. 3. Of particular interest is the precise overlap of the footfalls found for the forward and reverse running sequences. This overlap is predicted by the symmetry equations and is shown quantitatively in the plots of Fig. 2.

The symmetries under discussion specify sufficient conditions for steady-state locomotion, but they do not specify necessary conditions. A legged system can violate the motion symmetries and still travel in steady state. Why, then, do animals sometimes choose symmetric motions over the diverse range of alternatives? Perhaps features of their mechanical structure impose constraints that make symmetric motions attractive. For instance, the springlike characteristics of muscle and tendon may influence the pattern of motion that the dynamic system can make efficiently. Another explanation may be that animals use symmetry to simplify control. A legged system could avoid controlling the detailed variations of each joint, concentrating instead on providing initial conditions on each stride that would lead to steady-state forward travel. The legged robots I have studied use symmetry in this way to simplify their control.

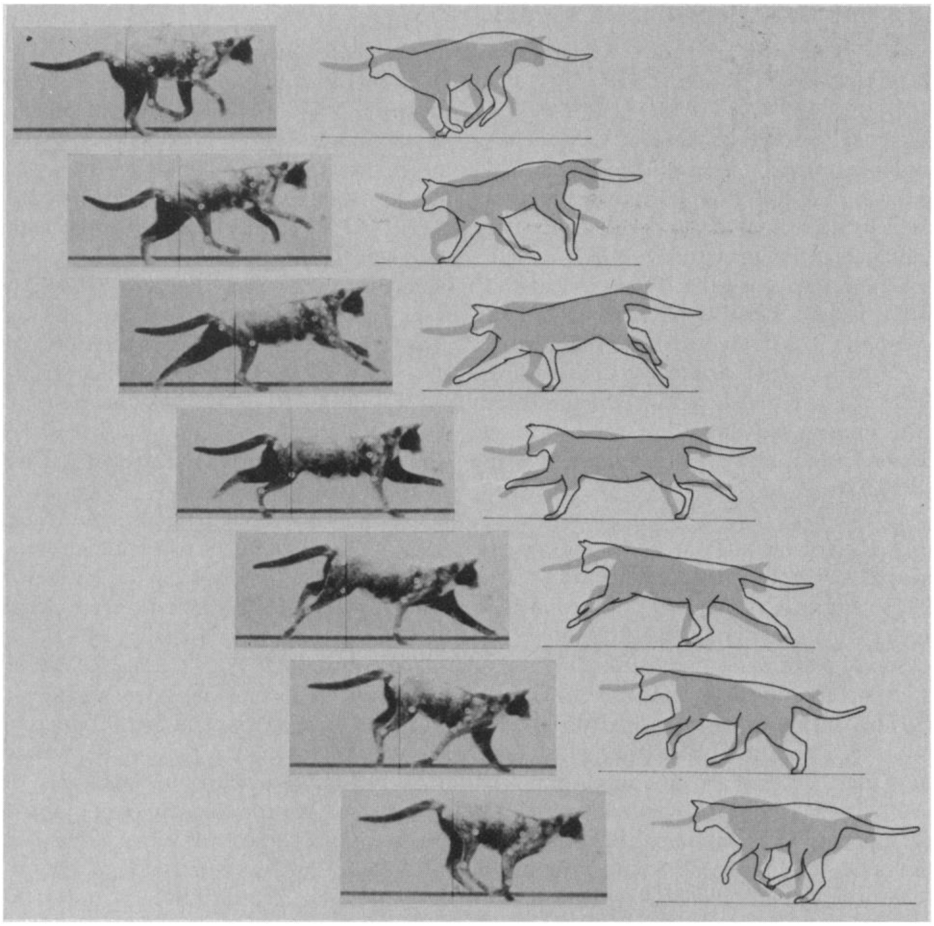

Fig. 3. Graphical interpretation of symmetry in the galloping cat. (Left) Photographs of galloping cat taken at 50-msec intervals. (Right) The shaded figures show the forward translation and the configuration of the cat during normal running, and the outlines show reverse running. The outlines were made from the same photographs as the shaded figures but were reflected about the vertical axis and are presented in reverse sequential order [$x(t) = -x(-t)$]. Therefore, the outline at the top was made from the photograph at the bottom after reversing its orientation. The positions of supporting feet and the rightward motion of the body correspond well in the two sequences, as predicted by symmetry. The relative placement of the figures for each sequence—the photographs, the shaded silhouettes, and the outlines—accurately reflects the forward progress of the cat with respect to the surface of the treadmill. After each set of figures was assembled according to the forward travel, the three sets were positioned relative to one another [photographs from (*13*)].

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2. M. H. Raibert, *Legged Robots That Balance* (MIT Press, Cambridge, MA, 1986).
3. A symmetry also plays an important role in controlling locomotion. While symmetric motion accounts for nominal, steady-state behavior, asymmetry in the motion accounts for the forces required to stabilize the system against external disturbances and for the accelerations needed to change running speed, posture, or direction. These components are illustrated by the exaggerated asymmetry displayed by someone running into a strong wind, by the runner at the start of a short foot race, and by the driver of a jinrikisha. The legged machines we have studied purposely generate asymmetric motions to stabilize and compensate for errors in running speed, once a nominal symmetric motion has been established. Asymmetric leg and body motion can also compensate for imperfections in the mechanics of the legged system, such as friction in the joints, unsprung mass in the legs, and body mass that is not distributed uniformly.
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7. For a system with more than one leg, the legs operate in pairs that have reciprocating symmetry. In this case the body symmetry equations remain unchanged, but the leg and actuator equations are subscripted to indicate the legs they describe. For example, the symmetry equations describing leg angle for a quadruped running with a rotary gallop would be $\theta_{RH}(t) = -\theta_{RF}(-t)$ and $\theta_{LH}(t) = -\theta_{LF}(-t)$, where LF is the left front leg, LH is the left hind leg, RH is the right hind leg, and RF is the right front leg. Similar pairs of subscripted equations describe symmetry for w, τ, and f. Quadrupeds may operate the legs with either of two pairings: (RF, RH) and (LF, LH), which makes lateral pairs of legs operate in reciprocation, or (RF, LH) and (LF, RH), which makes diagonal pairs of legs operate in reciprocation. The first pairing applies to the pace and rotary gallop in either direction. The

second leg pairing applies to the trot, the canter, and the transverse gallop. A perfect bound with no phase between either the front or hind legs could be represented by either pairing.

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13. Human measurements were made by digitizing 16-mm film of runners on the semicircular section of an outdoor cinder track. The camera (Bolex H16, operating at 50 frames per second) was mounted on a tripod at the center of the semicircle (18.5-m radius) and panned to track the runner. Ground markers spaced at 1.0-m intervals provided a scale reference and permitted alignment of each frame with respect to the next. Running speed was about 3.8 m $\sec^{-1}$. The data for the cat were obtained by digitizing 16-mm film provided by Wetzel and colleagues [M. C. Wetzel, A. E. Atwater, D. G. Stuart, in *Neural Control of Locomotion*, R. N. Herman, S. Grillner, P. S. Stein, D. G. Stuart, Eds. (Plenum, New York, 1976), pp. 99–136]. Treadmill markers spaced at 0.25-m intervals provided scale and alignment as before. Running speeds for the cat were about 2.2 m $\sec^{-1}$ for trotting and 3.1 m $\sec^{-1}$ for galloping. Small circular markers attached to the cat's skin made digitizing easier. When digitizing the data for both the human and the cat, I estimated the point of support provided by each foot visually. A straight line from this point to the hip (or shoulder for the cat's front legs) was used to find the leg length and the leg angle. The center of mass of the cat was taken as the point midway between the shoulder and the hip. The pitch angle of the body was the angle between the line connecting shoulder to hip and the horizontal, offset so that $\phi(0) = 0$.
14. Animals do not run with a pattern of motion that is precisely repeatable from one stride to the next, even for a single gait. This variability has been reported in studies of interlimb coordination in the cat [D. G. Stuart, T. P. Withey, M. C. Wetzel, G. E. Goslow, Jr., in *Control of Posture and Locomotion*, R. B. Stein, K. G. Pearson, R. S. Smith, J. B. Redford, Eds. (Plenum, New York, 1973), pp. 537–560; S. Miller, J. van der Burg, F. G. A. van der Meché, *Brain Res.* **91**, 217 (1975); A. W. English, *J. Neurophysiol.* **42**, 229 (1979)]. In principle, variability need not influence symmetry. A legged system can switch from one symmetric pattern of motion on one stride to a different symmetric pattern on the next stride. A legged system can maintain symmetry despite variations because the symmetry equations describe a class of body and leg motions rather than a particular motion. On the other hand, variations may have asymmetric components. Such asymmetric components are expected when a system accelerates as described in (*3*), but asymmetric steady-state variation is also possible. The reported variability has not been analyzed to reveal the relative contributions of symmetric and asymmetric components.

15. I thank M. Wetzel for providing film of the cat, J. Hodgins and J. Koechling for helping film the human runners, and J. Koechling for writing the computer programs used to digitize and process data. Supported by a grant from the System Development Foundation and by contract MDA903-81-C-0130 from the Engineering Applications Office of the Defense Advanced Research Projects Agency.

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Bacterial Gene Inserted in an Engineered RNA Virus: Efficient Expression in Monocotyledonous Plant Cells

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Brome mosaic virus (BMV) is a plant virus whose genome consists of three RNA components. A previously described viral complementary DNA expression system has been used to express both wild-type and altered genomic RNA's in barley protoplasts. Variants of BMV RNA3 were constructed in which the coat gene had been removed or replaced with sequences encoding chloramphenicol acetyltransferase (CAT). CAT sequences were also inserted near the 5′ end of the intact coat gene. When inoculated on protoplasts together with transcripts of BMV RNA's 1 and 2, all of these RNA3 derivatives were replicated and produced subgenomic RNA's analogous to the normal subgenomic coat protein messenger RNA. RNA3 derivatives in which the CAT coding sequences were oriented with the same polarity as viral genes produced significant CAT activity in protoplasts. CAT expression was improved by inserting the CAT gene in frame with the upstream coat protein initiation codon, and exceeded expression in plant cells transformed with Ti plasmid-based vectors.

APPROPRIATE LINKAGE OF HETEROLOGOUS sequences to a viral genome by recombinant DNA methods can allow those sequences to be amplified as part of an extrachromosomal replicon, transcribed into messenger RNA (mRNA), and translated into protein products. Accordingly, useful gene cloning and expression vectors have been derived from a wide range of bacterial, animal, and plant viruses that replicate by way of DNA intermediates (*1*). Most known viruses infecting eukaryotes, however, have genomes that replicate through only RNA intermediates. We show here that such RNA viruses may also be engineered for experimental purposes, including the efficient expression of foreign coding sequences.

We have developed an in vitro transcription system to express a plant RNA virus, brome mosaic virus (BMV), from cloned complementary DNA (cDNA) (*2, 3*), which allows recombinant DNA techniques to be used for engineering this virus for experimental purposes. Several attributes make BMV attractive for initial studies on designed modification of RNA viruses. Its genome is naturally divided among three segments (designated genomic RNA's), but only two components are necessary for replication in plant protoplasts (*4*), which demonstrates that the replication machinery acts in *trans* and suggests that altered replicating components could be constructed. The virus multiplies to high copy number in plant cells, many details of its biology are known, and its principal hosts are monocotyledonous plants (*5*), in which engineered expression of foreign genes has only recently been reported (*5a*).

Plasmids pB1PM18 (pB1), pB2PM25 (pB2), and pB3PM1 (pB3) contain cDNA copies of BMV RNA's 1, 2, and 3, respectively, adjacent to a modified *Escherichia coli* promoter (*2*). The mixture of capped in vitro transcripts from all three Eco RI–linearized plasmids is infectious to whole barley plants (*3*). To facilitate assays of replication and gene expression, infectivity studies were extended to protoplasts. We found that isolated barley protoplasts, which support BMV infection (*6*), could be efficiently infected with transcripts (Fig. 1B) if the template plasmid DNA was first removed, as by RNA precipitation with 2*M* LiCl (*7*). Typically, as judged by an antibody test (6), 60 percent of the protoplasts became infected when 10^5 viable protoplasts were inoculated (*8*) with a mixture of 1 μg each of pB1, pB2, and pB3 transcripts. Of all single and twofold component combinations, only RNA1 plus RNA2 gave rise to viral RNA replication (Fig. 1B). A previous study had shown that RNA 1 and 2 were sufficient to infect protoplasts (*4*), but these RNA's had not been tested singly. Thus, BMV resembles another tripartite RNA virus, alfalfa mosaic virus (*9*), in requiring two components for RNA replication in isolated cells.

The third BMV component, RNA3, is dicistronic (*10*), encoding genes for both a protein of molecular weight 32,000 (protein 3a) and the virion coat protein. In normal BMV infections, milligram quantities of coat protein are produced per gram of tissue (*5*) from translation of a subgenomic coat mRNA (RNA4) produced in large quantities from RNA3, probably by partial transcription of minus strand (*11*). Replacement of the coat gene with foreign coding sequences might provide high-level expression of the heterologous sequences at the level of both mRNA and gene product. To see if changes could be made in the coat region of RNA3 without preventing either genomic

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