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Simulations of neuromuscular control in lamprey swimming

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The neuronal generation of vertebrate locomotion has been extensively studied in the lamprey. Models at different levels of abstraction are being used to describe this system, from abstract nonlinear oscillators to interconnected model neurons comprising multiple compartments and a Hodgkin–Huxley representation of the most relevant ion channels. To study the role of sensory feedback by simulation, it eventually also becomes necessary to incorporate the mechanical movements in the models. By using simplifying models of muscle activation, body mechanics, counteracting water forces, and sensory feedback through stretch receptors and vestibular organs, we have been able to close the feedback loop to enable studies of the interaction between the neuronal and the mechanical systems. The neuromechanical simulations reveal that the currently known network is sufficient for generating a whole repertoire of swimming patterns. Swimming at different speeds and with different wavelengths, together with the performance of lateral turns can all be achieved by simply varying the brainstem input. The neuronal mechanisms behind pitch and roll manoeuvres are less clear. We have put forward a 'crossed-oscillators' hypothesis where partly separate dorsal and ventral circuits are postulated. Neuromechanical simulations of this system show that it is also capable of generating realistic pitch turns and rolls, and that vestibular signals can stabilize the posture during swimming.

Keywords: lamprey; simulation; neuromechanical model; neural oscillators

1. INTRODUCTION

Computer simulation is becoming an indispensable tool in neuroscience. This technique has many advantages; perhaps most importantly it makes it possible to relate results and models describing one system at different levels of abstraction or granularity. For example, the electrophysiological properties of a neuron may be accounted for by simulating mathematical descriptions of relevant subcellular mechanisms such as channel activations and ion currents. Similarly, the collective properties of a neuronal network may be examined by simulating large sets of interacting model neurons. Being able to synthesize and eventually explain a system in terms of its constituent parts in this way is a very important complement to the massive gathering of data which has been the focus of neuroscience to date. In fact, understanding a system in terms of its components may even be considered a vital constituent of scientific knowledge.

In neuroscience, one fundamental goal is to understand behaviour in terms of neurons and their properties. The use of computer simulation opens up new ways of approaching this goal, because it makes it possible to build realistically connected networks comprising model neurons and study the emergent properties on a behavioural level. When approaching the behavioural level, it eventually becomes necessary to simulate not only the neuronal system itself but also the environment in which it resides and operates. In this paper we shall describe one system, the swimming behaviour of the lamprey, where simulations have indeed been used to tie together cellular and network data with the behaviour of the animal as a whole.

The lamprey, and in particular its swimming behaviour, has been the subject of numerous experimental and theoretical studies (for a review see, for example, Grillner *et al.* 1995). The rationale behind such interest in this particular species is twofold. First, the lamprey is a true vertebrate sharing most of its neural architecture with higher vertebrates, so making it possible to extrapolate results up the evolutionary chain. Second, compared to most other vertebrates its nervous system is much simpler and fortunately also unusually accessible for experimental studies. A large body of knowledge has therefore been accumulated with data, in particular about the spinal neurons involved in the swimming rhythm generation together with their connectivity. Although there is still a lot to be learned about the details, our current knowledge of this system is complete enough to make biophysically realistic simulations feasible.

In this paper we shall give an overview of the simulation studies done on the lamprey, with special emphasis on those including the full neuromechanical system. Such simulations make it possible to include influences from various types of sensory feedback. We also present a new set of results where vestibular feedback is incorporated into the model. Such feedback, via a straightforward connectivity scheme to the spinal networks, has the ability to stabilize posture during swimming.

(a) *Lamprey swimming movements*

The lamprey swims by propagating a lateral wave along most of its body from the head towards the tail with a gradually increasing amplitude. The wavelength is approximately equal to the body length, which means that about one full wave is always present along the body regardless of the swimming speed. This makes sense from a hydrodynamic point of view, because the lateral forces can cancel each other out while the longitudinal forces give a resultant thrust which propels the body forwards. The lamprey has fins but they do not seem to be of much importance during normal swimming.

The mechanical waves are generated by coordinated contractions of longitudinal muscle fibres located on both sides of the body. These contractions are in turn driven by waves of motor neuronal bursts of activity alternating between the sides and travelling down the spinal cord. Separate motor neuron pools innervate dorsally and ventrally located muscle fibres (Wallén *et al*. 1985). These pools are normally active synchronously, but open up the possibility of moving the body out of the lateral plane.

The swimming movements cover a considerable frequency range, from about 0.3 Hz up to something like 8 Hz. Finding a neuronal mechanism capable of generating coordinated output over more than one order of magnitude has been a challenge throughout the modelling work of this system. In addition to the normal forward swimming, the lamprey also displays a large repertoire of other swimming patterns. These include lateral turns, pitches and rolls, swimming with different amplitudes and even backwards swimming (Ullén *et al*. 1995). Many of these manoeuvres can be seen as modifications of the normal swimming pattern. Lateral turning, for example, is accomplished by increasing the curvature during the contractions on one side of the body.

(b) *Isolated spinal cord preparation*

The central nervous system of the lamprey is capable of generating a swimming rhythm even without sensory feedback. This is particularly evident in the isolated spinal cord preparation where the spinal cord has been dissociated from the body and is kept alive in isolation in a bath. Under such conditions, the neuronal networks in the cord are still able to produce well-coordinated motor neuronal activity with most of the characteristics of intact swimming preserved (Grillner *et al*. 1981*a*). To achieve such fictive swimming, the cord can be activated by adding, for example, glutamate, to the bath. By varying the concentration of glutamate, different swimming frequencies can be attained; in fact the entire frequency range of intact swimming can be covered.

Having the operating network fixed in a bath makes it possible to conduct investigations using experimental techniques otherwise restricted to much simpler animal models. For example, by pharmacologically manipulating the surrounding bath solution, the role of many different signalling substances and channel types has been characterized. The possibility of carrying out intracellular recordings has also enabled detailed studies to be made of the intrinsic electrical and chemical properties of individual neurons. Paired intracellular recordings have allowed precise mapping of the local synaptic connectivity among the neurons participating in the swimming rhythm generation. In all, this makes these local rhythm generating circuits among the best described vertebrate neuronal networks (Grillner *et al*. 1995).

Over longer distances along the cord, paired intracellular recording is not a feasible technique. This is simply because the chance of finding pairs of synaptically connected neurons over long distances is minimal. Therefore, our knowledge about such intersegmental connectivity is much more diffuse. One source of information is the extent of the axonal and dendritic processes (Buchanan 1982; Ohta *et al*. 1991). A technique that addresses this issue is the split bath preparation, where the bath solution around the cord is divided into chemically separate pools by introducing one or several barriers across the cord. This makes it possible to study how changes in activity in one part of the cord affect the activity in neighbouring parts (Matsushima & Grillner 1992). Such experiments show that if one part of the cord receives higher excitation, the rest of the cord will also increase its frequency but with a phase delay depending on the distance to the barrier.

2. RHYTHM-GENERATING NETWORKS IN THE SPINAL CORD

Four main types of rhythmically active neurons have been identified in the lamprey spinal cord. Motor neurons (MN) are most easily recognized because they project directly to the muscles. Small excitatory interneurons (E) are active in phase with ipsilateral motor neurons. There are also two types of inhibitory interneurons: the L-type is a large laterally located neuron with an ipsilateral projection, while the C-type has a crossed descending projection (see figure 1).

The motor neurons are active in bursts, alternating between the two sides of the cord. It is known that the motor neurons do not participate in the actual rhythm generation but merely function as output devices (Wallén & Lansner 1984). The E- and C-neurons are the primary rhythm generating neurons, possibly with the aid of L-neurons at higher frequencies. From the paired intracellular studies we know that the E-neurons have excitatory synapses to all other ipsilateral neurons, including the motor neurons. The E-type is believed to be the cause of sustained activity during a burst. The C-neurons inhibit all contralateral neurons and their primary role may therefore be to ensure that only one side is active at a time. The role of the L-neurons is less clear. These are larger neurons with inhibitory synapses to ipsilateral C-neurons. They have been thought of as the primary source of burst termination, but recent findings are pointing in the direction that other burst terminating factors may be dominant, such as accumulation of intracellular calcium and intrinsic pacemaker properties of E- and C-cells (El Manira *et al*. 1994; Fagerstedt *et al*. 1997).

(a) *Simulations of the rhythm-generating networks*

The local spinal network has been simulated using different kinds of model neurons, from simple 'connectionist'-type non-spiking neurons (Ekeberg 1993; Buchanan 1992) to biophysically realistic models describing the most important membrane currents and

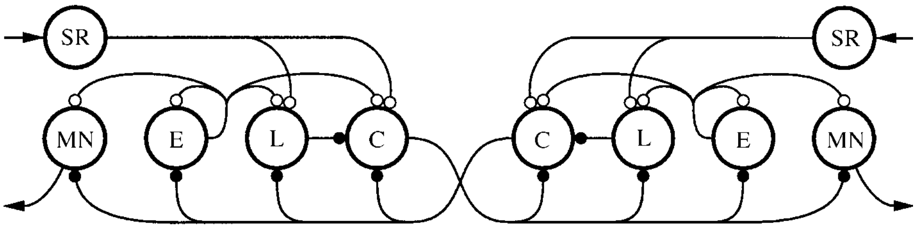

Figure 1. Local connectivity between different spinal neurons involved in the generation of the swimming rhythmicity. E, C and L refer to the different interneurons as described in the text. Motor neurons are labelled MN, while the stretch receptors are labelled SR. Open circles are excitatory synapses; filled circles are inhibitory synapses.

other relevant mechanisms (Ekeberg *et al*. 1991; Brodin *et al*. 1991). The simpler models have the advantage of being less dependent on specific parameters which are hard or even impossible to measure experimentally. The main advantage of using the biophysical models is that they make it possible to mimic a number of pharmacological conditions. Therefore, the simulation results can be compared directly with corresponding experimental data.

Simulations using a multicompartment model of each neuron were initially done with only one neuron of each type (Wallén *et al*. 1992) and later extended to populations of neurons (Hellgren *et al*. 1992). Such simulations revealed that it is not hard to generate oscillations with the proposed network, but a proper response to pharmacological treatments requires a much more precise selection of operating mechanisms. In particular, the mechanisms involved in the termination of bursts were found to be more complex than previously appreciated. The simulations have subsequently been refined by incorporating new membrane currents and other mechanisms that were found to be of importance (Tråvén *et al*. 1993; Brodin *et al*. 1991; Tegnér *et al*. 1997*a*,*b*; Tegnér & Grillner 1999; Ullström *et al*. 1998; Lansner *et al*. 1997).

(b) *Intersegmental coordination*

Since the exact connectivity between segments in the cord is not known, most models addressing intersegmental coordination are instead based on what is known about the resulting motor pattern. Many abstract models make the assumption that segmental oscillators influence each other depending on their mutual phase relations. Applying the mathematics of coupled nonlinear oscillators to such models has made it possible to make predictions about the nature of the coupling (Cohen *et al*. 1982, 1992; Kopell 1988).

A number of models where neurons are used have been based on the reasonable assumption that the connectivity pattern observed locally is also preserved between segments (Buchanan 1992; Williams 1992; Ekeberg 1993; Wadden *et al*. 1993, 1997). These simulations show that coordinated waves of activity can be generated without any extra mechanisms involved. If the rostrally located local networks receive stronger base excitation, this part of the cord will become the source of a travelling wave because of the phase differences between the subsequent oscillators along the cord. By varying the amount of such extra excitation, the spatial wavelength can be controlled independently from the temporal frequency (Ekeberg 1994).

Very few models have dealt with the separation of the dorsally and ventrally projecting motor neuron pools. This becomes important when trying to understand how movements in three dimensions, such as pitch turns and rolls, are controlled. We have put forward a 'crossed-oscillators' hypothesis (Ekeberg *et al*. 1999) which postulates that the premotor interneurons are also at least partly separated into a dorsal and ventral group. One important assumption of this hypothesis is that connections that cross the midline also primarily go ventral to dorsal or vice versa. This arrangement makes it possible to view the local oscillator as being composed of two partly separate oscillators, one left-ventral right-dorsal and one left-dorsal right-ventral. Under normal conditions, these two oscillators would be active synchronously and thus indistinguishable from their activity pattern. If, however, the brainstem input for some reason becomes asymmetrical there would be a phase difference between the two. When, for example, the left-ventral right-dorsal oscillator receives more excitation, the ventral muscles will contract before the dorsal ones when activity switches over to the left side, but the dorsal muscles will be ahead of the ventral ones when switching back. This gives rise to a rotating contraction pattern, consistent with a roll manoeuvre.

3. MODELLING MUSCLES AND MECHANICS

All simulations described so far have been aimed at mimicking the isolated spinal cord preparation. Under *in vivo* conditions, however, the rhythm generating circuitry is intimately linked to the actual movements of the body. Even if the spinal circuitry can operate without sensory feedback, it is evident that such signals do influence the rhythm. For example, simply bending the isolated cord modifies the rhythm to follow the imposed movements (Grillner *et al*. 1981*b*). This is known to be mediated by a set of stretch-sensitive neurons located in the lateral margin of the spinal cord (Viana Di Prisco *et al*. 1990). These stretch sensors synapse onto most of the neurons in the rhythm generator in a way which provides negative feedback, i.e. they tend to activate the stretched side and terminate bursts on the contracted side. If and how this influences the swimming behaviour is still not clear.

In order to address questions like these by means of computer simulation, it becomes necessary to extend the mathematical models of neurons and their interaction with models of the mechanical environment in which it operates. In the case of the lamprey, this involves models of muscle activation, body dynamics, forces from the surrounding water, and activation of the stretch receptors and other mechanosensors. This is a major undertaking and requires careful selection of adequately realistic models of each component. To be manageable, the models should not be unnecessarily complex and must allow interfacing with the other parts of the model mosaic.

(a) *Models of muscles, mechanics and hydrodynamics*

Most neuromechanical simulation studies of the lamprey have been done using a mechanical model where the body is represented as a chain of links (Ekeberg 1993; Bowtell & Williams 1991). Since the real lamprey does not have discrete vertebra, these links should only be viewed as an artificial subdivision of the body motivated by the mathematical treatment. The movements of the links can be calculated if we have reasonable estimates for the forces and torques acting upon them. There are two main sources for such forces, the muscle contractions and the counteracting forces from the surrounding water.

The muscles act on both sides of the body and in the two-dimensional (2D) version of the model this can be lumped together as a net torque at each joint between the links. For each muscle we used a pure linear elastic and viscous model. Motor neuronal drive is included in the calculations by letting the neural output level linearly adjust the spring constant of the elastic component. This simple model captures several fundamental properties of the real muscles, including the ability of the neuronal output to modify the stiffness of the mechanical system by means of co-contraction. Naturally, a lot of fine details of real lamprey muscles are left out of this model, but this may be better than using a too detailed model and be forced to arbitrarily set parameter values without proper support from experimental data. Investigations of lamprey muscle properties may enable more elaborate models to be used (Williams *et al*. 1998).

When it comes to estimating the forces exerted by the surrounding water, there are a number of different models to choose from, ranging from totally ignoring the water to a full three-dimensional (3D) fluid-dynamic calculation solving the Navier–Stokes equations. By using prescribed body kinematics the 2D Navier–Stokes solution can be calculated (Williams *et al*. 1995). This method does not, however, allow calculation of the body dynamics controlled by the neuronal output. In most of our neuromechanical simulations we have used a simpler approach, taking the corresponding static drag force as an approximate estimate of the true water force on the body (Ekeberg 1993). This model ignores all secondary effects of movements of the water, but is considerably simpler to calculate and interface with the body dynamics than any model which requires solving the Navier–Stokes equations.

(b) *Simulations of the neuro-mechanical system*

A simplified model of the spinal network was combined with the mechanical model to enable the study of the neuromechanical interaction (Ekeberg 1993). For these studies, a non-spiking leaky integrator model was used for the neurons, enabling concurrent simulation of the entire spinal network. Some parameter tuning was necessary to ensure that the strength of the muscles was appropriate to move the body fast enough to reach succeeding positions in phase with the neural oscillations. Many of the characteristic features of lamprey swimming naturally emerged out of the model such as the caudally increasing amplitude and a velocity through the water coupled to the frequency.

One striking feature of this neuromechanical model is the simplicity by which the normal motor pattern can be modified to produce other kinds of coordinated output. In fact, pure tonic input to selected parts of the simulated spinal cord results in a number of movement patterns resembling the natural behaviour of real lampreys.

By adjusting the overall tonic input to the spinal network, the speed of swimming can readily be controlled, but the current model does not cover the full frequency range of the real lamprey. It is primarily limited by the simplified neuron model used which does not, for example, include the pacemaker properties known to be of importance in the low-frequency range.

Giving extra excitatory input to the most rostral part of the cord results in a shortened wavelength (Ekeberg 1994). The resulting swimming pattern is less efficient but may, for example, be suitable for passing a narrow passage. Thus it seems as if the lamprey is not constrained to using only one built-in wavelength, but has the option of choosing whatever is suitable for the situation.

Extra input to the caudal end of the cord reverses the direction of the waves and results in backwards swimming. Alternatively, a reduced input to the rostral end has a similar effect. The real lamprey has the ability to swim backwards when necessary but, if free to choose, most often prefers to turn around instead.

Lateral turning is another behaviour which can readily be achieved within the current model. Extra input to one side of the cord results in stronger contractions on that side and a corresponding lateral turn. The strength of the asymmetrical input determines the sharpness of the turn, from a slight bend to a sharp turn.

In the 3D version of the neuromechanical model, it is also possible to mimic pitch turns by selectively exciting the dorsal or ventral parts of the network. Such input superimposes an upward or downward bend, respectively, on top of the ordinary propulsive waves.

Perhaps the most complex pattern achieved by selective tonic input is that producing a roll. With a model based on the 'crossed-oscillators' hypothesis, extra tonic input to one of the two coupled oscillators will result in a phase difference. Mechanically, this asymmetry gives rise to a narrow rotating spiral shape of the body which effectively produces the roll.

4. INCORPORATING SENSORY FEEDBACK

We shall here describe the effects of incorporating sensory feedback in the neuromechanical model. Two types of sensory feedback have been studied: lateral stretch receptor activation and vestibular feedback via brainstem projections.

(a) *Intraspinal stretch receptors and their role in swimming*

The intraspinal stretch receptors are activated when the cord itself is bent; they have a local effect on the locomotor oscillator. It is not clear what role, if any, these mechanoreceptors have during swimming. Equipped with

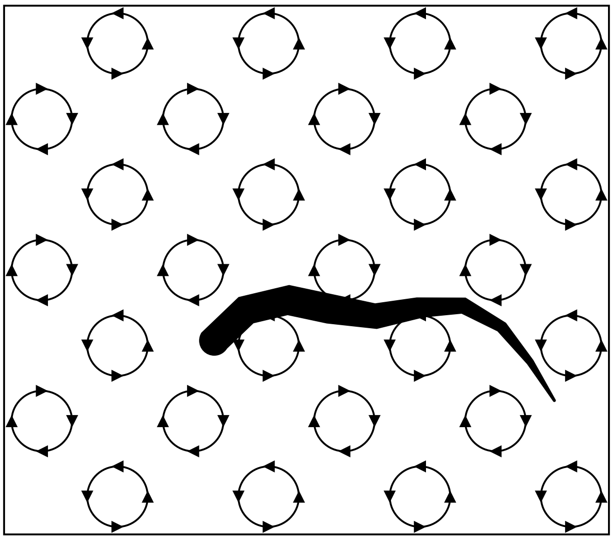

Figure 2. First version of perturbed swimming. The model lamprey experiences pseudo-random forces from a grid of simulated vortices. Incorporating the stretch receptors made the body generally stiffer, but no clear measure of improved performance could be identified. In this particular figure, the simulated lamprey has intact stretch receptor feedback.

a working neuromechanical model, it should be straightforward to address this question simply by comparing the resulting swimming pattern with and without these stretch receptors.

A linear model of the stretch receptor activation was used such that the output was proportional to the curvature of the body. A lower limit was included at zero so that no output was produced on the contracted side. It was found that adding or removing the stretch receptor feedback in the model had very little effect on the resulting movements. A slight increase in spatial wavelength could be observed when the feedback was removed, but this effect was small and well within the uncertainty of the parameters used. Considering the fact that the motor neuron output during fictive swimming resembles the intact pattern, it is not surprising that normal swimming can be produced without sensory feedback. This, however, emphasizes the question: what role do these mechanoreceptors have?

A reasonable assumption is that the sensory feedback is only necessary when the movements do not proceed as expected, so that the neuronal pattern generator has to adapt its rhythm to the actual movements. One way to test this in the model is to exert some sort of mechanical perturbation and see if the animal adapts better with sensory feedback. When choosing which kind of perturbation to use, we preferred those that would resemble disturbances that a real lamprey would be likely to encounter. Because lampreys naturally swim up rivers, unpredictable changes in water flow would be a reasonable kind of perturbation to use.

Two different variations of this theme were tested. First, the water was made to move in a pseudo-random fashion by using a mesh of vortices. The water speed and distance between vortices could be varied and its effect on the swimming model lamprey could be studied (figure 2). It turned out to be very hard to obtain any quantitative results from this experimental paradigm. Adding stretch receptor feedback had the general effect of stiffening the body, but since the model lamprey had no real goal it became hard to evaluate if it was performing better or not.

In the second kind of experiment, the model lamprey was set to swim through a region of water where the flow was directed against the direction of swimming (Ekeberg *et al*. 1995). Now one could study under which conditions the lamprey managed to swim through this barrier. The difficulty of this task could be varied by changing the width of the barrier and the speed of the water flow. This experimental paradigm was found to give clearer results. For a range of difficulties of the task the lamprey was able to penetrate the barrier when the stretch feedback was included but failed without it (figure 3). When the flowing water forced the head to the side, the stretch receptor feedback managed to counteract the diversion and keep the body straight enough to make it through. Without feedback the rostral region continued to be bent, eventually resulting in a complete change in swimming direction.

(b) *Vestibular influences on roll posture*

The lamprey has vestibular sensors in the form of bilateral labyrinths which are important for orientating the body during swimming. Visual input also influences the posture, because the lamprey tends to lean its darker dorsal side towards the light. The visual input can be seen as modifying the equilibrium point of the vestibular feedback system. Neurons in the brainstem have been found which respond to vestibular stimulation corresponding to non-equilibrium postures such as right or left tilt. It seems reasonable to assume that these neurons would act as command neurons by modifying the swimming pattern to change the posture towards equilibrium (Orlovsky *et al*. 1992; Deliagina *et al*. 1992*a*,*b*).

We have made a set of simulations where a model of the vestibular signal sets the tonic drive to the spinal network. We already know from previous modelling studies that a tonic diagonal stimulation results in a roll. The vestibular signal for left–right tilt was therefore connected likewise, such that a left tilt would induce a compensating right roll and vice versa.

As a measure of the left–right tilt we used the scalar product of a unit vector pointing right in relation to the head and a unit vector pointing upwards in the global (gravity) coordinate system. This value is zero when the body is level and becomes positive or negative for a left and right tilt, respectively, with a maximum value at 90°. When the body is upside down, this signal is again zero, but with a proper control mechanism this should be an unstable equilibrium.

Figure 4(*a*) shows the result of a suite of simulations with increasing strength of the vestibular signal. The simulations all start with the lamprey in a very unordered state: the neurons are randomly active but the body is straight with zero velocity. The stimulation eventually gives a swimming rhythm at about 5 Hz. It takes a few cycles to gain speed, during which the body rotates in an uncontrolled fashion regardless of the presence of any vestibular feedback. When the lamprey comes up to speed after about 1.3 s, the compensatory movements become effective and are capable of eventually maintaining a reasonably stable dorsal-side-up posture. Without feedback

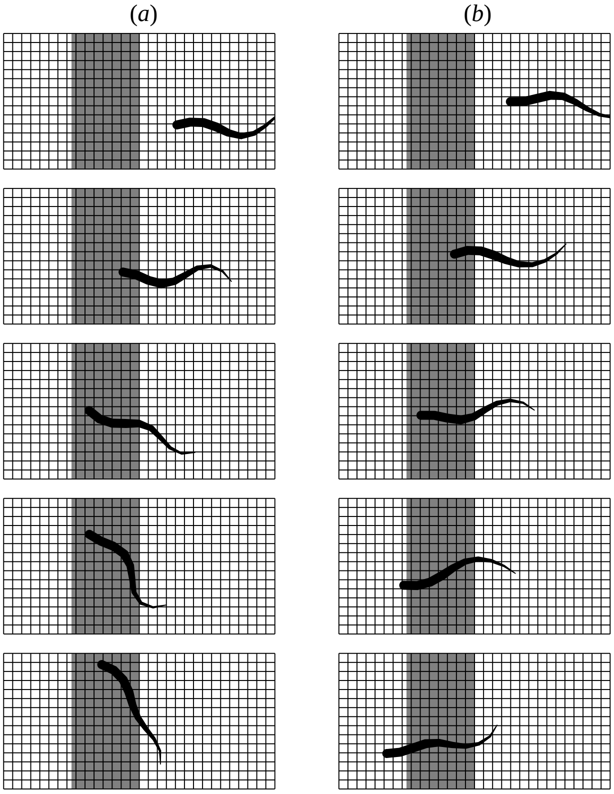

Figure 3. Second version of perturbed swimming (*a*) without feedback; (*b*) with feedback. The model lamprey is set to swim through a region (shaded area) where the water is rapidly moving towards the right. The result is shown with 250 ms between the frames. Without stretch receptor feedback, the lamprey was less successful in penetrating the barrier.

the posture still stabilizes but at a random angle, in this case almost upside down (figure 4*a*, solid curve).

With the pure position feedback there are remaining oscillations of the steady-state posture. This can be attributed to the considerable delay between arrival of the feedback in the spinal network and the compensatory change in tilt. A standard way of handing this in linear control theory is to use the derivative of the signal for faster response. This would imply that the rotational velocity should also be used as a feedback signal to gain a quicker response.

Figure 4(*b*) shows the result of gradually adding such a velocity feedback signal. The position feedback was kept at three (arbitrary units) being one of the best results from the previous experiment. Low values of the velocity feedback reduces the unwanted oscillations while larger values interfere with the position feedback so that it takes longer to reach the dorsal-side-up posture. Feedback from the rotational velocity sensors which is too strong makes the system unstable which can be seen in figure 4(*c*). The lamprey here continues to spin around its longitudinal axis for several seconds.

(c) *Vestibular control of pitch angle*

The pitch angle during swimming must also be controlled, for example in order to maintain a certain depth. We know from earlier simulations that pitch turns can be induced by a dorsoventral asymmetry in the brainstem input causing a superimposed upward or downward bend of the body. It should therefore be possible to stabilize the pitch angle by connecting a vestibular pitch signal to such brainstem neurons.

As a representative vestibular pitch signal, we used here the scalar product of a unit vector pointing forwards in relation to the head and the unit vector pointing upwards in the global coordinate system. This value is zero during level swimming, positive when the head is pointing upwards and negative when heading downwards. This value (properly scaled) was added to the ventral parts of the network and subtracted from the dorsal parts. When the head was pointing upwards, for example, this should then cause increased contractions of the ventral muscles, causing the body to bend downwards.

Figure 4(*d*) shows the result of adding such pitch control to the neuromechanical model. Because this kind of pitch control makes very little sense when the body is not in a dorsal-side-up situation, the vestibular roll control from previous section was active during this experiment. Without pitch control, the lamprey here stabilizes at a pitch angle around 15° upwards. This angle is completely dependent on the starting conditions because the lamprey in this situation has no notion of pitch. With the pitch control activated the lamprey adjusts to level swimming.

5. CONCLUSIONS

Formulating models is one way of presenting our current view of a system under study. This concept has been dominant in physics and other sciences for centuries and has more recently been adopted as a tool within biology. While our physical models have reached a level of exactness where they can often be used as a replacement for experiments (which is commonplace in engineering), biological models are often dealing with much more complex systems and the models are of a more approximate nature. One problem when using models in biology is that the systems are often built up of a large number of components which may all require different kinds of models for an adequate description. Computer simulation has become an enabling technology in that it makes it possible to make use of such complex mosaics of interacting models.

Here, we have presented the lamprey preparation and various models describing it on different levels of abstraction. For an adequate description of the generation and control of swimming movements, models are required for the spinal neuronal circuitry, the body dynamics including the surrounding water, muscle activation and mechano-sensory feedback. By using simplified models for each one of these components and their interaction, it has been possible to synthesize neuromechanical models which capture many of the fundamental features of swimming behaviour. One general observation from these studies is that some behaviours, such as turning and wavelength control, emerge without any explicit mechanisms for their execution.

Synthesized models such as these can serve several purposes apart from the pure description of our view of the system. Because all the constituent sub-models are approximate descriptions only valid within restricted operating conditions, the predictive power of the synthesized models may be limited. Perhaps more importantly,

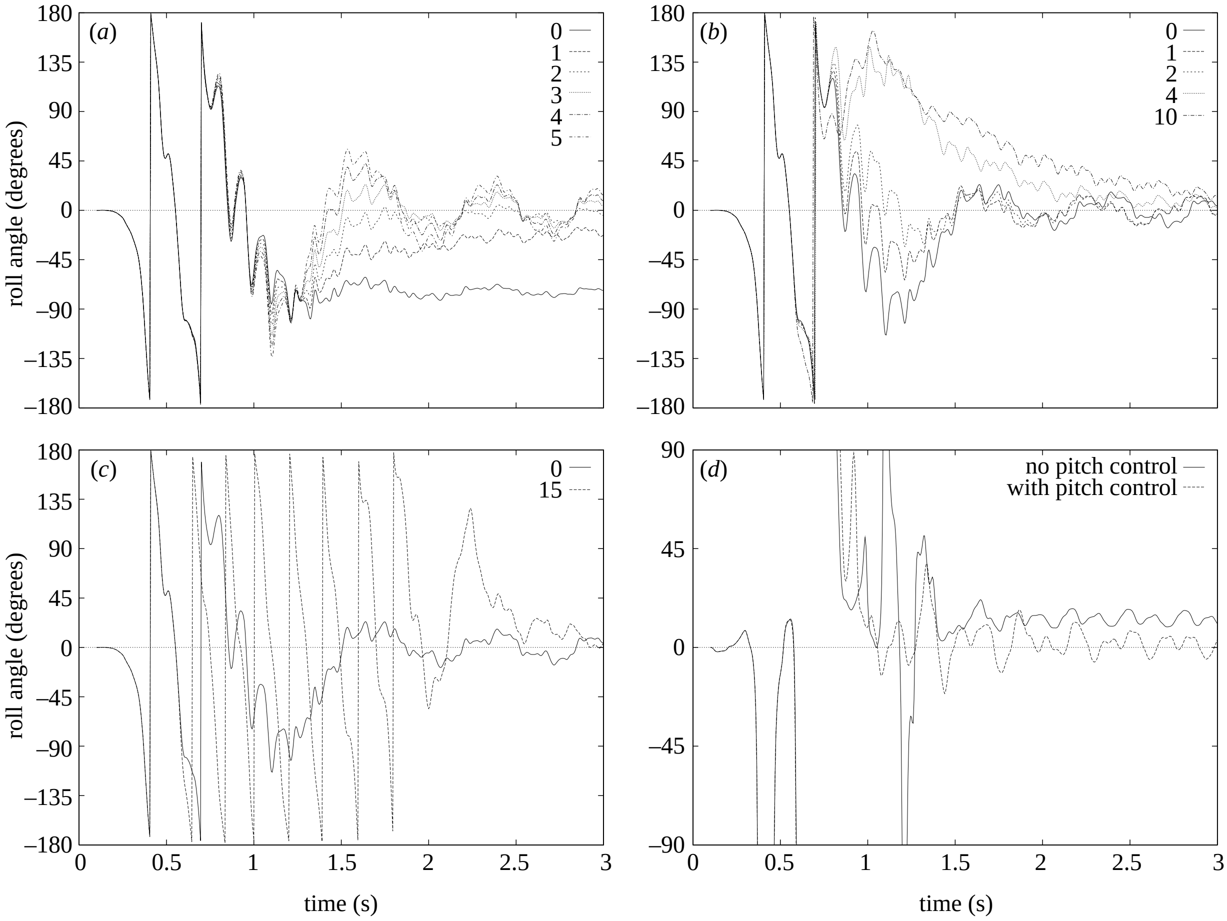

Figure 4. Stability during swimming, starting from standstill with a random neural state. The diagrams show the angle of the head (roll in *a–c*, pitch in *d*) in relation to the vertical as a function of time. (*a*) Effect of different amounts of feedback from a vestibular sensor signalling posture; the different curves correspond to different strengths of the feedback. (*b*) Effect of adding a velocity sensitive vestibular feedback; the position feedback of strength 3 (from *a*) was used with the addition of a roll-velocity dependent signal. (*c*) Increasing the velocity-dependent feedback above the values used in (*b*) results in an unstable control. (*d*) Pitch angle during initial stabilization of posture with and without pitch control through the vestibular feedback.

modelling can serve as a tool to identify which behaviours naturally emerge out of already known mechanisms, while others require more careful investigations. Here we have presented a set of experiments where a simple model of the vestibular signals is connected to the spinal rhythm generating circuitry in a straightforward manner. Simulations show that this mechanism is sufficient for stabilizing both pitch and roll posture during swimming. Whether the lamprey really uses this or some alternative mechanism remains an open question which requires further experimental evidence to be resolved.

Neuromuscular control systems generally make use of several feedback loops; this makes it necessary to include most parts of the system to make an adequate simulation model. This may be true even when the primary interest is only to study one part of the system in detail. A neuromechanical model comprising simplified sub-models can then serve as a framework for testing various more detailed models of the different components in an *in vivo* setting. The models described here were initially developed to provide the neuronal models with an adequate operating environment. They can, however, be used for testing more detailed models of other parts of the system; for example, muscle models, hydrodynamic models or models of sensor activation. Eventually, such work will increase our understanding of the parts and of the neuromechanical system as a whole.

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