Constrained optimization in human running

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Summary

Walking humans spontaneously select different speed, frequency and step length combinations, depending on which of these three parameters is specified. This behavior can be explained by constrained optimization of cost of transport (metabolic cost/distance) where cost of transport is seen as the main component of an underlying objective function that is minimized within the limitations of specified constraints. It is then of interest to ask whether or not such results are specific to walking only, or indicate a more general feature of locomotion control. The current study examines running gait selection within the framework of constrained optimization by comparing self-selected running gaits to the gaits predicted by constrained optimization of a cost surface constructed from cost data available in the literature. Normalizing speed and frequency values in the behavioral data by preferred speed and frequency reduced inter-subject variability and made group behavioral trends more visible. Although actual behavior did not coincide exactly with running cost optimization, self-selected gait and predictions from the general human cost surface did agree to within the 95% confidence interval and the region of minimal cost+0.005 ml O_2 kg^{-1} m^{-1}. This was similar to the level of agreement between actual and predicted behavior observed in walking. Thus, there seems to be substantial evidence to suggest that (i) selection of gait parameters in running can largely be predicted using constrained optimization, and (ii) general cost surfaces can be constructed using metabolic data from one group that will largely predict the behavior of other groups.

Key words: gait, locomotion, cost, control, human.

Introduction

It has been shown that humans and animals choose to move in a way that minimizes the cost of locomotion (Alexander, 2000; Alexander, 2001; Hoyt and Taylor, 1981; Saibene, 1990). Until recently, it was generally assumed that the least metabolically costly gait for any given forward speed (v), step frequency (f), or step length (d) could be described by a single functional relationship between these parameters. Thus, one should be able to generate a single behavioral relationship representing the least costly gait in speed–frequency–step length (v–f–d) space by controlling any one gait parameter, measuring the self-selected value of either one of the two other parameters, and calculating the value of the third using some form of the relationship $v=fd$.

However, Bertram and Ruina (2001) suggested in a walking study that not one but three different 'least costly' relationships are generally obtained by following such a procedure. The behavioral relationship obtained depends on which parameter is specified. Thus, one 'least costly' behavioral relationship was obtained by specifying v, another by specifying f, and yet another by specifying d. It is apparent from these results that

optimal gait is not rigidly predetermined by internal factors, but rather depends on the conditions presented to the individual and emerges from interaction between factors, both internal and external to the individual.

But how can three different curves all represent the least costly gait? To explain this apparent paradox Bertram and Ruina formulated the constrained optimization hypothesis (Bertram and Ruina, 2001). According to this hypothesis, gait parameters are selected to optimize (minimize) some objective function within the limitations of imposed constraints. In keeping with the original observation that animals and humans move in a way that minimizes cost, Bertram and Ruina (2001) proposed that cost of transport (metabolic cost/distance) serves as the objective function and that the controlled gait parameters serve as constraints. Bertram (2005) compared self-selected behavioral relationships to behavioral predictions obtained by applying constrained optimization to a metabolic cost surface and found that these were strikingly similar for walking. This suggests that metabolic cost does indeed strongly influence choice of gait parameters, and validates constrained optimization as a model for predicting gait selection.

Is this result specific to walking, or does it apply to other aspects of human movement control? There are many features of the mechanics of walking that differ substantially from running. Identifying a similar control strategy in both running and walking would indicate a general feature of movement control effective at levels beyond the mechanics of each specific gait. The objective of the present study was to test the applicability of the constrained optimization hypothesis to running. We did this by comparing self-selected running behavioral data collected under *v*-constrained, *f*-constrained and *d*-constrained conditions to predictions obtained by performing constrained optimization on metabolic data available in the literature. This allowed us to see whether or not constrained optimization of metabolic cost can reliably predict gait selection in other modes of terrestrial locomotion besides walking, and whether or not constrained optimization of metabolic cost data from one group of subjects can predict the gait selected by another group.

Materials and methods

Subjects

Five healthy subjects (one female and four males) participated in the study. Anthropometric data for each subject are given in Table 1. We obtained informed consent from all subjects prior to experimentation. All testing was done according to the guidelines set by the Florida State University Human Subjects Committee Review Board.

Self-selected running behavior

We employed methods similar to those detailed in Bertram and Ruina (2001) and Bertram (2005) for human walking, but used constraint values appropriate for running. Since steady state locomotion can be defined by the simple relationship $v=fd$, we evaluated running behavior under three different constraint conditions: *v*-constrained, *f*-constrained and *d*-constrained. In each case one variable was controlled (either *v*, *f* or *d*), one variable was directly measured, and the third variable was calculated using the relationship $v=fd$. We briefly outline the specific procedures below.

For constrained *v*, subjects ran on a treadmill (Desmo Pro, Woodway, Wakeshaw, WI, USA) at constant belt speed. Eleven different belt speeds were used, ranging from 0.49 to 4.32 m s^{-1}. We presented the belt speeds at random to reduce

the potential for systematic bias and cross-trial interference. Between trials the subjects walked at a comfortable speed until they had fully recovered. At each *v*, *f* was measured by timing the duration of two sets of 20 steps using an electronic stopwatch. The two trial results were averaged to obtain a reliable measure of *f* for that speed and individual. We calculated step length using $d=v/f$. Measurements were made after at least 1 min of running at each *v*.

For constrained *f*, subjects ran in time to the beat of an electronic metronome (KDM-1, Korg Inc., Tokyo, Japan) at ten different frequencies ranging from 2 to 3.33 steps s^{-1}. Again, step frequencies were randomly presented and subjects were allowed to fully recover between trials. We measured *v* by timing how long it took subjects to travel a 10 m segment of a 30 m level runway (using a portion of an outdoor athletic track). Accurate measurements of speed were facilitated by use of two portable cameras (TK-S241U, JVC, Victor Co., Yokohama, Japan), mounted perpendicular to the path of the runner on tripods placed at the starting and ending points of the 10 m distance along the straight portion of the track. We combined the signals from both cameras into a single viewing channel *via* a signal inserter (SCS splitter/inserter, American Video Equipment, Houston, TX, USA) and fed the signal into a video monitor (Panasonic, Matsushita Electric Industrial Co., Ltd., Kadoma, Japan). This allowed the timer a perpendicular view of the starting and ending points. We timed each 10 m run using an electronic stopwatch. We calculated step length using $d=v/f$.

Finally, for constrained *d*, subjects ran by stepping on evenly spaced markers (2 inch roofing nails with colored plastic washers inserted into a grass athletic field) over level ground at ten predetermined step lengths, ranging from 0.3 m to 2 m. Some subjects were unable to reliably maintain 2 m step lengths, so only nine step lengths were used for these individuals. Step lengths were randomly presented and subjects were allowed to fully recover between trials. We also gave the subjects one or more practice trials at each step length and did not take measurements until the subject felt fully comfortable with the step length requirements of the trial. This was especially necessary for step lengths approaching 2 m. We measured *f* at each speed by timing the duration of 2 sets of 20 steps within 30 markers for each given step length. We then averaged the two measured frequencies to obtain *f*. We calculated speed using $v=fd$.

Data analysis

Self-selected running behavior

All self-selected running behavioral data were pooled to evaluate general gait selection trends. Before pooling the data, we normalized *v* data by apparent preferred *v* (v_p), *f* data by apparent preferred *f* (f_p), and *d* data by $d_p=v_p/f_p$ for each subject. We considered normalizing the data by speed and frequency of variants of the Froude number, but rejected this normalization since it did not improve the fit of the linear regressions. We determined v_p and f_p by estimating the location of the point of intersection of the *v*-constrained, *f*-constrained, and *d*-constrained *v*–*f* relationships (Fig. 1). The point of intersection should indicate the absolute minimum cost of

Table 1. *Physical characteristics of subjects*

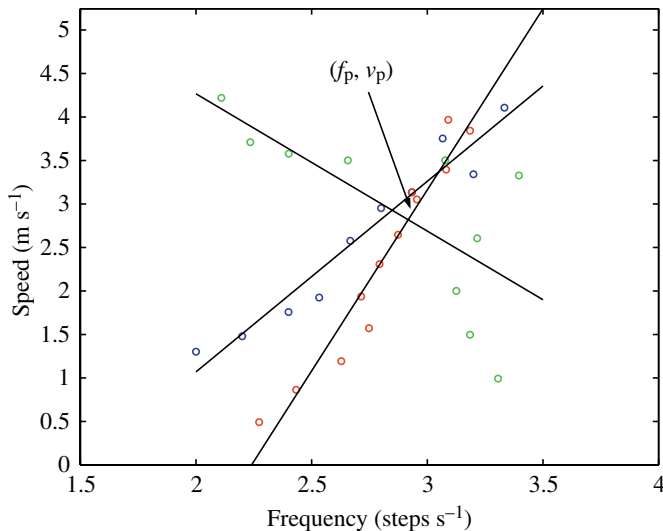| Subject	Sex	Mass (kg)	Height (m)	Leg length (m)
1	M	90.8	1.85	0.930
2	M	58.5	1.73	0.910
3	M	69.3	1.78	0.950
4	M	103.7	1.84	0.906
5	F	53.9	1.60	0.845

M, male; F, female.

Fig. 1. A plot of speed–frequency relations for a single subject running under the three constraint conditions imposed in this study. Red circles show frequencies selected when speed is constrained in treadmill running, blue circles show speeds selected when frequency is constrained in over-ground running to a metronome beat, and green circles indicate the speed–frequency combinations selected when step length is constrained by stepping in registry with ground markers. Each relation was fit with a least-squares linear regression with the constrained parameter as the independent variable, then the relationship determined was converted to speed–frequency for comparison (see text for details). The point of intersection of the v-constrained, f-constrained and d-constrained relationships gives apparent preferred speed and frequency (v_p and f_p).
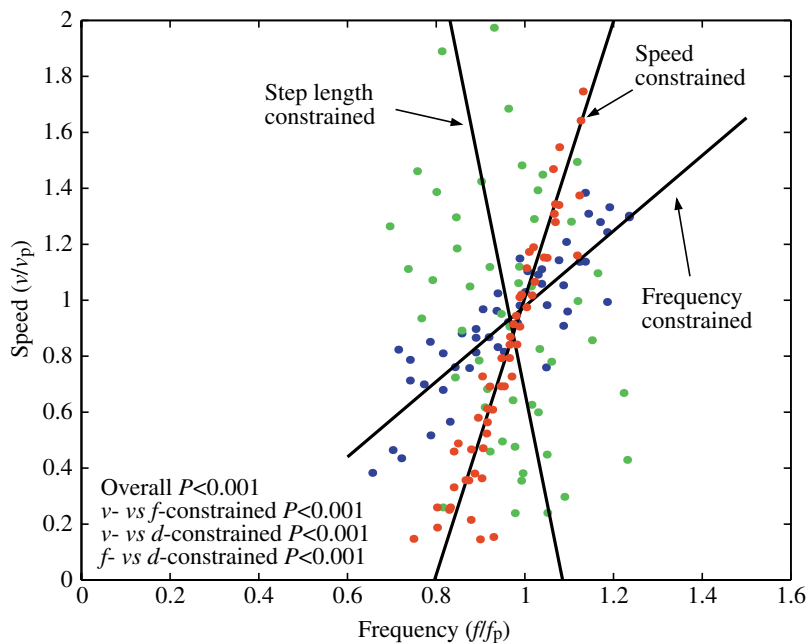

Fig. 2. Behavioral data for all subjects with least-squares linear regressions determined as in Fig. 1. Data for v-constrained conditions, red circles; f-constrained conditions, blue circles; d-constrained conditions, green circles. All three slopes are significantly different from one another, $P<0.001$. v-constrained conditions, $f/f_p=0.202(v/v_p)+0.796$; f-constrained conditions, $v/v_p=1.347(f/f_p)-1.3684$; d-constrained conditions, $f/f_p=0.117(d/d_p)+1.078$.

transport for each individual and, therefore, should also correspond to the freely chosen v and f selected by an individual during unconstrained running, as it does for walking (Bertram and Ruina, 2001; Bertram, 2005).

The pooled self-selected running behavioral data were fit with least-squares linear regressions (SigmaStat, SPSS, Chicago, IL, USA). Since the constrained variable (independent variable) was different for each constraint condition, regression analyses were performed with the data plotted on different axes for each constraint. Frequency-constrained data were plotted with f on the x-axis and v on the y-axis; v-constrained data with v on the x-axis and f on the y-axis; and d constrained data with d on the x-axis and f on the y-axis. However, for the sake of consistency and ease of comparison, each linear regression equation was converted into $v(f)$ form and replotted in v-f space (Fig. 2), as per Bertram (2005).

The slope of the v–f relationship for each of the three constraint conditions was obtained from the linear regressions and the standard error for each slope was computed. A one-way analysis of variance (ANOVA) was used to determine whether or not the three slopes were significantly different from one another. Once statistical significance was determined, a Tukey *post hoc* comparison (also in SigmaStat) was used to identify where the significant differences lay. We defined statistical significance as $P \leq 0.05$.

Cost surface

We compiled and evaluated cost data from several sources available in the literature (Cavanagh, 1982; Knuttgen, 1961; Liefeldt, 1992) as well as from an undergraduate student honors project done in our laboratory at Florida State University (Rouviere, 2002). See Appendix for an outline of the methods used in this thesis. Information on these data is displayed in Table 2. We used data from the single-subject studies directly and average values from multiple-subject data.

Although the above data represented a reasonable assemblage of running metabolic cost data, all data sets did not agree well. Two sets of data, v-constrained data from Knuttgen (1961) and from Liefeldt (1992), differed substantially from the other data available. The cost values reported by Liefeldt (1992) were unusually low (0.1611–0.1769 ml O_2 kg^{-1} m^{-1}). These levels are approximately 70% of those reported by the remainder of the studies (0.1930–0.2992 ml O_2 kg^{-1} m^{-1}). Knuttgen (1961) reported v-constrained data in which f remained virtually constant over a wide range of speeds. This is in contrast to observations from our study as well as v–f data from Minetti et al. (1998), indicating that subjects increase f as v increases (at least under the speeds considered here). The differences between these two sets of data and the other sets

Table 2. *Information on metabolic data*

Study	Constraint	Number				
		Data points in Fig. 3	Subjects	Trials/subject	Trials/study	% of total trials
Cavanagh (1982)	*d*-constrained	7	1	7	7	6.1
Knuttgen (1961)	Fully constrained	9	1	9	9	7.9
	v-constrained	11	1	11	11	9.6
Liefeldt (1992)	*v*-constrained	6	9	3	27	23.7
Rouviere (2002)	Fully constrained	12	5	12	60	52.6
	Total	28			114	100.0
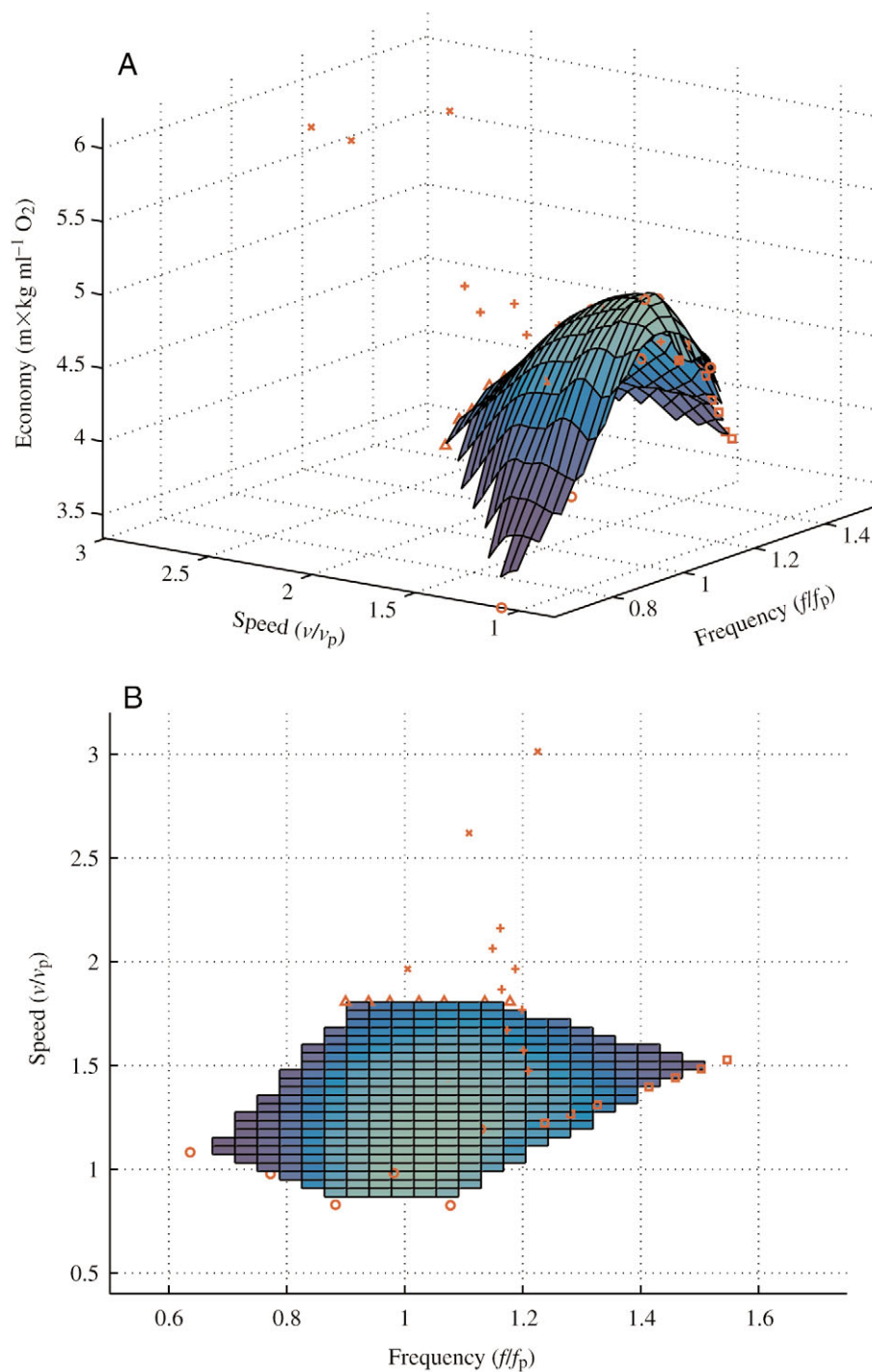
Fig. 3. Economy (the inverse of cost of transport) as a function of normalized speed (v/v_p) and frequency (f/f_p). (A) The 3-D surface; (B) a flattened, overhead view of the surface, showing the distribution of the data points more clearly. Economy is used instead of cost of transport simply for visual clarity in depicting the surface shape. The surface is interpolated based on metabolic measurements from Cavanagh (1982) (red triangles), Rouviere (2002) (red circles), and Knuttgen (1961) (red squares), in which running parameters were fully constrained. The *v*-constrained metabolic measurements from Knuttgen (1961) ($\times$), were considered to be outliers by virtue of the peculiar frequency selection of the subject in comparison to frequencies selected by subjects in other studies. The measurements of Liefeldt (1992) (+), were considered to be outliers because the costs were considerably lower than those reported in other studies under similar conditions. These two sets of outliers were not used to generate the cost surface. The color of the surface is determined by the height of the surface. Dark blue indicates regions of low economy (high cost), bright green indicates regions of high economy (low cost), and blue-green indicates regions of intermediate economy (intermediate cost).

of data may be due to differences in method, differences in equipment, or peculiarities of the subjects. In any case, it seems safe to assume that these two sets of data do not represent standard responses, so these two data sets were not included in the metabolic cost profile evaluated in the current study.

Gross (no baseline correction) metabolic cost measurements (ml O_2 kg^{-1} min^{-1}) were converted to cost of transport (ml O_2 kg^{-1} m^{-1}), C, and the data points plotted in C–v–f space. Since the data set was composed of only 28 points once data points had been averaged for multiple subject studies and outliers rejected, the resolution of the raw data was inadequate to reliably predict behavior. Therefore, we used the 'griddata' function in MATLAB (MATLAB 5.3, The MathWorks Inc., Natick, MA, USA), a triangle-based cubic interpolation algorithm, to construct a continuous cost surface between the data points (Fig. 3) that would facilitate appropriate mathematical analysis of optimization (see below).

Next, we calculated the partial derivatives, $\partial C(f,v)/\partial f$ and $\partial C(f,v)/\partial v$, for the cost surface, $C(f,v)$, to generate gait predictions for the applied constraints. According to the principle of constrained optimization, individuals should choose v–f combinations that correspond to points where one of the partial derivatives is zero in order to minimize the cost of transport. This is equivalent to finding points where a constraint curve is tangent to a cost contour (Bertram and Ruina, 2001; Bertram, 2005) (Fig. 4). For v-constrained conditions (v held constant), running cost is minimized when f is chosen such that $\partial C(f,v)/\partial f=0$. Likewise, for f-constrained conditions (f held constant), running cost is minimized when v is chosen such that $\partial C(f,v)/\partial v=0$. Therefore, we predicted self-selected v–f relationships under v- and f-constrained conditions

by plotting regions where both $\partial C(f,v)/\partial f=0$ and $\partial C(f,v)/\partial v=0$. We also plotted regions that contain points <0.001 ml O_2 kg^{-1} m^{-1} and <0.005 ml O_2 kg^{-1} m^{-1} from minimal cost (C_{min}) for each constraint to show how sensitive cost of transport is to changes in v–f (Fig. 5A,B). A narrow region indicates high sensitivity to changes in v and f, whereas a wide region indicates relative insensitivity to differences in these values. For d-constrained conditions, we replotted cost of transport data in d–f space and the data were fit to a new cost surface. We then calculated new partial derivatives $\partial C(f,d)/\partial f$ and $\partial C(f,d)/\partial d$ and plotted as $\partial C(f,d)/\partial f=0$ to show the predicted v–f relationship. We also plotted regions containing points <0.001 ml O_2 kg^{-1} m^{-1} and <0.005 ml O_2 kg^{-1} m^{-1} from minimal cost for d-constrained conditions (Fig. 5C). We did not plot solutions to $\partial C(f,d)/\partial d=0$ since they duplicate the $\partial C(f,v)/\partial v=0$ curve.

We chose to fit a new surface to the data points once we had replotted the data in C–d–f space to make the numerical calculation of $\partial C(f,d)/\partial f$ simpler. It is relatively straightforward to numerically calculate partial derivatives parallel to the axes of the plot, whereas more involved calculations are required to determine partial derivatives along other directions. This is because the 'griddata' interpolation algorithm generates points on the surface in a rectangular grid aligned with the plot axes. However, one downfall of replotting the data is that the two interpolated surfaces are not identical. Still, we do not feel that the two surfaces differ enough to substantially affect the behavioral predictions. This is supported by Fig. 6, which shows a comparison of the curves generated by plotting points satisfying (i) $\partial C(f,v)/\partial v=0$ and (ii) $\partial C(f,d)/\partial d=0$.

Most of the metabolic data were taken under a single applied constraint condition, so we did not have enough information
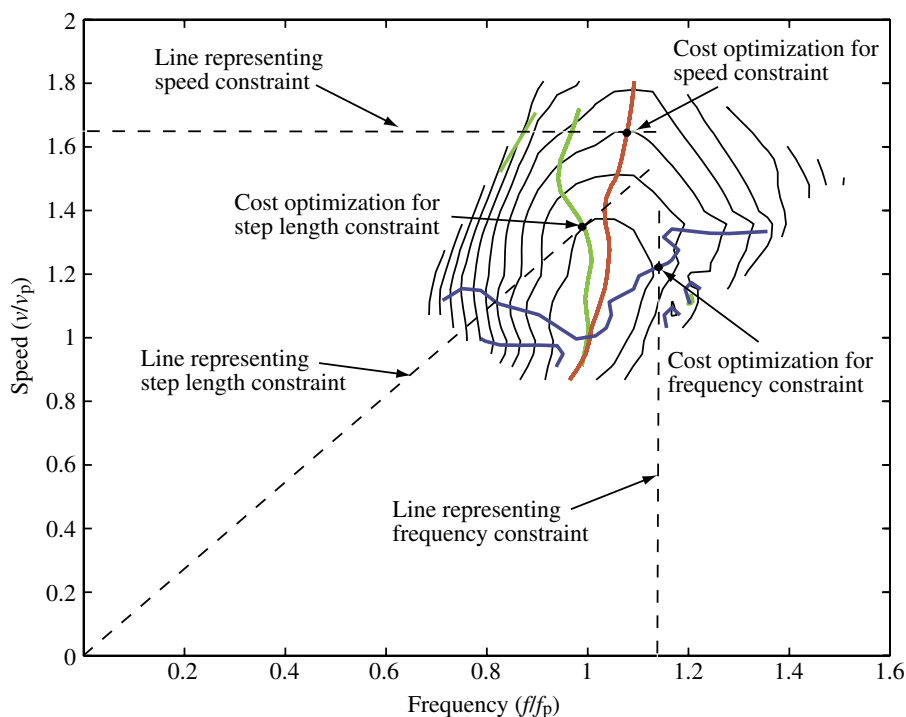

Fig. 4. Predicting optimal behavior by finding the points where constraint lines are tangent to cost contours. Cost contours are shown as black curves. Cost is least in the region bounded by the central curve and greater for curves lying outside each other. Constrained optimization predicts that for any given constraint gait, parameters will be chosen such that cost of transport is minimized. This occurs at the tangent of the constraint line and a cost contour, because any other point on the constraint line lies outside the contour and indicates a greater cost. This method is equivalent to predicting optimal behavior by finding the points where one of the partial derivatives is equal to zero and may be used to verify the optimal behavior predictions shown in Fig. 5. Speed and frequency constraints can be visualised as horizontal and vertical lines, respectively, and step length constraints can be visualised as lines radiating from the origin whose slopes are equal to the specified step lengths – i.e. lines whose equations are of the form $v=fd$, where d=constant.
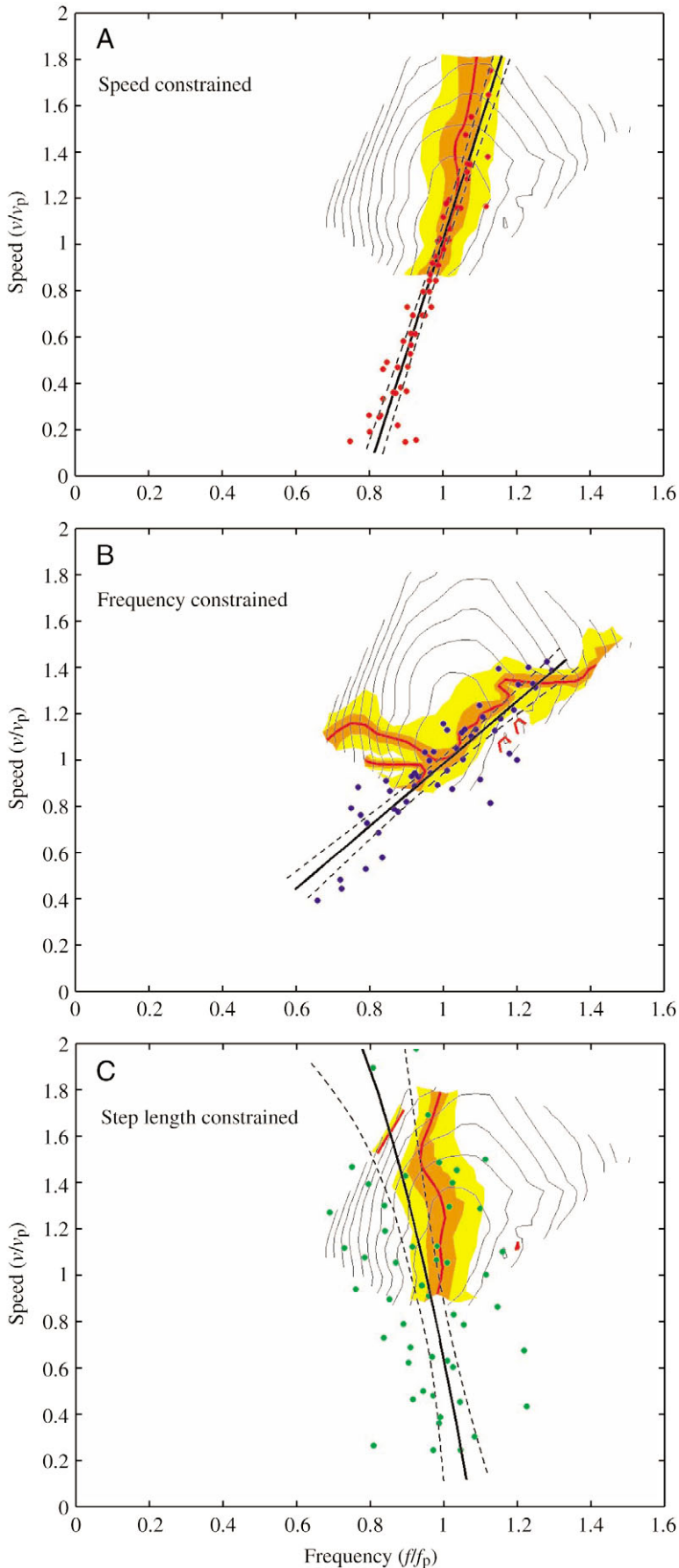
Fig. 5. Predicted and measured running gait parameter selection for all subjects. Solid circles indicate measured parameter selection under specific constraint conditions; (A) red circles, *v*-constrained; (B) blue circles, *f*-constrained; (C) green circles, *d*-constrained. Thick black lines indicate least-squares linear regression of the behavioral data, as determined using each constrained parameter as the independent variable. The broken black lines give 95% confidence intervals of the regression. Contours lines indicate equivalent cost of transport with the region of least cost surrounded by the inner contour and cost increasing outward from that. The bold red lines indicate the optimal predicted behavior (zero slope/minimum cost), the orange area represents the region of C_{min} + 0.001 ml O_2 kg^{-1} m^{-1}, and the yellow area that of C_{min} + 0.005 ml O_2 kg^{-1} m^{-1}.

to obtain v_p, f_p and minimum cost of transport for each data set. Therefore, we normalized predicted *v–f* relationships from the metabolic data by v_p and f_p for the pooled data in order to compare the predictions made using the metabolic data to the self-selected behavioral data. We determined v_p and f_p for the pooled data by finding the coordinates of the absolute minimum metabolic cost.

Results

Self-selected running behavior

The slopes of the three different *v–f* relationships were significantly different (Fig. 2). The *v–f* relationships for *v*-constrained and *f*-constrained conditions were particularly well defined (Table 2). The overall *P*-values from the ANOVA and the pairwise *P*-values from the Tukey *post hoc* analysis were all <0.001. This strongly suggests that the observed differences between the slopes are caused by subjects choosing gait parameters in specific response to the imposed constraints.

Shape of metabolic cost surface

The metabolic cost surface has an ovoid bowl shape when plotted in *C–v–f* space (Fig. 3). The long axis of the bowl lies along the line of the *v*-constrained behavioral curve. The bowl has relatively little curvature along the long axis (contour lines are widely spaced), and thus along the *v*-constrained behavioral curve, and higher curvature perpendicular to it (contour lines closely spaced) (Figs 4 and 5).

Self-selected vs predicted behavior
Speed constrained

Predicted and self-selected running behavior data agreed within the region of minimal cost (C_{min})+0.005 ml O_2 kg^{-1} m^{-1} and 95% confidence interval for *v*-constrained conditions (Fig. 5A). In the
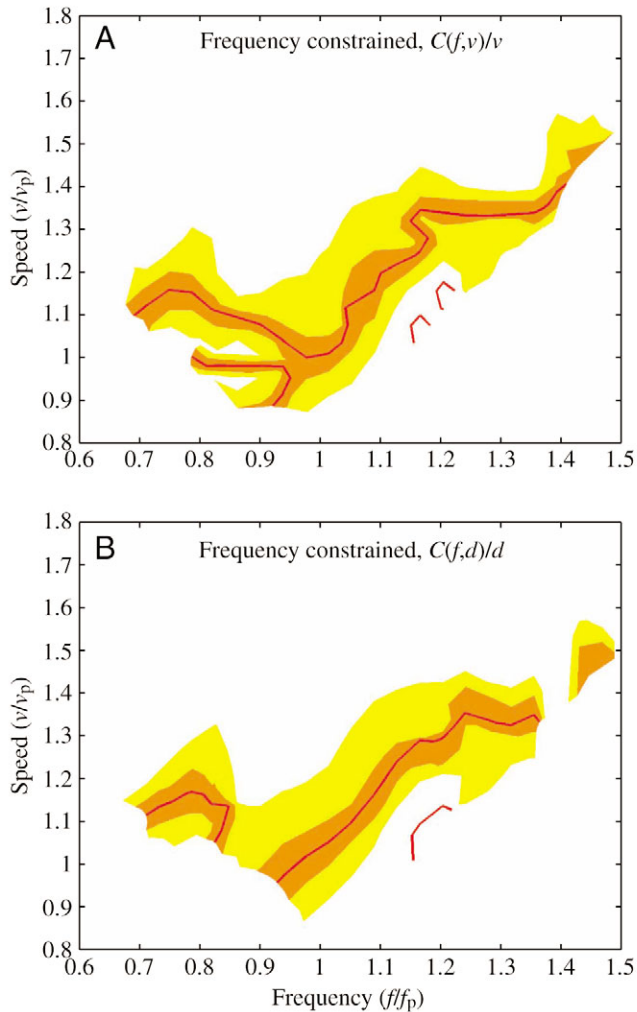
Fig. 6. Comparison of optimal minimal cost behavior predictions for constrained frequency running using cost regions calculated for (A) speed–frequency–cost space and (B) frequency–step length–cost space. For comparison, both predictions are displayed on equivalent speed–frequency plots. Thick red lines represent optimal predicted behavior (zero slope), the orange area represents region of minimal cost+0.001 ml O_2 kg^{-1} m^{-1} , and the yellow area that of minimal cost+0.005 ml O_2 kg^{-1} m^{-1}. The general features of the predicted behavior are not affected by method of calculation.

area where metabolic data were available, 21 out of 24 data points fell within the region of C_{min}+0.001 ml O_2 kg^{-1} m^{-1}, and two of the remaining points fell within the region of C_{min}+0.005 ml O_2 kg^{-1} m^{-1}, while only one point fell outside these regions. There was more scatter in the data for speeds roughly in the middle third (~0.8–1.4v/v_p) and for the lowest speeds (~0.14v/v_p).

Frequency constrained

Predicted and self-selected running behavior data also agreed within the region of C_{min}+0.005 ml O_2 kg^{-1} m^{-1} and 95% confidence interval for f-constrained conditions (Fig. 5B). In the area where metabolic data were available, 17

out of 35 data points fell within the region of C_{min}+0.001 ml O_2 kg^{-1} m^{-1}, 13 of the remaining points fell within the   region of C_{min}+0.005 ml O_2 kg^{-1} m^{-1}, and five points fell outside these regions. There was somewhat more scatter in the data for higher speeds: ~1.05–1.2v/v_p.

Step length constrained

Likewise, predicted and self-selected running behavior agreed within the   region of C_{min}+0.005 ml O_2 kg^{-1} $m^{-1}$and 95% confidence interval for d-constrained conditions (Fig. 5C). However, unlike v- and f-constrained conditions, only 7 out of 22 behavioral data points fell within the   region of C_{min}+0.001 ml O_2 kg^{-1} m^{-1} in the area where metabolic data were available, and only five more fell within the   region of C_{min}+0.005 ml O_2 kg^{-1} m^{-1}, whereas ten fell outside these regions. This reflects a relatively high degree of scatter over all step lengths.

For all three constraint conditions, the data points that fall outside the region of C_{min}+0.005 ml O_2 kg^{-1} m^{-1} came from a variety of individuals. This indicates that scatter in the behavioral data was not due to the peculiar behavior of any one individual.

Discussion
Shape of metabolic cost surface

It is well known that cost of transport (metabolic cost/distance) for running is relatively constant when measured under v-constrained conditions at commonly used speeds, and that cost of transport increases more dramatically under f-, d- or fully constrained conditions (Cavanagh, 1982; Diedrich and Warren, 1995; Hreljac, 1993; Knuttgen, 1961; Kram and Taylor, 1990). However, there is evidence that cost of transport does increase under v-constrained conditions at extremely high and low speeds – i.e. at speeds much higher or lower than v_p (Hreljac, 2002). The metabolic cost surface we created reflects these observations, since there is relatively low curvature along the v-constrained behavioral curve and higher curvature perpendicular to it.

Normalization

Normalizing v–f values of the metabolic data after pooling can be thought of as normalizing by an average v_p and f_p. This normalization method did not reduce inter-subject variability. The sole purpose of using this method was to facilitate comparison between normalized self-selected behavior and predicted behavior. However, if self-selected behavior does indeed reflect the shape of the metabolic cost surface, then successfully collapsing the behavioral data into generalized behavioral trends *via* normalization (i.e. scaling to reduce inter-subject variability) implies that one should be able to successfully generate any subject's cost surface by scaling a generalized cost surface by the v_p, f_p, and minimum cost of transport of that subject. Table 3 and Fig. 7 show that inter-subject variability in behavioral trends was indeed reduced by the normalization method used in this study.
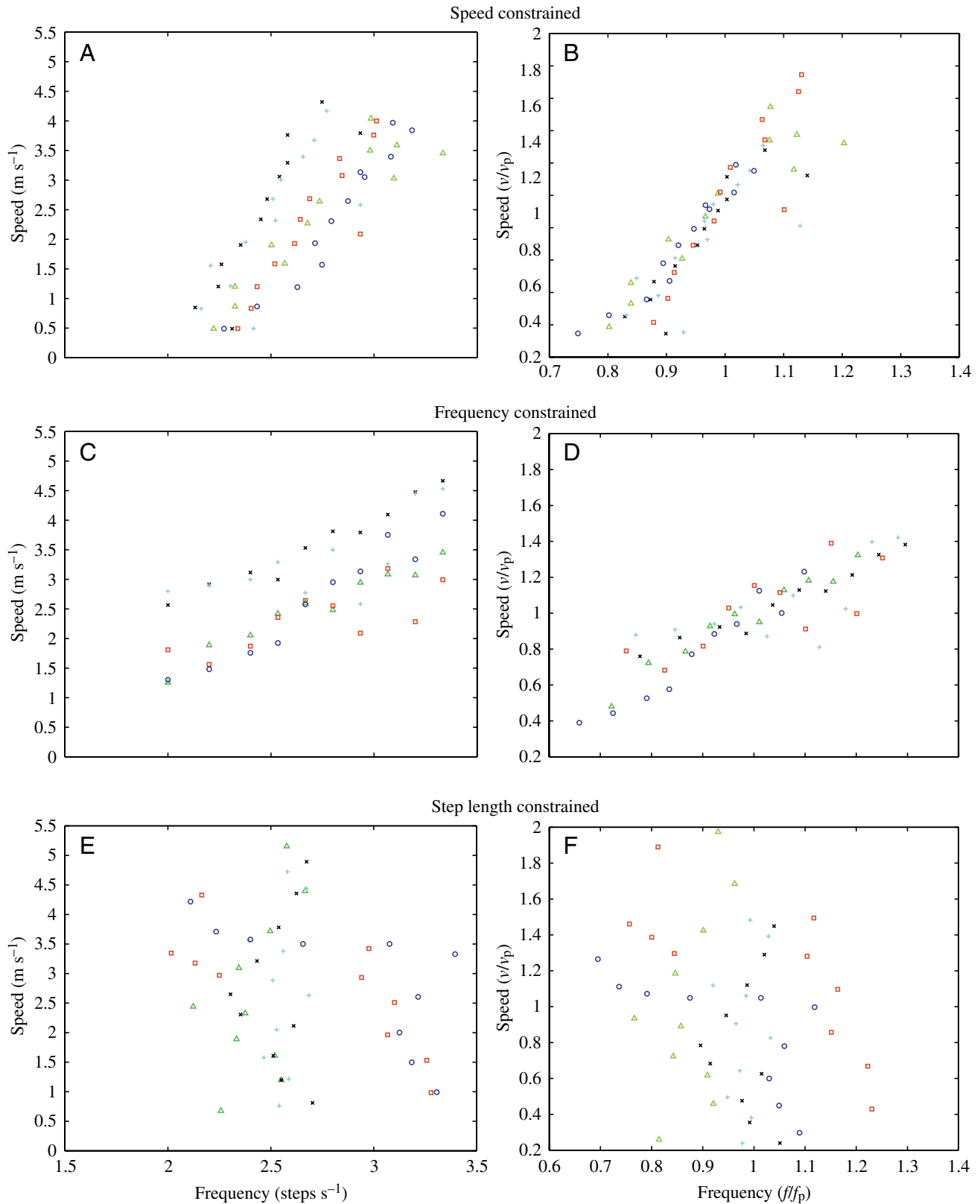
Fig. 7. Comparison of raw (A,C,E) and normalized (B,D,F) gait parameter selection data for all five subjects. Speed and frequency are normalized according to v_p and f_p, respectively. Normalization reduced inter-subject variability for all constraint conditions, but the reduction of variability is most noticeable for *v*-constrained (A,B) and *f*-constrained (C,D) conditions. Subject 1, green triangles; Subject 2, black ×; Subject 3, blue +; Subject 4, red squares; Subject 5, blue circles.

Table 3. *R^2 values for linear regressions run on raw and normalized behavioral data*

	Behavioral linear regression R^2	
Constraint	Raw	Normalized
Speed	0.61	0.88
Frequency	0.52	0.78
Step length	0.20	0.24

Data were normalized by v_p and frequency.

Actual behavior vs predicted behavior

Speed constrained

The narrow region of C_{min}+0.005 ml O_2 kg^{-1} m^{-1} slope indicates that the cost of transport increases quite rapidly for f values to either side of the optimal gait along horizontal lines representing v-constraints. Therefore, there is a stiff energetic penalty associated with deviating from the optimal gait under v-constrained conditions. So, we would expect to see little scatter in the behavioral data. And, indeed, the f-constrained data has the highest R^2 value (R^2=0.88) (Table 3).

Frequency constrained

As with v-constrained running, a narrow region of C_{min}+0.005 ml O_2 kg^{-1} m^{-1} indicates that cost of transport increases quite rapidly for v values to either side of the optimal gait along vertical lines representing f-constraints. So again there should be a reasonably stiff energetic penalty associated with deviating from the optimal gait under f-constrained conditions and, consequently, little scatter in the data. And again, prediction matches the observed behavior fairly well since the f-constrained data has the second highest R^2 value (R^2=0.78) (Table 3).

One interesting feature of the predicted behavior for f-constrained conditions is that multiple optima appear to exist for each frequency at lower frequencies. This is similar to the predictions for constrained walking (Bertram, 2005) in which multiple optima were predicted at higher frequencies under f-constrained conditions. However, in walking, observed behavior within the subject population was distributed between the optima, whereas all observed behavior in the present study was concentrated at the lowest speed optimum. This concentration could be due to the low number of subjects recruited for the behavioral part of the study. It is possible that if more subjects were included, some may have chosen the higher speed optimum. It is also possible, however, that the lowest speed optimum was chosen because it corresponds to a slightly lower metabolic cost than the higher speed optimum (the method we used to locate optima does not distinguish between local and global optima). This hypothesis is supported by the slope of the metabolic cost contour lines. Contour lines at lower frequencies have roughly positive slopes. Thus, for any given frequency, a lower speed should, in general, have a lower metabolic cost. Since the lowest speed optimum is near the edge of the cost surface, more low speed metabolic data

would be needed to conclusively confirm this hypothesis. A third possibility is that the lower speed optimum would provide an adequate cost/distance solution and lower cost rate (cost/time). Possibly this appealed to the subjects involved in this study because this study involved more rigorous activity than the previous walking study. At this time the interaction between factors potentially influencing the objective function are not established (Bertram, 2005).

Step length constrained

As under v- and f-constrained conditions, the fairly narrow region of C_{min}+0.005 ml O_2 kg^{-1} m^{-1} indicates that cost increases quite rapidly for v–f combinations along diagonal lines representing d-constraints. This indicates that a rather large energetic penalty should be associated with deviating from the optimal gait under d-constrained conditions. However, this does not agree with the measured behavioral response of the subjects studied. The d-constrained behavioral data is the most scattered of all three constraint conditions. One possible explanation for this discrepancy is that the shape of the cost surface was distorted because we were not able to normalize speed, frequency and cost values for each individual before pooling the metabolic data. Another explanation is that other types of metabolic cost such as cost per time may modify the shape of the cost surface under d-constrained conditions (Bertram, 2005). Cost per step would not alter the results for d-constrained conditions because cost per step and cost per distance differ by only a constant, d, so both cost per step and cost per distance surfaces would have the same minima along lines of constant d. (Note that similar logic holds for cost per distance and cost per time surfaces under v-constrained conditions.)

Implications

Although the predicted and actual behaviors do not coincide exactly, they do agree quite well considering the confounding factors with this study, e.g. small number of metabolic data points available, inability to normalize metabolic data prior to pooling, etc. This indicates that minimizing cost per distance can largely account for the complex behavior observed in human running. This is especially important because walking and running employ fundamentally different mechanics (Cavagna et al., 1977). Walking is generally modeled using an inverted pendulum to emphasize exchange of kinetic and potential energy, whereas running is generally modeled using spring mass system to emphasize storage and release of elastic strain energy. The fact that self-selected gait correlates well with gait predicted *via* constrained optimization of metabolic cost for both walking and running indicates that the control of these two gaits might be quite similar. This, in turn, suggests that constrained optimization might even be capable of predicting gait parameters for forms of motion with even more radically different mechanics.

However, there is substantial evidence that constrained optimization of metabolic cost would not successfully predict the self-selected behavior for cycling or other human–machine

forms of locomotion. It has been shown that experienced cyclists train themselves to pedal at a cadence that is significantly higher than that which minimizes metabolic cost per distance cycled for a given speed. Interestingly, less experienced cyclists spontaneously choose cadences that are closer to (although still higher than) the energetic optimum (Marsh and Martin, 1997). One possible explanation for this is that the body might judge

optimality in a way that is inappropriate for locomotion when a machine intervenes. For example, the body might optimize whole body muscle work to minimize cardio-pulmonary metabolic cost per distance as appears appropriate for walking and running, when localized muscle fatigue is a more important limitation for performance in cycling (Foss and Hallén, 2005). Therefore, experienced cyclists train themselves to override their instincts in order to optimize race performance in the artificial human–machine integration of cycling.

Although some discrepancies exist between the behavior predicted by constrained optimization of cost per distance and the observed self-selected behavior, the basic form of the predicted and observed behavioral curves agreed. This was similar to the level of agreement demonstrated for walking (Bertram, 2005). Optimization of alternative objective functions such as metabolic cost per time and cost per step did not predict running gait as well as metabolic cost per distance (Fig. 8). However, it is likely that these other types of cost might still help shape the objective function and influence features of gait parameter selection (Bertram, 2005). Also, other factors not directly related to metabolic cost, such as local muscle fatigue and body temperature, might play a role in running, which places specific demands on the locomotory system due to the vigor of the activity. Finding a way to measure the extent to which these elements contribute to the objective function, and under which circumstances, would be a worthy and challenging goal for future studies.

Appendix

Summary of methods used in Rouviere's thesis

The purpose of C. Rouviere's honors thesis (Rouviere, 2002) was to examine a few hypotheses regarding signals that might trigger the transition between running and walking. Testing one of these hypotheses involved determining the shape of the cost surfaces for walking and running near their intersection.

To build these cost surfaces, Rouviere measured the metabolic cost of walking and running near the gait transition for 5 subjects; 3 male, 2 female (age=25±1.87 years, mass=79.1±10.8 kg, height=179.4±13.2 cm). Subjects came to
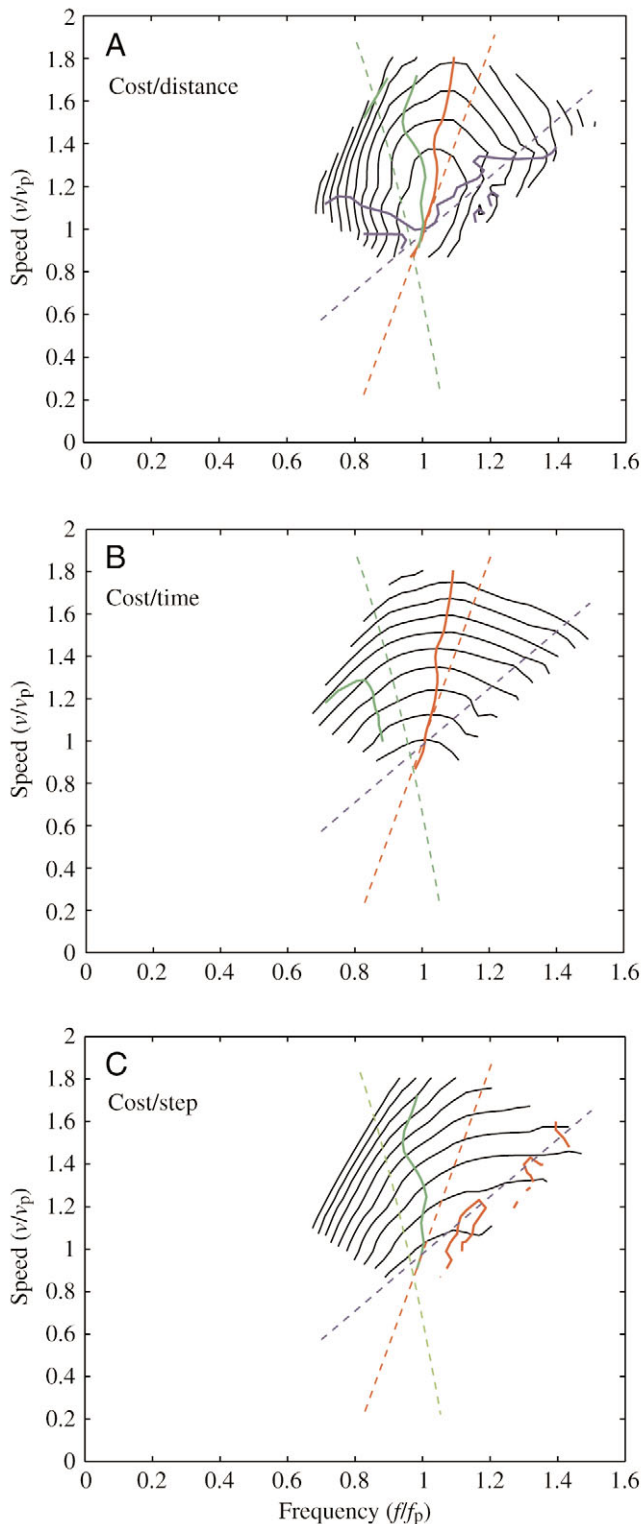

Fig. 8. Comparison of optimal behavior predictions generated using (A) cost per distance, (B) cost per time, and (C) cost per step surfaces. Cost contours from each surface are shown as black curves. Colored broken lines represent least-squares regressions of self-selected behavioral data and colored solid lines represent optimal predicted behavior. Red lines are used for v-constrained conditions, blue for f-constrained conditions and green for d-constrained conditions. The cost per time plot predicts v-constrained and d-constrained behavior quite well, but does not predict f-constrained behavior (no solid blue line). The cost per step plot also does not predict f-constrained behavior and predicts that the v-constrained behavior should occur where, instead, we observe f-constrained behavior. Only the cost per distance plot correctly predicts three different self-selected behaviors and places all three curves in the correct regions of v–f space. Therefore, minimization of cost per distance seems to be the best predictor of running behavior.

the laboratory twice and performed 12 walking or running trials on the treadmill over a complete range of constrained speed, frequency and step length conditions. The order of frequencies and gaits were originally randomly assigned, but all subjects used the same random sequence. A recovery period of at least 5 min was provided between trials to reduce the effects of fatigue and ensure valid metabolic measurements.

Oxygen consumption and carbon dioxide release rates were obtained using standard metabolic analysis techniques (TrueMax 2400, Parvo Medics, Salt Lake City, UT, USA). Subjects were tested at least 2 h post-prandial. A 7 min baseline consumption level was determined prior to each test session. This was used to normalize the metabolic rates of the two testing days. Values for the metabolic data points were calculated by averaging metabolic data from the last 3 min of each 5 min trial. None of the running trials were particularly strenuous as the highest running speed was in the range of 3 m s^{-1}, only slightly faster than the natural gait transition speed. However, to ensure that all metabolic data were obtained during steady state exercise, only trials where the rate of oxygen consumption had reached a steady value by the third minute were used. Also, RER was monitored and values for all trials were 0.92 or below.

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