Sensorimotor Integration in Lampreys and Robot I: CPG Principles

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Movement through the world requires that the environment be fully integrated and understood. Biological systems are well known to be superb at integrating sensory and motor information during the production of movement. In our daily interactions with the world we are all familiar with the seamless way in which our nervous system combines sensory and motor information. The optimization of this integration has evolved over millions of years of natural selection. We suggest that a useful strategy for designing artificial organisms, that is robots, may be to copy the methods seen in such evolved systems. In this presentation, we will present first some biological observations and then some conclusions that seem most relevant to robotic systems. Finally, we will briefly illustrate how we have used the observations to implement efficient control of a robotic limb. In the paper by Lewis et al., this proceeding, these results are presented in more detail.

In the presentation by Trevor Drew (this proceedings), the concept of a central pattern generator (CPG) is introduced. Here we summarize the basic notion. In biological systems, it is well known that the motor output from all studied rhythmic movements is generated in part by neural circuits that are capable of operating in the absence of sensory feedback or external control (Delcomyn, 1980). This holds, for example, for locomotion (Grillner ref). These neural circuits generate a rhythmic output that provides periodic forcing of the required musculature. The neural circuits while not requiring external control for their basic operation, are highly sensitive to both sensory feedback and external control from such structures as the brain. The lamprey, a primitive fish-like organism, like all other vertebrates studied to date, has a CPG that provides periodic neural activity to drive locomotion (Cohen chapt). Such periodic forcing from spinal cord circuits can be produced in the absence of sensory feedback or brain input (Cohen and Wallén, 1980). However, sensory feedback from stretch receptive inputs along the spinal cord is extremely effective in entraining the rhythm (McClellan and Sigvardt, 1988).

The CPG in the lamprey and other organisms, appears to be a distributed system of coupled non-linear oscillators (Cohen, in press) that have been modeled using dynamical systems of non-linear differential equations (Cohen et al., 1980; 1992). Each neural oscillator is considered, on the basis of some experimental evidence (Cohen and Wallén, 1980) to be a single segment of the spinal cord with its own preferred frequency. The coupling, that maintains the whole ensemble at a single frequency, is known to be bi-directional and quite strong (Mellen et al., 1995)

It is clearly evident that sensory feedback is required to provide information regarding the status and position of an organism in its environment, and the nature of that environment. Feedback provides both a cycle by cycle regulation of the rhythm and phase dependent corrections elicited by perturbations. The traditional view of sensory feedback to the spinal cord has been that the feedback provides information regarding the position of the organism in space. Appropriate to this role, the feedback may correct a CPG on a cycle by cycle basis to maintain the organism in a proper relationship to the environment (Rossignol, et. al. 1988). For example, the hip joint angle of the cat can trigger a new step cycle as the body is propelled over its respective limb on the ground (Andersson and Grillner, 1983). Pearson and is colleagues have also recently found that stretch of muscle spindles can trigger a new step cycle through contractions of appropriate muscles. In these ways, the cycle periods will accommodate changes in the velocity of the animal (Pearson, 1995; Hiebert et al., 1996). Similarly, the bending of the tail fin in dogfish or lamprey entrains the swimming so that swim cycle are appropriate lengths for the environmental conditions (Grillner and Wallén, 1982). Thus, if the body is not able to adequately bend against a strong current, this will be compensated for by a longer cycle. This type of sensory regulation is accomplished at the level of the spinal cord and requires no descending input although descending input is likely to influence the responses if present (Forssberg, 1979). All CPGs must have some stimulus that can trigger or prolong a new cycle as necessary in order to guarantee the CPG's movements are adaptive.

Another well documented role for sensory feedback is to elicit reflexive responses to environmental perturbations. This is also accomplished at the spinal level where sensory inputs are gated through the CPG during ongoing activity (Rossignol, et. al., 1988). A sensory stimulus can elicit phase dependent responses that are quite unlike the reflex responses that such stimuli would induce in the absence of CPG activity. For example, an obstacle encountered by the paw dorsum will produce an enhanced flexion during the flexion phase of the step cycle, but it will produce an enhanced extension during the extension phase (Forssberg, 1979). This guarantees that the limb is properly supported at the moment that it is raised to avoid the obstacle. The contralateral limb is also integrated with such responses. That is, the limb opposite the stimulus must be positioned to support the responsive limb before it will flex over such an obstacle (Hiebert et al., 1994). Such phase dependent responses to perturbations are very common across CPGs. For each rhythmic movement there are classes of stimuli that elicit such responses (Rossignol et al., 1988). In the case of locomotion the response requires no input from descending systems and is seen in spinal animals as well as intact animals (Forssberg, 1979).

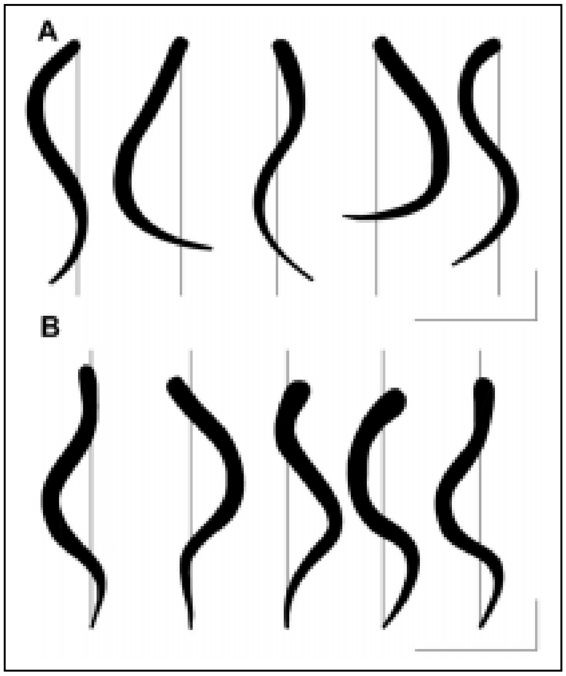
Both cycle by cycle and phase dependent corrections are required for adaptive locomotion. The interaction between the CPG and sensory feedback can be shown to be complex than these examples suggest (review, Cohen and Boothe, 1999). For example, the CPG feedforwards to the sensory receptor input to provide a filtering mechanism. This type of feedforward combined with feedback is ubiquitous throughout motor control systems.

Another role for sensory feedback has been suggested by Cruse and his colleagues (1995) . They suggest that sensory feedback can provide a gain setting mechanism. We have recently found evidence that, indeed, in the lamprey this is true (Kiemel and Cohen unpublished).

To perform these experiments, we dissect the spinal cord free from the brain, the musculature and viscera. We then induce activity in the isolated spinal cord of the lamprey by bath application of an excitatory amino acid, D-glutamate. The resultant motor output pattern is termed "fictive swimming" because it is so similar to the motor pattern seen during the normal swimming of fully intact lampreys (Wallén and Williams, 1984). Fictive swimming in lampreys is typically highly stable and periodic, and lasts continuously during the exposure to excitatory amino acids.

When one bends the spinal cord during fictive swimming, the rhythm can be entrained by intrinsic stretch receptive mechanoreceptors as noted by others (McClellan and Sigvardt, 1988). In addition to this cycle by cycle entrainment effect, Kiemel and Cohen report that the baseline frequency of the locomotor rhythm is increased following the termination of the bending, with the frequency increase decaying only over one or more cycles. This slowly decaying excitation (SDE) can be so strong as to prevent entrainment by a bending at a frequency slower than the baseline.

The bending required to elicit SDE is very small, and the effect is seen with even one cycle of bending. The SDE is also impacted by the amplitude of the bending. Given the small amplitude of bending that can induce the effect, it seems highly likely that natural swimming in the intact animal will induce just such an increase in frequency of the CPG. *Thus, it appears that the gain of the system is increased by the movement of the animal.* Moreover, the gain will be increased whenever the animal begins movement. This type of slowly decaying excitation seen in lamprey seems to be an example of positive feedback. That is, the CPG generates movement that in turn causes the CPG to go faster. This phenomenon would also appear to guarantee that movement persists until actively terminated. There is also the implication that the gain remains less than 1, as the system is highly stable even with the bending (Prochazka et al., 1997).

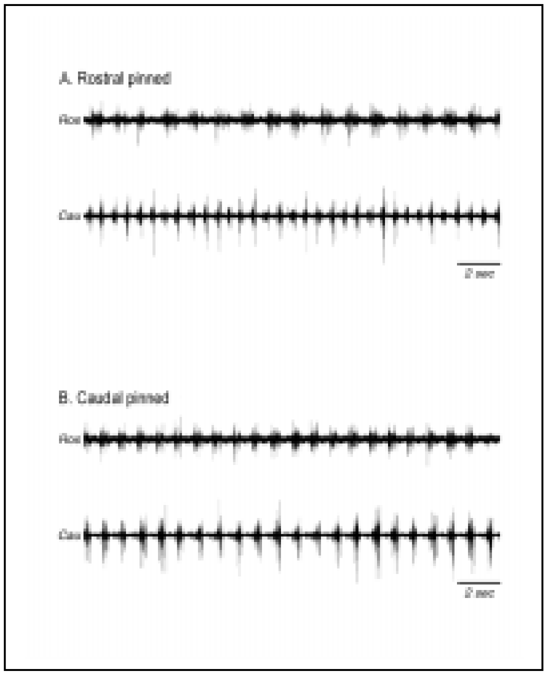


We have recently begun to use a semi-reduced lamprey preparation. This preparation is essentially the lamprey body in the absence of the brain or tail, with the spinal cord exposed to the bathing solution. Thus, the body is induced to swim with the mechanical properties and sensory feedback almost intact, and uninfluenced by the brain. This preparation, therefore, allows us to gain some insight into the roles of both mechanical aspects of the body, and the sensory feedback when interacting with the CPG, but without the brain to filter it.

In this reduced preparation, we show that the increased frequency caused by movement is indeed a factor when the body is driven by the CPG. In figure 1, above, we present two sets of images to illustrate this. In the upper set of images, the body is loosely pinned at the rostral or head end of the body. In the lower set of images, the body is pinned at the caudal or tail end. The calibration bars indicate one centimeter (vertical bar) and 0.33 seconds for the head end pinned, and 0.66 seconds for the tail end pinned. (horizontal bar). Note, that with the head pinned there is more movement at the free end of the body, than there is when the tail is pinned. Presumably, this is because the tail is thinner and provides less damping than does the head end. It seems reasonable to propose that the greater degree of bending at the tail end will create a greater degree of frequency increase than will the lesser movement of the head end.

Indeed, we find that the mechanical properties of the body apparently do have an impact on the degree of this increased frequency. Thus, the increased amplitude of tail end movement, while expected, causes an unexpected alteration in the motor pattern as the movement interacts with the spinal mechanism for increasing the frequency of swimming. What we see is that the head-end segments are not as speeded up as the tail-end segments. If we weaken the intersegmental coupling among the segments with some acute lesions, we see, with the head end pinned, that the alterations in the frequency in the tail end segments can be so great that it causes the head and tail segments to lose their 1:1 phase locking. This is shown in figure 2, below. The upper traces are with the head end pinned; the lower traces are with the tail end pinned. Notice, the head end pinned produces bursting that is 2:1, with the tail twice the frequency of the head. What impact this would have on the intact animal is not yet clear, but it seems likely to have an impact on the phase lags between segments (cf. Cohen et al., 1982).

From the insights into rhythmic movements described above, we take several principles that will be applied to the control of a robot limb. The first is that locomotion is best driven by a periodic feedforward forcing mechanism that is similar to that of a non-linear



oscillator. Furthermore, sensory feedback will be essential in stabilizing the pattern on a cycle by cycle basis, and finally, that there will be a gain control initiated by movement that will cause the pattern to be increased in its frequency and requiring an active termination mechanism. All of these factors appear to improve the control of a robot limb. These principles are demonstrated in the accompanying contribution by Lewis et al., this proceeding. Another example of similar use of these principles successfully controlling a limb is found the work of Kimura and his colleagues (this proceeding).

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