Oscillatory network controlling six-legged locomotion.
Optimization of model parameters

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Abstract

The model of a legged locomotory system is optimized to ensure stable motion, reliable with respect to different initial conditions. The cost function suggested is based on the frequency of the model’s loss of stability evaluated for randomly chosen initial leg positions. The optimized model can start from the majority of allowed leg configurations, demonstrating stable walking at low and moderate speeds. Furthermore, an acceleration procedure is designed to permit the model to pick up practically every speed and then walk successfully.

Keywords: Legged locomotion; Stick insect model; Oscillatory network

1. Introduction

The problem of controlling a legged walking system has been intensively investigated by engineers and biologists. By now the widely accepted basic scheme of locomotion control has been formulated. It is assumed that control is conducted by a hierarchical system with several levels. An inferior level is represented by a network of locally coupled oscillatory subsystems, where each subsystem corresponds to a single appendage (von Holst, 1943; Orlovsky and Shik, 1976; Grillner, 1981; Cruse, 1990). An oscillator comprises a separate system consisting of a neural controller including the sense organs and a mechanical part including the muscles (Wendler, 1964; Bässler, 1972; Feldman, 1979; Cruse, 1990). Interleg coordination is based on the complex dynamics of the system of coupled oscillators. Different locomotor patterns are generated by different modes of synchronization between the oscillators (Graham, 1977; Cohen et al., 1982; Kopell and Ermentrout, 1988; Schöner et al., 1990; Collins and Stewart, 1993). Perturbations and external disturbances of the gait are autonomously processed by the “inferior” level to avoid critical situations and to re-establish the gait. By “critical situation” we mean loss of balance. The “superior” levels of the control system determine the velocity and the direction of motion, and possibly may resolve the critical situations appeared to be difficult for the “inferior” level. Following Tsetlin (1973), we suppose that the expeditiously aligned “inferior” level must operate autonomously to the utmost with respect to the “superior” levels.

It is of interest to investigate potentialities inherent in the “inferior” level system to avoid critical situations, without any influence of the superior level being taken into account. To approach this aim we examine our previously described model of a six-legged locomotory system (Müller-Wilm et al., 1992). Our previous investigations of the model have faced the problem of many starting configurations being unfavorable in the sense that the system may not maintain postural stability during the first steps (Cruse et al., 1993; Cruse et al., 1995). We suggest a cost function evaluating a frequency of downfall of the system beginning its motion from different initial conditions. We adjust parameters determining the interaction between the oscillators of the model to minimize the cost function. Finally, we consider gaits demonstrated by the optimized model.

The approach employed here has a twofold purpose. First, the model optimized can be implemented to control a real walking robot. Second, insofar as we use a biologically inspired model based on experiments with stick insects, it
is interesting to observe whether the model gaits are in agreement with experimental data and to discuss the approach in the context of animal learning.

Our study is based on the notion of static stability during walking, which is a simplification borrowed from robotics. The gaits keeping static equilibrium at every moment of motion are widely used in robot control (McGhee and Frank, 1968; Bessonov and Umnov, 1973; Okhotsimski and Golubev, 1984; Song and Waldron, 1989). Note that animals with six or more legs appear to keep static stability within a wide range of speeds (McGhee and Sun, 1974; Dean and Wendler, 1984; Ting et al., 1994). Thus, the requirement of static stability during walking is of interest both in the context of modeling of living locomotory systems and for possible application to walking machines.

Some animals seem to learn to walk “by trial and error”, i.e. by reinforcement learning. This method has the following salient features (Tsetlin, 1973; Barto et al., 1983; Sutton, 1984; Grossberg and Kuperstein, 1989):

1. learning is conducted without a teacher, so a learning subject does not receive any detailed information about how to act, but, instead, is provided with a measure evaluating the current performance. It is the external world or environment that is mostly considered as the source of this information. The measure of performance is also called a punishment/reward, reinforcement value or cost function;
2. reinforcement is delayed. It becomes available with a delay after an action has been finished.

Following this method, it is supposed that a required gait is not known in advance. The system should learn how to walk by minimizing or maximizing the cost function (Maes and Brooks, 1990; Beer and Gallagher, 1992; Müller-Wilm, 1993). For example, a genetic algorithm has been successfully applied to adjust the parameters of the control system of a six-legged walking apparatus (Beer and Gallagher, 1992). The cost function considered in this case was the measure of performance also called a punishment/reward, reinforcement value or cost function.

In this paper we suggest cost functions based on the frequency of the loss of static stability (FLSS), with initial leg positions chosen at random. Literally speaking, following the “trial-and-error” method an animal performs a number of walks starting at different leg positions. During the walk the animal falls down or succeeds in moving. A signal indicating that it has fallen down terminates the particular walk and represents the “punishment”. The frequency of the animal’s “punishment” should be minimized. An initial configuration is determined by the positions of all appendages and by the velocity of movement. The velocity does not change during a single walk. Depending on the definition, the cost function evaluates either FLSS for the particular speed or the average of FLSS over a range of speeds.

We consider the model of a six-legged walking system which has been described in a number of studies (Dean, 1991; Dean, 1992; Müller-Wilm et al., 1992). The model is based on experimental data concerning the locomotion of stick insects. To fit the experimental data, local coordinative mechanisms have been formulated which determine the interaction between oscillatory subsystems (Cruse, 1990; Dean, 1991; Dean, 1992; Müller-Wilm et al., 1992). Since only qualitative information about these mechanisms is available from the experiments, the question of how to choose the values of the interaction parameters remains to be solved.

The values of parameters of the model are adjusted during learning to obtain the minimum of the cost function. For a fixed value of velocity, the optimal set of interaction parameters is found, providing the minimum of the FLSS, i.e. the cost function. Repeating the minimization procedure for different values of velocity, we obtain the dependence of the minimum value of the cost function on the velocity. This dependence is called an “ideal” dependence.

Then we consider the cost function which averages the FLSS over the domain of velocities. Two different cases of the dependence of the parameters on the velocity are examined. In the first case, a “hard-wired” system (HWS) is examined, where parameters do not depend on the velocity. It turns out that for this case the “ideal” dependence of the FLSS is reached only within a comparatively narrow range of speeds. In the second case, we design the system with the parameters depending on the velocity. We show that introducing the linear dependence of just one parameter on the velocity is enough to make the system (LDVS) demonstrating the dependence of FLSS close to “ideal”. The optimal values of the parameters obtained are discussed.

As the minimal FLSS for high velocities remains high, we introduce an accelerating procedure which enables the system to pick up any desired speed without losing stability. The system begins the motion with a low enough speed and then reaches a desired velocity with constant acceleration. This procedure allows the model to have a low FLSS over a wide range of velocities.

The model is described in Section 2. The cost function is thoroughly defined in Section 3. The gaits of the model adjusted are described in Section 5.3.

2. Model

Direct forward locomotion of a six-legged animal over the horizontal plane is modeled. To check static stability, it is sufficient to consider a projection of the animal on the plane of support. Let $OY^2$ be a Cartesian coordinate system on the supporting plane, with the origin located at the projection of the center of mass (Fig. 1). For $OY^2$ we choose the projection of the symmetry axis of the animal, considering the rostral direction as positive. The positive direction of $OY^2$ is from right to left.

Suppose the distal point of a leg moves along the defined line which is parallel to $OY^2$ (Fig. 1). To describe this
A moving leg can be in one of two states: a retraction state (power stroke) and a protraction state (return stroke). During the protraction state, the distal point of a leg is lifted off the support surface and moves forward with a constant speed along the body. While in retraction, the leg is placed on the surface, supports the body and moves backward with a constant speed.

The measurements (millimeters) are taken from stick insects: $D_1 = 18$, $D_2 = 20$, $D_3 = 15$, $D_4 = 24$, $D_5 = 24$, $D_6 = 20$.

Fig. 1. The scheme of the stick insect model with basic measurements. In contrast to our previous work (Müller-Wilm et al., 1992), we neglect the duration of the transition between the states.

The movement of every leg is described by the pair of variables $(x, s)$, where $x_i$ is the coordinate of the distal point of the leg $i$ on its own coordinate axis $O_i X_i$, $s_i \in \{0, 1\}$, is the state of the $i$th leg ($s = 0$ for the protraction state, and $s = 1$ for the retraction state). Suppose for a moment that there is no interaction between the systems controlling the legs. Then the tip of every leg moves within the range of $[\text{PEP}_0, \text{AEP}_0]$. The dynamics of leg movement are described by the following system of difference equations:

$$x_i(t + \Delta t) = x_i(t) - V_i \Delta s_i(t) + V_i \Delta [1 - s_i(t)]$$

(1)

$$s_i(t + \Delta t) =
\begin{cases} 
1, & \text{if } x_i(t + \Delta t) > \text{AEP}_0, s_i(t) = 0 \\
0, & \text{if } x_i(t + \Delta t) < \text{PEP}_0, s_i(t) = 1 \\
s_i(t), & \text{otherwise}
\end{cases}$$

(1')

where $V_i$ ($V_p = \text{const}$) is the velocity of the distal point of the leg being in the protraction state, $V_r$ ($V_i = \text{const}$) is the velocity of the leg being in the retraction state. The function $s_i(t)$ is a piecewise linear periodic function ($i = 1, \ldots, 6$).

We suppose that parameters $V_p$, $V_r$ are identical for all the legs. Then the velocity of the center of mass is equal to $V_p$. Based on the experimental data, it is postulated that $V_p$, $\text{PEP}_0$, $\text{AEP}_0$ are not dependent on $V_i$. By scaling the time, we can choose $V_p = 1$, then the system of Eq. (1) takes the form

$$x_i(t + \Delta t) = x_i(t) - V_i \Delta s_i(t) + V_i [1 - s_i(t)]$$

Obviously, the static stability holds only if $V_i < V_p$, hence $V_i \in [0, 1]$, $i = 1, \ldots, 6$.

A coordination of leg movements results from local interactions of their control systems. The interaction implies that the extreme positions of the leg depend on the positions of distal point and states of other legs which are close “neighbors”. Thus, a leg can only be influenced by the ipsilateral anterior and posterior legs (if these legs do exist) and the symmetrical contralateral leg; the movement of each leg can be influenced by either two or three legs.

The influences are described as four mechanisms, where the first three mechanisms determine the dynamics of the PEP changes and the fourth one determines the dynamics of the AEP changes. A PEP is allowed both to increase and decrease. To avoid unlimited backward protruding of a leg, a minimal value $\text{PEP}_{\text{min}}$ of PEP is set. If PEP reaches $\text{PEP}_{\text{min}}$, the leg changes its state without any regard to incoming influences. Note that introducing $\text{PEP}_{\text{min}}$ does not mean that the ranges of the movement of neighboring legs cannot overlap. Changes of an AEP are so fashioned that $\text{AEP}_0 \geq \text{AEP}(t)$ for every $t$. Therefore, the tip of leg does not leave the interval $[\text{PEP}_{\text{min}}, \text{AEP}_0]$.

Mechanism 1 describes the effects on the PEP which come from the ipsilateral rear leg (if it exists) and the contralateral one. The effects are only present if the influencing leg is in the protraction state. The influence $\Delta \text{PEP}_{i, r}$ is determined by the equation

$$\Delta \text{PEP}_{i, r}(t + \Delta t) = [s_i(t) - 1]P_{i, r}$$

(2)
Here $P_{d,e}^0$ is the ‘‘coupling weight’’. $d$ is the number of the leg $(d = 1, 2, \ldots, 6)$, which is the destination of influence, $e$ is the number of the effecting leg, $e \in N_3^d$, where $N_3^d$ is the set of the numbers of legs, influencing the leg $d$ via mechanism

\[
N_3^d = \begin{cases} 
(d + 1, d + 3), & \text{if } d = 1, 2 \\
(d + 3), & \text{if } d = 3 \\
(d + 1, d - 3), & \text{if } d = 4, 5 \\
(d - 3), & \text{if } d = 6
\end{cases}
\]

Mechanism 2 describes the effect on the PEP which come from the ipsilateral rear leg (if it exists). It prescribes transition of the leg from the retraction state to the protraction state at the instant when the next rear leg begins the retraction phase:

\[
\Delta_{d,e}(t + \Delta t) = \begin{cases} 
(AEP_0 - PEP_{\min})P_{d,e}^2, & \text{if } s_d(t) = 1, s_e(t - \Delta t) = 0 \\n0, & \text{otherwise}
\end{cases}
\]

where $d = 1, \ldots, 6$; $e \in N_3^d$ where

\[
N_3^d = \begin{cases} 
(d + 1), & \text{if } d = 1, 2, 4, 5 \\
\{ 0 \}, & \text{if } d = 3, 6
\end{cases}
\]

$P_{d,e}^0$ is the binary parameter taking either 0 or 1. $P_{d,e}^2$ allows the elimination of the mechanism from the model, if necessary.

Mechanism 3 describes the influences of the anterior and contralateral legs on the PEP of the leg. The value of the influence depends on the position of the distal point of the influencing leg. The parameter $P_{d,e}^{\mu}$ is a ‘‘neutral position’’ of the mechanism 3. It introduces the dependence on the velocity in the LDVS model: $P_{d,e}^{\mu} = P_{d,e}^0 + P_{d,e}^3V_e$. In the case of the HWS model the parameters of the model do not depend on the velocity, i.e., $P_{d,e}^{\mu} = 0$ for every $d$ and $e$.

\[
\Delta_{d,e}(t + \Delta t) = \begin{cases} 
P_{d,e}^{\mu}P_{d,e}(t)|P_{d,e}^{\mu} - x_d(t)|, & \text{if } s_d(t) \leq P_{d,e}^{\mu} \\
P_{d,e}^{\mu}P_{d,e}(t)|P_{d,e}^{\mu} - x_d(t)|, & \text{if } s_d(t) > P_{d,e}^{\mu}
\end{cases}
\]

where $d = 1, \ldots, 6$; $e \in N_3^d$ where

\[
N_3^d = \begin{cases} 
(d + 3), & \text{if } d = 1 \\
(d - 1, d + 3), & \text{if } d = 2, 3 \\
(d - 3), & \text{if } d = 4 \\
(d - 1, d - 3), & \text{if } d = 5, 6
\end{cases}
\]

$P_{d,e}^{\mu}$ and $P_{d,e}^3$ are the weights of the influence.

Mechanism 4 describes the change of an AEP. The construction of the model allows the tip of the ipsilateral leg to be located behind the tip of the given leg. This can happen if the anterior leg moves backward until it is within the range of movement of the given leg and, moreover, it is crossed by the given leg, as it moves toward its own AEP$(t)$. Mechanism 4 acts to prevent this problem. When legs intercrossing just occurs, the given leg is forced to change its state, i.e. to begin retraction. This influence is similar to targeting behavior described in the work by Cruse (1979) Dean and Wendler (1984) and Dean (1990).

Mechanism 4 takes into account the positions of the given leg and ipsilateral anterior leg on the plane $OY^3$ associated with the body of the animal. The projections $v_d$ and $v_e$ of the tips of the legs on the axis $OY^3$ are compared. The equation for $\Delta_{d,e}^4(t)$ may be written in the form

\[
\Delta_{d,e}^4(t + \Delta t) = \begin{cases} 
|PEP_{\min} - AEP(t)|P_{d,e}^4, & \text{if } y_d(t) \geq y_e(t) \\
0, & \text{otherwise}
\end{cases}
\]

where $d = 1$, ..., 6; $e \in N_3^d$ where

\[
N_3^d = \begin{cases} 
(d - 1), & \text{if } d = 2, 3, 5, 6 \\
\{ 0 \}, & \text{if } d = 1, 4
\end{cases}
\]

$P_{d,e}^4$ is binary and takes either 1 or 0.

Taking into account all four mechanisms, the dynamics of each leg are described by the following system of difference equations:

\[
x_d(t + \Delta t) = x_d(t) - V_d\Delta \bar{t} + \Delta t[1 - s_d(t)]
\]

\[
\begin{cases} 
1, & \text{if } x_d(t + \Delta t) > AEP_d(t + \Delta t), \\
0, & \text{if } x_d(t + \Delta t) < AEP_d(t + \Delta t), \\
x_d(t) + 1, & \text{if } x_d(t + \Delta t) \geq 4
\end{cases}
\]

\[
AEP_d(t + \Delta t) = AEP_d(t + \Delta t)
\]

where $N_d^m$ is the set of the numbers of the legs previously determined for the given mechanism $m$ ($m = 1, 2, 3$), and the leg $d$, $(d = 1, \ldots, 6)$, in the description of mechanisms.

In the LDVS model, mechanism 1 is determined by ten parameters, mechanism 2 by four parameters, mechanism 3 by 40 parameters and mechanism 4 by four parameters. Thus in this case the total number of parameters is 58. In the case of the HWS model $P_{d,e}^{\mu} = 0$ for every $d$ and $e$ and, hence, the number of the parameters is 48.

To reduce the number of parameters to be adjusted we suggest that the system has symmetries. Let the values of the parameters determining the influence on any leg on the left side of the body be equal to the values of the like parameters determining the influences on the corresponding leg at the
right side of the body. Thus we introduce the symmetry of the left and right sides. Moreover, we suppose translation symmetry, imposing equality of the values of the like parameters determining every interaction of ipsilateral legs. For example, we suggest that in the case of mechanism 1 the influence of the middle left leg on the front left leg is determined by the same value of the parameter as the influence of the left hind leg on the left middle leg, i.e. \( P_{1,2} = P_{2,1} \).

Introduction of the symmetries allows us to decrease the number of model parameters significantly. In addition, in the case of contralateral interactions due to mechanism 3 we suppose that

1. the neutral position does not depend on the velocity, \( P_{i,3}^{0} = 0 \),
2. the weights of the influence are equal to each other, \( P_{i,2}^{0} = P_{i,3}^{0} \).

Finally, the LDVS model is determined by ten parameters: \( P_{i,1}^{0}, P_{i,2}^{0}, P_{i,3}^{0}, P_{i,4}^{0}, P_{i,1}^{3}, P_{i,2}^{3}, P_{i,3}^{3}, P_{i,4}^{3}, P_{i,5}^{3}, P_{i,6}^{3} \).

The interactions of the HWS model are determined by nine parameters (\( P_{i,4}^{3} = 0 \)). The complete list of the parameters is given in Appendix A.

### 3. Cost function

Consider an object with weightless legs, bearing on a plane, as statically stable at instant \( t \) if and only if the vertical projection of the mass center of the body locates strictly within a supporting polygon. The supporting polygon is the two-dimensional minimal convex domain, stretched on leg tips located on the plane at instant \( t \).

A function of the loss of static stability \( d(x, \bar{p}, V) \) detects whether a statically unstable configuration of the system has at least once appeared before instant \( t \). To introduce this function, consider the trajectory of the system of difference equations in Eq. (6) with an initial configuration. If parameters of the model \( \bar{p} \), initial leg positions \( x \) and velocity \( V \) are known, the trajectory of the system is uniquely determined. Then

\[
d'(x, \bar{p}, V) = \begin{cases} 0, & \text{if unstable configuration has not occurred before } t \\ 1, & \text{otherwise} \end{cases}
\]  

Denote by \( J'(\bar{p}, V) \) the mean value of \( d'(x, \bar{p}, V) \) over domain \( S \)

\[
J'(\bar{p}, V) = \frac{\int_{S} d'(x, \bar{p}, V) \, dx}{\int_{S} \, dx}
\]  

where \( S \) is the domain of the allowed initial leg positions. A vector of the initial leg coordinates and the states belongs to the domain, \( x \in S \) if all legs are initially located on the supporting surface and their tips are within “normal” ranges of movement:

\[
S = \{ x \} \quad \text{PEPu} < x_i < \text{APEbo}, \quad s_i = 1 \}
\]

where \( x_i \) is the coordinate and \( s_i \) is the state of the leg with number \( i, \bar{i} \), \( i = 1, 2, ..., 6 \).

Function \( J'(\bar{p}, V) \) evaluates the FLSS of the system starting from initial configurations belonging to the domain \( S \) at the fixed velocity \( V \), i.e. the fraction of the configurations leading to the loss of static stability.

To estimate \( J'(\bar{p}, V) \) we use \( J_s'(\bar{p}, V) \) evaluated using a sample of \( N \) initial configurations \( \bar{x} \) uniformly distributed over \( S \)

\[
J_s'(\bar{p}, V) = \frac{\sum_{i=1}^{N} d'(x_i, \bar{p}, V)}{N}
\]  

where \( x_i \) is the vector determining the \( i \)th set of initial leg positions. Thus we use the finite approximations of the integrals in Eq. (8). We suggest that for a large enough value of \( N \) the estimation \( J_s'(\bar{p}, V) \) tends to \( J'(\bar{p}, V) \).

We intend to find the optimal parameters \( \bar{p}^* \) to minimize \( J_s'(\bar{p}, V) \). As \( J_s'(\bar{p}, V) \) is a function of \( V \) it is of interest to consider two different optimization problems.

**Problem 1.** For a fixed value of velocity \( V^* \), to determine an optimal set of the parameters \( \bar{p}^* \) such that a cost function \( G(\bar{p}^*) \) is minimal, \( G(\bar{p}) = J_s'(\bar{p}, V^*) \).

**Problem 2.** To find such “universal” set of parameters \( \bar{p}^* \) which is, in some respects, optimal for every velocity \( V \) from the domain of allowed velocities \( W \). For this purpose we consider a “generalized” FLSS which is defined as the FLSS averaged over domains \( S \) and \( W \):

\[
J_s(\bar{p}) = \frac{\sum_{i=1}^{N} d'(x_i, \bar{p}, V)}{N}
\]  

Problem 2 is to find an optimal set of parameters \( \bar{p}^* \) providing the minimum of \( G(\bar{p}) \), \( G(\bar{p}) = J_s(\bar{p}) \).

**4. Minimization of cost function**

Usually an estimation of a cost function consists in evaluating a multidimensional integral by the Monte Carlo method and takes an enormous amount of computer time. To reduce the computations, we subdivide the minimization procedure into two stages. First, we try to find some point sufficiently “close” to the global minimum. For this purpose we employ an evolutionary algorithm. At this stage the cost function is calculated roughly, with a relatively small number of starts for the Monte Carlo method. Second, further local minimization is achieved by the downhill simplex method (Press et al., 1992) having the advantage that it does not require evaluation of the derivatives of the cost function.
4.1. Evolutionary algorithm

Up to now many different algorithms have been proposed inspired by the principles of natural evolution (Holland, 1975). All of them simulate the evolution of individuals, encoding possible solutions of the problem by employing computational representations of the natural processes of selection, mutation and reproduction. These algorithms are simple to implement and are robust. They have been widely used for global optimization in complex search spaces in many applications.

Our model incorporates two rules of coupling, containing binary parameters. This leads to some combinatorial minimization. Taking into account this feature of the problem, an evolutionary algorithm appears to be of particular assistance.

We use an evolutionary algorithm to find a point in the vicinity of the global minimum of the cost function $G(p)$ for problem 1. Commonly, the algorithm finds a solution in about 100 iterations. As a rule, further work of the algorithm does not lead to any sensitive decrease of the function.

Let us describe the algorithm used here. We consider a population $Q^*$, composed of individuals $q_i^k$, $i = 1, \ldots, L$, $L = 10$. The individual $q_i^k$ is an array of the values, corresponding to the values of the model parameters $p$. The values of the array $q_i^k$ are related to the arguments of the cost function $G(p)$ (recall that the number of the parameters is nine for the HWS model and ten for the LDVS model). An individual which has all values equal to zero will be called the “0”-individual.

An evolutionary algorithm applies three procedures to a population $Q^*$: (1) computation of the cost function for each individual; (2) “selection”, providing “survival and reproduction of the fittest individuals”, where the fitness is determined by the value of the cost function; (3) “mutation”, producing “diversity” within the population. As a result of sequential applications of all three procedures to population $Q^*$, we get the new “generation” $Q^{k+1}$.

The initial population $Q^*$ consists of the “0”-individual and of individuals with sets of numbers uniformly distributed over some domain. By doing so, some initial diversity is introduced at the start of the algorithm.

4.1.1. Selection

“Selection” is the procedure determining the fittest creatures which survive and take part in reproduction in the next generation, i.e. at the next iteration of the algorithm. Selection is conducted according to the value of the cost function; the probability of reproduction of an individual at the next generation is greater if the value of the corresponding cost function is smaller. The evolutionary algorithm is designed so that at every iteration there is an individual whose corresponding cost is not greater than the smallest value of the cost function at the previous iteration.

Selection may be viewed as having two stages.

(1) Choosing the individual $q_i^{k+1}$. The individual $q_i^{k+1}$ is exactly the one having the smallest corresponding value of the cost function among all other individuals in the population of the previous generation $Q^* = \{q_i^k\}$, $q_i^{k+1} = \min_{q_i^k \in Q^*} \{G(q_i^k)\}$.

(2) Determining the other $L - 1$ individuals $q_i^{k+1}$, $k = 2, \ldots, L$. First of all, the procedure selects the survivors $q_i^k$, $k \in \{2, \ldots, L\}$, with the cost function taking values strictly smaller than that of the first individual $q_i^1$, $G(q_i^1) < G(q_i^k)$. Suppose that there are $K > 0$ such individuals. Let us enumerate them: $q_{i_1}^k, j = 1, \ldots, K$. A new generation is formed by these $K$ individuals according to probabilistic rules of reproduction. An individual $q_i^{k+1}$, $i = 2, \ldots, L$ in the next population is a copy of the individual randomly chosen from $K$ individuals. The probability $P(q_i^{k+1})$, of an individual $q_i^{k+1}$, $i \in \{1, \ldots, K\}$, to be selected is

\[
P(q_i^{k+1}) = \frac{G(q_i^k) - G(q_{i_1}^1)}{\sum_{j=1}^{K} [G(q_i^j) - G(q_{i_1}^1)]}
\]

If $K = 0$, the new population consists of the copies of the individual $q_i^1$.

After, we obtain a population consisting of $L = 10$ individuals.

4.1.2. Mutation

Mutation provides diversity when the fittest creatures are replicated. By doing so, “local” search in the vicinity of the fittest creature is conducted.

Parameters of the best individual $q_{i_1}^k$ are kept unchanged; they serve as a standard within the procedure of selection. Parameters of other $L - 1$ individuals are to be modified. A random, normally distributed component with mean value equal to zero and standard deviation $\sigma$, $\sigma = 0.3$, is added to every parameter in the set, where $i$ is the number of the individual, $i = 2, \ldots, L$.

5. Results

5.1. Results of minimization

5.1.1. Problem 1

Consider problem 1. Having adjusted the parameters of the HWS model separately for the different fixed velocities, we find the dependence of the minimal FLSS on the velocity (the “ideal” dependence). Figure 2 demonstrates that the FLSS steadily increases with the velocity. At velocity $V = 0.1$, the FLSS is 0.004, then up to $V = 0.4$ the frequency is less than 0.3, and for the high velocities exceeding $V = 0.7$ the frequency is more than 0.8. For comparison, the dependence of the FLSS for the model without coordinative mechanisms is presented in the same figure. It can be seen that coordinative mechanisms appropriately adjusted allow a substantial decrease in the FLSS for a wide range of velocities.
Consider the optimal values of parameters resulting from the procedure of minimization. The first stage of minimization always sets $P^0 = 0$ for every velocity. Thus mechanism 2 does not improve the model in respect to the cost function and is eliminated from the model before the second stage of minimization. In contrast, mechanism 4, which also has a binary parameter, is retained for every velocity. Therefore, at the second stage of minimization, $P^3$ is not treated as an argument of the cost function. It is fixed at $P^3 = 1$. Mechanism 3 for the HWS model is characterized by parameters: $P^{3,1}, P^{3,2}, P^{3,3}$. It turns out that for every velocity $P_{c,2}$ and $P_{c,3}$ are smaller than $P^{3,2}$ at least by a factor of ten.

Fig. 2. The FLSS during walk. Initial leg positions are chosen at random. The × symbols plot the “ideal” dependence of the FLSS on velocity (same as in Fig. 2). The curve marked by circles represents the FLSS of the model without coordinative mechanisms; the curve with bars presents the FLSS of the HWS models optimized for the corresponding velocity. Frequency is calculated on the base of 1000 starts. The means are calculated from samples of seven values. $\Delta t = 0.1$

```
\begin{align*}
P^n_{1} & = 1.1, \\
P^n_{2} & = 5.999, \\
P^n_{3} & = -9.32, \\
P^n_{4} & = 0.083, \\
P^n_{5} & = 0.998, \\
P^n_{6} & = 0.999, \\
P^n_{7} & = 0.999.
\end{align*}
```

5.1.2. Problem 2

Considering problem 2, we optimize two different models, the HWS model and the LDVS model.

**Problem 2 for HWS model.** We take the system with the same parameter values at every velocity (HWS) as suggested in Section 2. If the cost function is calculated, with $V$ being uniformly distributed in the range $[0.1, 0.7]$, the HWS cannot be adjusted well enough to produce a dependence of the FLSS close to the “ideal” dependence. As a rule, the result is spoiled in the whole range. Nevertheless, if we only consider the range $[0.1, 0.45]$, then, as can be seen by comparing Fig. 2 with Fig. 3, within this range the dependence of the FLSS of the “hard-wired” system is “close” to the “ideal” dependence. Note that for $V = 0.4$ and $V = 0.45$ the FLSS curve of HWS fits the “ideal” dependence. The frequency is calculated on the base of 1000 starts. The means are calculated from samples of seven values. ($\Delta t = 0.1, a = 0.00008, P^0_1 = 11.998, P^0_2 = 5.999, P^0_3 = -9.32, P^0_4 = 6.23, P^0_5 = 0.083, P^0_6 = 16.058, P^0_7 = -2.063, P^0_8 = 0.081.$)

Problems 2 for LDVS model. A better performance can be obtained if we consider the LDVS model. We choose the neutral position to be dependent on the velocity ($P^n_{10} = P^n_1 + P^n_4 \times V_j$) because it is known from numerical investigation that the parameter $P^n_{10}$ controls the phase relationships between the movements of the ipsilateral legs. For the LDVS model, as shown in Fig. 4, the dependence of the FLSS is in good agreement with the “ideal” dependence in the range $[0.1, 0.5]$. Comparing Fig. 4 and Fig. 3, one can see that in the second case the FLSS is smaller for every velocity in the range.

```
\begin{align*}
P^n_{11} & = 0.45, \\
P^n_{12} & = 0.00008, \\
P^n_{13} & = 0.00008. \\
\end{align*}
```

Nevertheless, for a high velocity the FLSS is high even for the “ideal” model. Note that when picking up a high velocity immediately after starting the animals also appear to stumble (Cruse, H., unpublished observations from stick insects). To overcome this difficulty in the model we introduce an accelerating procedure.
5.2. Accelerating procedure

The limit oscillatory regime, which permanently satisfies the condition of static stability, corresponds to a statically stable gait, otherwise it corresponds to a statically unstable gait. Consider the trajectory initiated from a randomly chosen point of phase space. A loss of static stability can occur if the system following the path to the attracting regime takes a statically unstable configuration, the attracting regime is statically unstable, or both.

The FLSS is about zero at low velocities. This suggests that at a low velocity: (1) the system only has statically stable limit regimes; and (2) most trajectories do not contain statically unstable configurations.

It appears that the adjusted system only demonstrates statically stable limit regimes at high velocities as well. If we check the static stability of the system after a long enough period of time then the FLSS diminishes drastically. For example, if this period of time is greater than five periods of a single leg oscillator, then the FLSS is about zero up to the velocity \( V = 0.6 \). The higher the velocity, the greater is the period of time required. Up to \( V = 0.85 \) statically unstable limits regimes are not detected.

Let \( V_r \) be the desired velocity of motion. The accelerating procedure is described by

\[
V_r(t) = \begin{cases} 
V_r(0) + a \times t, & \text{if } V_r(t - \Delta t) < V_r^* \\
V_r^*, & \text{if } V_r(t - \Delta t) \geq V_r^* 
\end{cases}
\]

where \( V_r(0) \) is an initial velocity, \( a \) is an acceleration.

Employing this accelerating procedure, the system has a better chance to attain an attracting limit regime at the required velocity. Suppose that the limit regime is statically stable at a low velocity. If the system begins its motion at the low velocity and the acceleration \( a \) is small enough and the limit regime has no bifurcations during the growth of \( a \); then: (1) the limit regime is not "significantly" changed at each moment; (2) the system remains in the close vicinity of the statically stable limit regime. Thus the condition of static stability will most likely be held during the acceleration.

The constant \( a \) is chosen to reconcile two contradicting demands: (1) the desired velocity must be reached as fast as possible; (2) the FLSS should be kept at FLSS corresponding to the initial low velocity.

In Fig. 4 one can see that, for the LDVS model, the accelerating procedure allows the system to keep the FLSS below the level of 0.05 for the range of velocities \([0.1, 0.9]\). Under the same conditions for the "hard-wired" model the FLSS can be kept below the level of 0.1 (Fig. 3).

5.3. Model gaits

To describe the model gaits, we consider the trajectories demonstrated by the system of equations in Eq. (6). The trajectories can be conveniently classified according to their limit behaviors. The adjusted models only demonstrate periodic oscillations with the same period for all legs. Hence a stable periodic oscillation, i.e. the model’s gait, can be related to a regime of synchronization of leg movements and described by a set of relative phases.

To investigate the gaits demonstrated by the system moving with a given velocity from different initial leg positions, a set of \( N \) different randomly chosen initial configurations \((N = 100)\) is used. Here only the trajectories which meet the condition of static stability are taken into consideration. Numerical simulations are conducted using the accelerating procedure. The set of relative phases for different pairs of legs is determined after a stable period and relative phases between oscillatory movements of all six legs have been set up. Then the diagrams of relative phases for different pairs of legs are drawn and investigated.

For any velocity chosen, every diagram shows a single narrow peak. This suggests that the gait observed is a unique statically stable regime of synchronization of the system. Investigation of stationary phase relationships has shown that, in all gaits observed, phase relationships for neighboring ipsilateral legs are the same: \( \Phi_{i-3} = \Phi_{i-4} = \Phi_{i-5} = \Phi_{i-6} = \phi_i \), where \( \Phi_{i,j} \) means the time lag of the movement of the \( i \)th leg relative to the \( j \)th leg, normalized by the period of the movement. Similarly, phase relationships for neighboring contralateral legs are also the same: \( \Phi_{i+1} = \Phi_{i+2} = \Phi_{i+3} = \phi_{i,c} \). Thus, every observed stationary gait can be described by a pair of numbers \((\phi_i, \phi_{i,c})\). This result appears to follow from the symmetry imposed on the parameters of the model.

Consider first the gaits of "hard-wired" model demonstrated by the adjusted HWS model. If \( V = 0.1 \), the ipsilateral relative phase is \( \phi_i = 0.65 \). For \( \phi_i > 0.5 \), protraction phases of different legs appear in the following order: hind, middle, front (positive metachrony). It can be seen from Fig. 5, that \( \phi_i \) grows from 0.65 to 0.7, with the velocity growing up from 0.1 to 0.4. Thus if the velocity is taken from the range \([0.1, 0.4]\), the ipsilateral relative phase is \( \phi_i = 0.67 \), so phases \( \Phi_{1-1}, \Phi_{2-2}, \Phi_{3-3} \) are distributed almost equidistantly on the circle. With the velocity increasing above 0.4, \( \phi_i \) continuously decreases, the relative phase \( \phi_{i,c} \) tending to 0.5, when the velocity tends to 1 (Fig. 5). The relative phase \( \phi_{i,c} \) does not depend on velocity \((\phi_{i,c} = 0.5)\). Thus if \( \phi_i = 0.5 \), the tripod gait is observed.

Now consider the gaits of LDVS model. Fig. 6 shows that if \( V_r = 0.1 \), then \( \phi_i = 0.91 \); \( \phi_i \) tends to 0.5 with the velocity tending to 1. The neighboring contralateral pairs of legs move in anti-phase \((\phi_{i,c} = 0.5)\) and \( \phi_i \) does not vary with the velocity. Note that this dependence reproduces Gait II, in particular the one described by Wilson (1966). It can be seen that Wilson’s gait closely fits the data received from the adjusted model (Fig. 6). Let us describe the gaits known from the experiments.

Animals having more than four legs mostly demonstrate metachronal wave gaits (von Holst, 1943; Wilson, 1966;
Graham, 1972; Graham, 1985). A formal description of metachronal gaits can be found in Smolyaninov and Karpovich (1975a); Smolyaninov and Karpovich (1975b). The protraction phases of ipsilateral legs appear shortly one after another, creating the impression of a propagating wave. In many species the wave propagates from rear to front. This is called positive metachrony. In this case the rear leg is the first to begin the protraction phase, the neighboring middle leg starts shortly after the rear leg has finished the protraction phase and, similarly, the front leg does the same after the middle leg has completed its protraction. For some species the wave propagates from the front to the rear. This is called negative metachrony. In both cases of metachrony the contralateral pairs of legs are usually moving nearly in anti-phase. In addition, there is a metachronal gait which is intermediate between these two. It is the case of a standing metachronal wave, commonly called the tripod gait. During this gait the neighboring legs are alternating, i.e. moving in anti-phase.

Observing the locomotion of the 1st instar nymph of the stick insect, Graham (1972) described two basic velocity-dependencies of the gait as Gait I and Gait II. Also, he has shown that an adult stick insect only demonstrates Gait II (Graham, 1972).

Gait I represents the tripod gait for the whole range of velocities. The duration of the protraction phase depends linearly on the period (Graham, 1972).

Gait II represents a positive metachronal wave. In

Fig. 5. The phase shifts of ipsilateral leg movements of the HWS model optimized for a range of velocities. The upper line represents the phase of the 2nd leg relative to the 1st leg, the lower line depicts the phase of the 3rd leg relative to the 1st leg. The phase $\phi_2$, increasing from 0.65 to 0.7, with the velocity growing up from 0.1 to 0.4. If the velocity is taken from the range [0.1, 0.4], the ipsilateral relative phase is $\phi_1 = 0.67$, so phases $\Phi_{1-2}, \Phi_{2-3}$ are distributed almost equidistantly on the circle. ($\Delta \tau = 0.01, P^1_1 = 10.85, P^1_2 = 6.73, P^1_3 = -2.48, P^2_1 = 4.75, P^2_3 = 0.191, P^3_1 = 0.0, P^3_2 = -0.34, P^3_3 = 0.09$.)

Fig. 6. The phase shifts of ipsilateral leg movements of the LDVS model optimized for a range of velocities. The upper line represents the phase of the 2nd leg relative to the 1st leg, the lower line depicts the phase of the 3rd leg relative to the 1st leg. The crosses represent the phase shifts of Gait II (Wilson, 1966; Bessonov and Umnov, 1973). It can be seen that Gait II closely fits the data received from the adjusted model ($\Delta \tau = 0.01, P^1_1 = 11.998, P^1_2 = 5.999, P^2_1 = -9.32, P^2_2 = 6.23, P^2_3 = 0.083, P^3_1 = 16.058, P^3_2 = -2.063, P^3_3 = 0.081$).
contrast to Gait I, the duration of the protraction phase for Gait II does not depend on the period, i.e. on the velocity of the motion. Graham notes that the protraction phases of ipsilateral legs appear one after another with some delay. This delay also depends on the velocity. As the velocity increases, the metachronal wave is transformed into the tripod gait.

A simple scheme reproducing a particular example of Gait II has been introduced earlier by Wilson (1966) and is widely used in robotics (Bessonov and Umnov, 1973; Okhotinski and Golubev, 1984; Song and Waldron, 1989). It can be obtained by setting the delay equal to zero. The duration of the protraction phase and the ranges of the leg motion are fixed for all velocities. Then as the velocity increases, the fraction of the protraction phase in the cycle also increases and tends to 0.5, at which point the metachronal wave becomes the tripod gait. The dependence on the velocity of this Gait II is depicted in Fig. 6 by X symbols.

6. Discussion

At present, much experimental data has been provided about the design and properties of systems controlling animal locomotion. Nevertheless, the question concerning the learning-adjustment of the systems remains unclear. Among different algorithms of learning, the learning by "trial-and-error" appears to be a biologically plausible algorithm, in particular when learning also includes "learning" during the evolution process. This algorithm seems to be more realistic than algorithms implying a teacher who possesses detailed knowledge about a desired locomotor pattern. The gist of learning by "trial-and-error" is a cost function.

The cost function is considered here as an integral index of "quality" of the control system. The cost function describes the ability of the system to perform a statically stable walk. The cost function averages the index of motion efficiency during a fixed period of time over many trajectories starting from randomly chosen initial configurations. In other words, it presents the frequency of the loss of static stability during the motion of the system. Recall that the model considered contains an explicit parameter corresponding to the velocity of motion. Considering the velocity as one of the coordinates determining the initial condition of the system, we thereby design the cost function taking into account the performance at different speeds. It turns out that for low and moderate velocities the parameters providing the FLSS smaller than 0.1 can be found. In contrast, at "high" velocities the FLSS exceeds 0.7 and it appears to be impossible to decrease the FLSS by adjusting the parameters. This means that at a high velocity the start from arbitrarily chosen leg positions in most cases leads to the loss of static stability.

Another way to pick up a high velocity successfully can be represented by the accelerating procedure. The procedure makes it possible to perform a stable walk with a high velocity starting from arbitrary initial leg positions. The motion is initiated with a low velocity so that the system could easily "find" a statically stable gait. Then the velocity gradually increases to the value desired. This procedure allows the system to achieve a good efficiency of walking (the FLSS is smaller than 0.1) at high velocities.

Moreover, it should be noted that the FLSS of the system beginning the motion from randomly chosen initial configurations can be used as a measure of performance to compare not only different sets of parameters of the same model, but to compare different models as well (Cruse et al., 1993). It would be useful to design a set of tests to compare different control systems. We think that the cost function proposed can be used as a representative of this set.

The investigation of the parameters chosen as optimal suggests that the strict rostrally directed excitatory influence (mechanism 2) is inappropriate, or at least not helpful, for the maintenance of static stability under the conditions tested. We suggest that more "smooth" coordinative mechanisms are more preferable in the context of stability balance. Contrary to our model, the contralateral version of mechanism 1 was not found in the stick insect (Cruse and Epstein, 1982), although several authors have postulated it to exist in insects. On the other hand, mechanism 2 has been found in stick insects (Cruse and Schwarze, 1988). Therefore, it might be possible that mechanism 2 may improve stability under special walking conditions.

The cost function is an integral characteristic taking into account different arbitrarily chosen initial leg positions. This feature allows one to consider the stability of the system not only with respect to different starting positions, but also in situations when the ongoing motion is subjected to perturbations. Suppose that a moving system has been affected by an "obstacle" at some instant of motion. This leads to the disturbance of motion. In terms of the model, the action of the "obstacle" can be viewed as the termination of motion. Then the motion is initiated from new leg positions produced due to the "obstacle".

Note that the above reasons concerning the static stability of the system are only valid with respect to the "obstacles" at low velocities, where the FLSS is small. At higher velocities the influence of an "obstacle" results in frequent losses of static stability. The advantages of the accelerating procedure imply that the system can promptly decrease the velocity down to a small enough value at the moment when an "obstacle" has been encountered. This behavior is observed in stick insects. It should be noted though that the requirement of static stability seems to be too strong. It is more realistic to consider dynamic stability (Ting et al., 1994).

Three strategies should be of interest in the context of the model's sensitivity to motion disturbances:

1. it should be useful to determine a small set of allowed leg positions "close" to those appearing during walking at
this velocity. Then the system could reorganize the leg positions disturbed by the obstacle by choosing a position from this set, which is the nearest to the current one. This approach can lead to a drastic decrease of the FLSS.  

2. superior levels of the control system may be useful for avoiding the loss of stability in complex cases;  

3. the balance might be kept by grasping the surface. This method is widely used by insects which have a large arsenal of specialized tools, but is not generally applicable to walking machines because most of them have no suckers.  

The coordinative mechanisms have been previously formulated to fit the experimental data obtained on stick insects. Therefore, one might expect the walking behavior of the model to be similar to that observed in the experiments. The LDVS model can produce different dependencies of the walking pattern on the velocity (compare, for example, Fig. 5 with Fig. 6). It turns out that the LDVS model’s gaits are in good agreement with the experimental data and correspond to the Wilson (1966) case of Gait II. Moreover, it is interesting to note that this gait, appearing here as a result of learning without a teacher, has been widely used in robotics (Bessonov and Umnov, 1973; Okhotsimski and Golubev, 1984; Song and Waldron, 1989).  

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Appendix A

\[
P_1^l = P_{1.2}^l = P_{2.3}^l = P_{4.5}^l = P_{5.6}^l  
\]

\[
P_2^l = P_{1.4}^l = P_{2.5}^l = P_{4.6}^l = P_{5.1}^l = P_{3.2}^l = P_{6.3}^l  
\]

\[
P_3^l = P_{1.3}^l = P_{3.2}^l = P_{4.5}^l = P_{5.6}^l  
\]

\[
P_i^{3.1} = P_{2.1}^i = P_{3.2}^i = P_{4.3}^i = P_{5.4}^i = P_{6.5}^i  
\]

\[
P_i^{2.3} = P_{2.1}^i = P_{3.2}^i = P_{4.3}^i = P_{5.4}^i = P_{6.2}^i  
\]

\[
P_i^{3.2} = P_{2.1}^i = P_{3.2}^i = P_{4.3}^i = P_{5.4}^i = P_{6.3}^i  
\]

\[
P_i^{3.3} = P_{2.1}^i = P_{3.2}^i = P_{4.3}^i = P_{5.4}^i = P_{6.3}^i  
\]

\[
P_i^{3.4} = P_{2.1}^i = P_{3.2}^i = P_{4.3}^i = P_{5.4}^i = P_{6.4}^i  
\]

\[
P_i^{1.1} = P_{2.1}^i = P_{3.2}^i = P_{4.3}^i = P_{5.4}^i = P_{6.3}^i  
\]

\[
P_i^{2.2} = P_{2.1}^i = P_{3.2}^i = P_{4.3}^i = P_{5.4}^i = P_{6.2}^i  
\]

\[
P_i^{3.5} = P_{2.1}^i = P_{3.2}^i = P_{4.3}^i = P_{5.4}^i = P_{6.3}^i  
\]

\[
P_i^{4.2} = P_{2.1}^i = P_{3.2}^i = P_{4.3}^i = P_{5.4}^i = P_{6.2}^i  
\]


