Partly Shared Spinal Cord Networks for Locomotion and Scratching

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Synopsis Animals produce a variety of behaviors using a limited number of muscles and motor neurons. Rhythmic behaviors are often generated in basic form by networks of neurons within the central nervous system, or central pattern generators (CPGs). It is known from several invertebrates that different rhythmic behaviors involving the same muscles and motor neurons can be generated by a single CPG, multiple separate CPGs, or partly overlapping CPGs. Much less is known about how vertebrates generate multiple, rhythmic behaviors involving the same muscles. The spinal cord of limbed vertebrates contains CPGs for locomotion and multiple forms of scratching. We investigated the extent of sharing of CPGs for hind limb locomotion and for scratching. We used the spinal cord of adult red-eared turtles. Animals were immobilized to remove movement-related sensory feedback and were spinaly transected to remove input from the brain. We took two approaches. First, we monitored individual spinal cord interneurons (i.e., neurons that are in between sensory neurons and motor neurons) during generation of each kind of rhythmic output of motor neurons (i.e., each motor pattern). Many spinal cord interneurons were rhythmically activated during the motor patterns for forward swimming and all three forms of scratching. Some of these scratch/swim interneurons had physiological and morphological properties consistent with their playing a role in the generation of motor patterns for all of these rhythmic behaviors. Other spinal cord interneurons, however, were rhythmically activated during scratching motor patterns but inhibited during swimming motor patterns. Thus, locomotion and scratching may be generated by partly shared spinal cord CPGs. Second, we delivered swim-evoking and scratch-evoking stimuli simultaneously and monitored the resulting motor patterns. Simultaneous stimulation could cause interactions of scratch inputs with subthreshold swim inputs to produce normal swimming, acceleration of the swimming rhythm, scratch-swim hybrid cycles, or complete cessation of the rhythm. The type of effect obtained depended on the level of swim-evoking stimulation. These effects suggest that swim-evoking and scratch-evoking inputs can interact strongly in the spinal cord to modify the rhythm and pattern of motor output. Collectively, the single-neuron recordings and the results of simultaneous stimulation suggest that important elements of the generation of rhythms and patterns are shared between locomotion and scratching in limbed vertebrates.

Introduction

Animals produce a wide variety of behaviors using a limited number of neurons and muscles. Thus, the same muscles and motor neurons are used for many different behaviors. Networks of neurons within the central nervous system, or central pattern generators (CPGs), can produce the basic patterns of motor neuron activity underlying rhythmic behaviors such as locomotion, breathing, chewing, and scratching (Marder and Calabrese 1996; Marder and Bucher 2001). Are there separate CPGs for different rhythmic behaviors that involve the same motor neurons and muscles or does a single CPG produce all types of rhythmic activity in a given set of motor neurons and muscles?

This question has been addressed in the greatest depth in several invertebrate model systems. In some of these systems, a single CPG can be reorganized or reconfigured to produce multiple, distinct kinds of rhythmic activity (Getting and Dekin 1985; Weimann et al. 1991; Dickinson and Moulins 1992; Pearson 1993; Morton and Chiel 1994; Weimann...
Locomotor or breathing movements, because each breathing may produce distinct forms of mammalian behaviors involving the same motor neurons and muscles (Heitler 1985; Ramírez and Pearson 1988; Hennig 1990; Pearson 1993; Morton and Chiel 1994; Marder and Calabrese 1996).

The vertebrate spinal cord is able to produce several kinds of rhythmic behaviors, including multiple forms of locomotion and scratching. It is much more difficult to identify CPG components in vertebrates (and even in larger invertebrate nervous systems), due to the large number of neurons in each network, as well as technical challenges, such as the difficulty of performing paired intracellular recordings between synaptically coupled neurons. Traditional criteria for membership in a CPG include the ability to reset or stop rhythmic output by depolarizing or hyperpolarizing a given neuron (Marder and Calabrese 1996). Such criteria are arguably unworkable for larger CPGs, however, because no single neuron has such a large effect on motor output.

Recordings from individual vertebrate neurons, however, can still provide strong circumstantial evidence that a neuron is a member of a CPG. Such evidence could include (1) that the neuron has rhythmic activity that is phase-locked to the activity of the motor neurons, (2) that the neuron has synaptic connections consistent with it having an effect on the activity of the motor neurons, (3) that the neuron has synaptic and/or intrinsic properties consistent with a role in rhythmogenesis, and (4) that activation or inhibition of all neurons of this type alters the rhythm fundamentally.

This kind of approach has been used for a few vertebrate systems to assess whether the same or different CPGs produce distinct kinds of rhythmic behaviors involving a given set of muscles. Thus, the central networks for two kinds of axial locomotion, forward swimming and struggling, are largely but not entirely shared in tadpoles and larval zebrafish (Soffe 1993; Ritter et al. 2001; Li et al. 2007; Liao and Fetch 2008; Satou et al. 2009; Berkowitz et al. 2010). Also, the same brainstem CPG (Lieske et al. 2000) or largely overlapping CPGs (Shiba et al. 2007) may produce distinct forms of mammalian breathing.

Limb movements are more complex than axial locomotor or breathing movements, because each multi-jointed limb adds several degrees of freedom to each rhythmic behavior. Yet it is crucial to understand the neural control of rhythmic movements of limbs, both to elucidate the mechanisms that produce multiple forms of locomotion in limbed animals and potentially to address important clinical issues, such as how to improve the lives of patients with injuries to the spinal cord. Few studies, however, have addressed whether distinct types of rhythmic limb movements in vertebrates are produced by the same or different CPGs.

We used the adult turtle to assess the extent to which distinct kinds of limb movements are produced by the same or different spinal cord CPGs. The turtle spinal cord can generate the motor patterns underlying multiple forms of locomotion and scratching, even without input from the brain or movement-related sensory feedback (Stein 2005). The three forms of hind limb scratching, rostral, pocket, and caudal, can each be evoked by gentle rubbing within a zone on the body surface (Morton et al. 1985; Robertson et al. 1985). Hind limb forward swimming can be evoked by electrical stimulation of descending axons in the midbody contralateral lateral funiculus (Lennard and Stein 1977; Juranek and Currie 2000). These four kinds of rhythmic motor patterns for each hind limb are reliably distinguished by the relative phases of knee extensor muscle or motor nerve activity within the cycle of hip flexor/hip extensor alternation, combined with the relative amplitudes of muscle or nerve activities (Fig. 1). In addition, physiological experiments on turtles take advantage of their remarkable tolerance to hypoxia, which allows reduced preparations to remain healthy for much longer than is the case for comparable mammalian preparations (Hounsgaard and Nicholson 1990; Lutz and Milton 2004).

We have taken two approaches to assess the extent to which the CPGs for forward swimming and the three forms of scratching are shared (Fig. 1). For several years, we have recorded from individual spinal cord interneurons while generating each kind of hind limb motor pattern in immobilized animals. Using this approach, we have obtained some, but certainly not all, of the kinds of circumstantial evidence required to assess adequately the membership of each neuron (or each type of neuron) in one or multiple CPGs (Berkowitz 2010). Recently, we have also taken a second approach, in which we deliver two stimuli simultaneously, each of which evokes one kind of rhythmic behavior of the hind limb on its own, and analyze the resulting motor patterns for clues to the extent of sharing between the networks...

**Individual spinal interneuron recordings**

We initially used single-neuron recordings to address whether the same set or separate sets of spinal cord interneurons are activated during the motor patterns for the three forms of scratching, in immobilized and spinal transected animals (Fig. 1). The vast majority of spinal interneurons that were rhythmically activated during one form of ipsilateral hind limb scratching were rhythmically activated during all three forms of ipsilateral scratching; many were rhythmically activated during contralateral hind limb scratching as well (Berkowitz and Stein 1994b; Berkowitz 2001b). Nonetheless, these neurons typically showed some selectivity, being broadly tuned to one region of the body surface and progressively less strongly activated at greater distances from this region (Berkowitz and Stein 1994a; Berkowitz 2001a). Rhythmically active interneurons typically maintained a particular preferred phase of firing within the hip activity cycle for all three forms of scratching (Berkowitz and Stein 1994b; Berkowitz 2001b), although there were exceptions to this rule (Berkowitz 2001b). Intracellular recordings and injections of dye showed that at least some of these rhythmic interneurons had axon terminal arborizations in the ventral horn in the hind limb enlargement of the spinal cord, as would be expected if these neurons affect motor neurons of hind limb muscles relatively directly (Berkowitz 2005). These data provide some of the kinds of circumstantial evidence required to show that CPGs for the three forms of scratching are largely shared.

Are the CPGs for scratching and locomotion shared or separate? An early hypothesis, based on pioneering extracellular recordings from individual cat spinal interneurons during scratching motor patterns and spontaneous slow oscillations, was that one CPG produces both scratching and locomotion (Berkinblit et al. 1978; Gelfand et al. 1988). In addition, studies of either locomotor (Feldman and Orlovsky 1975; McCrea et al. 1980; Pratt and...
and reach high firing rates during each depolarizing phase. Their very rhythmic firing makes T neurons good candidates to be CPG neurons and/or last-order premotor interneurons. Their high peak firing rates also make them good candidates to be premotor interneurons, which might be expected to have high firing rates and thereby depolarize each large motor neuron beyond its action potential threshold. At least some T neurons have axon terminal arborizations in the ventral horn of the spinal cord hind limb enlargement (Berkowitz et al. 2006). All T neurons studied thus far were activated during both scratching and forward swimming motor patterns (Fig. 3), while some non-T neurons were activated during scratching but not swimming (Berkowitz 2008). This provides some circumstantial evidence that T neurons are CPG members and/or premotor interneurons for both scratching and locomotion.

In addition to T neurons and other scratch/swim interneurons, a substantial minority of extracellularly recorded spinal interneurons were rhythmically activated during scratching but not activated at all during forward swimming motor patterns (Berkowitz 2002). Intracellular recordings showed that at least some of these scratch-specialized interneurons received hyperpolarizing inhibition throughout the swimming motor pattern (Fig. 4) (Berkowitz 2008). Even if the interneurons we happened to record were not members of the scratching CPG, this demonstrates that spinal interneurons exist that receive rhythmic input (directly or indirectly) from members of a scratching CPG but not from members of the forward swimming CPG. Therefore, there must also be important control elements that are not shared between locomotion and scratching. Thus, it is still not clear to what extent locomotor and scratching CPGs are shared. Interestingly, we have not yet encountered cells that were strongly activated during swimming and not activated during scratching, though, of course, this does not mean they do not exist. One possibility is that there is asymmetry in specialization of cells for different behaviors because these behaviors evolved during different periods (Berkowitz 2002), as has also been suggested for leech crawling and swimming (Briggman and Kristan 2006).

In addition, we have found spinal interneurons that are activated during limb withdrawal (flexion reflex) motor patterns but inhibited during both swimming and scratching motor patterns, including during the hip flexor phase, demonstrating that there is at least one other kind of behaviorally specialized spinal interneuron (Berkowitz 2007). While we continue to acquire additional kinds of evidence using...
single-interneuron recordings, we are also taking an additional approach to the question of shared versus separate CPGs.

**Dual stimulation**

A potentially powerful, but less common approach to assess whether CPGs are separate or shared is to deliver simultaneously two stimuli, each of which on its own evokes one of two distinct rhythmic motor patterns (Figs. 1 and 5). If the two interneuronal CPGs are entirely separate and have convergent inputs to a common set of motor neurons, then simultaneous activation of these two CPGs should produce a superposition of the two rhythms in each of these motor neurons. This has been experimentally demonstrated for flight and walking rhythms in locusts (Ramirez and Pearson 1988) and for flight and stridulation rhythms in crickets (Hennig 1990). If the two CPGs are separate, yet have either one-way or mutual inhibitory connections between them, then one CPG may simply

![Diagram of interneuron recordings](https://example.com/diagram.png)
override the other when the two are activated simultaneously; in this case, one of the two rhythms, unchanged, will be recorded from motor neurons. This seems to be the case, for example, for two forms of swimmeret beating in crayfish (Heitler 1985), escape swimming versus feeding in the mollusk Pleurobranchaea (Jing and Gillette 1995, 2000), and feeding versus swimming or crawling in leeches (Misell et al. 1998).

Two rhythmic behaviors involving the same muscles may be biomechanically compatible if they have very different cycle periods, so that several cycles of one behavior can occur during one phase of one cycle of the other rhythmic behavior. In such cases, the two CPGs might be largely separate, with some inhibitory and/or excitatory connections between them, or might be largely shared. In such a case, dual or intermediate stimulation might produce...
two simultaneous and coordinated rhythms in motor neurons. This appears to occur, for example, for scratching and hopping in rabbits (Brown 1911), walking and paw-shaking in cats (Carter and Smith 1986a, 1986b), and crawling and swimming with intermediate saline levels in leeches (Esch et al. 2002). In these examples, sensory feedback was available and might account for some or all of the coordination between rhythms. Such coordination between rhythms with different cycle periods has also been seen in vitro, however, including between gastronomic and pyloric rhythms in crabs (Weimann et al. 1991; Marder and Weimann 1992; Bartos and Nusbaum 1997; Bartos et al. 1999) and between feeding and locomotor rhythms in the mollusk _Lymnaea_ (McCrohan and Kyriakides 1992). In these cases, the coordination must be produced by shared CPG components or central interactions between two CPGs.

For two rhythmic behaviors involving the same muscles and having similar cycle periods,
simultaneous delivery of stimuli that evoke each rhythmic behavior might produce switching of motor patterns from cycle to cycle. This occurs during stimulation of a single site within a transition zone between two forms of scratching (Mortin et al. 1985; Robertson et al. 1985), as well as during dual stimulation in a rostral scratch zone and a caudal scratch zone (Stein et al. 1986). We have recently found that scratch/swim dual stimulation can also evoke switches between a scratch and a swim motor pattern (Fig. 5D and Table 1) (Hao et al. 2010, 2011). The occurrence of switches suggests that there either are strong interactions, probably inhibitory, between components of two separate CPGs, or cycle-by-cycle reconfiguration of a single CPG. The speed of these switches back and forth, however, argues against neuromodulation as the sole causal mechanism of such a reconfiguration.

It has been suggested that there may be separate spinal cord circuitry for generating the basic rhythm or oscillation (i.e., rhythm generation) and for shaping the relative timing of activity of each motor neuron pool (i.e., pattern generation) (McCrea and Rybak 2008). Whether or not there is such a separation, if the CPGs for two rhythmic behaviors have important common components or strong interactions between individual components (which may amount to the same thing, the difference being primarily semantic), then dual stimulation may cause fundamental changes to generation of the pattern and/or the rhythm, so that the dual-stimulation pattern is distinct from either motor pattern alone and from a superposition of the two. Such fundamental changes could involve modifications of the motor pattern within each cycle, which can be termed a hybrid motor pattern (Mortin et al. 1985), and/or modifications of the timing of a series of consecutive cycles, which can involve a reset or an acceleration of the rhythm. Hybrid motor patterns suggest sharing of pattern-generating components; resets and acceleration suggest sharing of rhythm-generating components.

One kind of hybrid motor pattern occurs when two rhythmic behaviors have a similar motor synergy, allowing biomechanical compatibility. In such cases, a single CPG might be able to generate both individual behaviors, as well as hybrids of the two. An example of this may be forward swimming and rostral scratching in turtles (Lennard and Stein 1977; Mortin et al. 1985; Robertson et al. 1985; Juranek and Currie 2000). In both of these motor patterns, the knee extensor muscle or nerve is active during the latter portion of hip flexor activity (Fig. 1). Thus, forward swimming and rostral scratching share a common knee-hip synergy. These two motor patterns differ, however, in the relative amplitudes of activity of muscles and nerves. Hip extension is the power stroke for forward swimming, but hip flexion is the power stroke for rostral scratching. When rostral scratch/forward swim dual stimulation was delivered in a moving animal, a hybrid rhythm was generated in which each cycle differed from the normal cycle of both individual movements (Earhart and Stein 2000). In each cycle, knee extension occurred in the latter portion of hip flexor activity and both the hip extensor and the hip flexor were strongly activated, meeting the goals of both forward swimming and rostral scratching in each cycle. The tight

<table>
<thead>
<tr>
<th>Level of swim stimulation</th>
<th>Resulting Motor Pattern(s)</th>
<th>Swim stimulus alone</th>
<th>Scratch + swim stimulation</th>
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<tr>
<td>Very weak</td>
<td>No response or</td>
<td>Normal scratching</td>
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<td></td>
<td>Tonic hip extensor activity</td>
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<td>Stronger, but subthreshold</td>
<td>No response or</td>
<td>Normal swimming</td>
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<td>Tonic hip extensor activity</td>
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<tr>
<td>Near threshold</td>
<td>Weak swimming</td>
<td>Scratch-swim switches or</td>
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<td>Intermediate motor patterns or</td>
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<td>Hip flexor deletions or</td>
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<td>Rhythm cessation</td>
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<tr>
<td>Suprathreshold</td>
<td>Normal swimming</td>
<td>Faster swimming</td>
<td></td>
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<tr>
<td>Overly strong</td>
<td>Tonic hip extensor activity</td>
<td>Normal swimming</td>
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coordination between these two kinds of rhythmic movements could be due to coordinating or common CPG components, but it could also be due to movement-related sensory feedback.

Another kind of hybrid motor pattern can be evoked even for two motor patterns that have substantially different motor synergies. In these cases, double bursts or prolonged bursts of one motor nerve can occur within a single cycle of other motor nerves, with each period of bursting achieving the goal of one of the two motor patterns. This can occur, for example, with a single stimulus in the transition zone between two forms of scratching in turtles (Robertson et al. 1985) or with simultaneous stimulation in a rostral scratch zone and a caudal scratch zone (Stein et al. 1986). During each cycle of alternation of hip flexor and hip extensor, the knee extensor is active in the phase appropriate for one form of scratching as well as the phase appropriate for the other form of scratching, thus achieving the goals of both motor patterns in each cycle. We have also recently evoked such hybrids of forward swimming with pocket scratching and caudal scratching motor patterns during scratch/swim dual stimulation in immobilized animals; in these cases, the knee extensor motor nerve was active in the phases appropriate for both behaviors on several consecutive cycles (Table 1) (Nguyen and Berkowitz 2007; Hao and Berkowitz 2008; Hao et al. 2010, 2011). These findings also suggest sharing of elements of rhythm and of pattern generation between locomotion and scratching.

Sharing or tight coordination of rhythm generation may be demonstrated when activation of one motor pattern temporarily overrides the ongoing rhythm of the other motor pattern, and also permanently resets the timing of the ongoing rhythm. This has been shown, for example, for escape and swimming in goldfish (Svoboda and Fetcho 1996), for forward swimming and rostral scratching in turtles (Juranek and Currie 2000), and for the flexion reflex and each form of scratching in turtles (Currie and Stein 1989).

A related effect that we have recently obtained was that when stimulation for forward swimming was combined with stimulation for any of the three forms of scratching, the rhythmic motor pattern during dual stimulation was often accelerated (Fig. 5E and Table 1) (Hao and Berkowitz 2008; Hao et al. 2010, 2011). The resulting motor patterns were most often swim-like, based on the relative phases and amplitudes of the motor nerve bursts. The resulting swim cycles, however, often had a substantially reduced cycle period (i.e., they occurred at a higher rate). Also, a swim-inducing stimulus that was too weak to evoke a swim by itself (because the amplitude or the rate of the electrical pulses was reduced) could evoke a normal forward swim when it was combined with a normal scratch stimulus (Fig. 5B and Table 1) (Nguyen and Berkowitz 2007; Hao and Berkowitz 2008; Hao et al. 2010, 2011).

The ability of scratch stimulation to combine with subthreshold swim stimulation to produce a normal swim motor pattern and to combine with suprathreshold swim stimulation to accelerate a swim motor pattern suggests that swim-inducing and scratch-inducing excitatory inputs converge at, or prior to, generation of the swim rhythm. In other words, there may be summation of excitation from scratch-evoking and swim-evoking inputs. Thus, the increased total excitation may bring a subthreshold swim stimulus above threshold and may accelerate the rhythm evoked by a suprathreshold swim stimulus. An analogous example from a small nervous system with identified neurons is that two neurons that each individually evoke a rhythmic feeding motor pattern in the mollusk Lymnaea evoke a much faster feeding rhythm when they are depolarized simultaneously (McCrohan and Kyriakides 1992). Analogous convergence of scratch-inducing and swim-inducing inputs prior to generation of a rhythm in turtles would suggest that rhythm-generating mechanisms are largely shared by forward swimming and each form of scratching. The fact that this was seen when swim stimulation was combined with pocket scratch or caudal scratch stimulation suggests that rhythm-generating mechanisms may be shared even when the two motor synergies differ substantially. A related finding provides evidence of convergence of excitatory inputs for two forms of scratching. Currie and Stein delivered a stimulus for pocket scratching following the end of another scratching motor pattern (Currie and Stein 1988). Delivery of a subthreshold pocket scratch-inducing stimulus following a rostral scratch-pocket scratch blend evoked a pocket scratch; delivery of a suprathreshold pocket scratch-inducing stimulus following a rostral scratch re-initiated the rostral scratch (Currie and Stein 1988).

Forward swimming shares a knee-hip synergy with rostral scratching, but not with pocket scratching or caudal scratching (Lennard and Stein 1977; Robertson et al. 1985; Juranek and Currie 2000). Thus, it might be that forward swimming movements would be biomechanically incompatible with pocket scratching or caudal scratching movements and that movement-related sensory feedback would
mediate the shutting down of one motor pattern when the other is strongly activated in a moving animal. We made our observations of fundamental changes in generation of pattern and rhythm in immobilized animals, which may have allowed us to uncover some CPG interactions that would not have been evident in moving animals.

A second, although less common result of scratch/swim dual stimulation was that the rhythm completely ceased during the period of dual stimulation, then immediately reappeared after one of the two stimuli was discontinued (Fig. 5C and Table 1) (Hao and Berkowitz 2008; Hao et al. 2010; Hao et al. 2011). This result suggests that there may also be incompatibilities in the central networks for swimming and scratching, which might include strong mutual inhibition between certain components of the two networks. The fact that the rhythm ceased, rather than one rhythm simply shutting down the other, suggests that common components of rhythm-generating mechanisms were affected in incompatible ways by the two stimuli.

In cases in which the rhythm ceased, prior to complete cessation there were sometimes cycles of rhythmic hip extensor activity, with no intervening hip flexor activity (i.e., hip flexor deletions; Fig. 5C) (Hao and Berkowitz 2008; Hao et al. 2010, 2011). Hip extensor deletions are commonly observed during rostral scratching (Stein and Grossman 1980; Stein et al. 1982; Robertson et al. 1985; Mortin and Stein 1989; Stein and Daniels-McQueen 2002), but hip flexor deletions do not normally occur during scratching or swimming. The fact that the rhythm ceased completely just after these hip flexor deletions suggests that either (1) rhythm generation and pattern generation are tightly coupled in scratch and swim central networks or (2) rhythm generation actually continued in a rhythmogenic module, but was not evident in any of the motor nerves we monitored. The former explanation seems more likely, as we monitored several motor nerves to knee and hip muscles (but see Rybak et al. 2006).

Given the variety of effects of dual stimulation, we wondered what might determine which effect we obtained. We found that by systematically increasing the frequency of swim-inducing electrical pulses, while keeping the scratch-inducing mechanical stimulation approximately constant, we could evoke several of these different effects reliably (Fig. 5 and Table 1) (Nguyen and Berkowitz 2007; Hao and Berkowitz 2008; Hao et al. 2010, 2011). At the lowest swim stimulation pulse frequency, dual stimulation evoked scratching motor patterns (Fig. 5A). At slightly higher pulse frequencies, but still subthreshold to evoke a swim, dual stimulation evoked normal swimming motor patterns (Fig. 5B). At slightly higher pulse frequencies, dual stimulation could cause either cessation of the rhythm (Fig. 5C) or switches between swimming and scratching motor patterns (Fig. 5D). At still higher pulse frequencies, dual stimulation generated a faster swim rhythm (Fig. 5E). These results suggest that different levels of swim stimulation differentially activate different CPG components or different kinds of interactions between scratch and swim CPG components, which might include both excitatory and inhibitory interactions.

Collectively, the observations of hybrid motor patterns, summation that brings subthreshold swim stimulation to threshold, summation that causes rhythm acceleration, and cessation of the rhythm during dual scratch/swim stimulation suggest that locomotion and scratching CPGs share important components and/or have strong interactions between them. Combined with the evidence from single-neuron recordings that many, but not all, rhythmic spinal interneurons are activated during both forward swimming and scratching motor patterns, these findings suggest that the central networks that generate locomotion and scratching include both shared and specialized components. More research will be required to elucidate the specific roles played by each shared and each specialized component.

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References


