Spinal Cord Coordination of Hindlimb Movements in the Turtle: Interlimb Temporal Relationships During Bilateral Scratching and Swimming

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Field, Edelle C. and Paul S. G. Stein. Spinal cord coordination of hindlimb movements in the turtle: interlimb temporal relationships during bilateral scratching and swimming. J. Neurophysiol. 78: 1404–1413, 1997. Hindlimb interlimb coordination was examined in turtles during symmetrical “same-form” behaviors in which both hindlimbs utilized the same movement strategy (“form”) and during asymmetric “mixed-form” behaviors in which the form exhibited by one hindlimb differed from that of its contralateral partner. In spinal turtles, three forms of scratching were examined: rostral, pocket, and caudal. Bilateral symmetrical same-form scratching was studied for each of the forms. Asymmetric mixed-form scratching (rostral scratching of a hindlimb and pocket scratching of the other hindlimb) was also examined. In intact turtles, two forms of swimming were examined: forward swimming and back-paddling. The symmetrical behavior of bilateral forward same-form swimming and the asymmetric behavior of turning mixed-form swimming (forward swimming of 1 hindlimb and back-paddling of the other hindlimb) were studied. For all behaviors examined, most episodes displayed absolute or 1:1 coordination; in this type of coordination, during each movement cycle that began and ended with the onset of ipsilateral hip flexion, there was a single onset of contralateral hip flexion. For most of these episodes there was out-of-phase coordination between hip movements; the onset of contralateral hip flexion occurred near the onset of ipsilateral hip extension midway through the ipsilateral movement cycle. Bilateral caudal/caudal same-form scratching displayed out-of-phase 1:1 coordination during some episodes and in-phase 1:1 coordination during other episodes. During in-phase coordination, the onset of contralateral hip flexion occurred near the onset of ipsilateral hip flexion close to the start of the ipsilateral movement cycle. In a few cases of bilateral same-form scratching there were episodes of relative or 2:1 coordination; in this type of coordination, during each movement cycle of the slowly moving limb that began and ended with ipsilateral hip flexion, there were two distinct occurrences of the onset of contralateral hip flexion. The observation that out-of-phase movements of the hip occurred during symmetrical as well as asymmetric behaviors is consistent with the hypothesis that timing signals related to hip movement play a major role in interlimb phase control. The neural mechanisms responsible for interlimb phase control are not well understood in vertebrates. The present demonstration of bilateral scratching in spinal turtles suggests that this preparation may be suitable for additional experiments to examine mechanisms of vertebrate interlimb phase control.

INTRODUCTION

Limbed vertebrates coordinate their limb movements during rhythmic behaviors. During out-of-phase movements, e.g., walking and trotting, a limb’s movements alternate with those of its contralateral partner; during in-phase movements, e.g., quadrupedal galloping, the movements of a pair of limbs occur nearly at the same time (Grillner 1981; Hildebrand 1976). The hindlimbs of marine turtles, for example, usually move in phase during forward swimming, but can move out of phase during slow swimming (Davenport et al. 1984); the hindlimbs of freshwater red-eared turtles move out of phase during forward swimming, but can move in phase during the initial backward-directed portion of escape swimming (Davenport et al. 1984; Zug 1971). Some out-of-phase behaviors, such as stepping in humans, begin with an in-phase movement (bilaterally symmetrical dorsiflexion of the ankles) preceding the out-of-phase movements characteristic of the steady state (Herman et al. 1973). These studies establish that interlimb phase is controlled according to the specific demands of the movement strategy (Stein 1976).

Most studies of rhythmic limb movements have focused on symmetrical same-form behaviors in which left and right limbs perform the same movement pattern; these symmetrical patterns may be in phase (hopping) or out of phase (stepping). There are cases of asymmetric mixed-form behaviors, however, in which left and right limbs perform different movements. During bipedal galloping in humans, one leg displays walking and the other leg displays running or leaping behavior (Whitall 1989; Whitall and Caldwell 1992). During turning behavior in insects, ipsilateral limbs display forward stepping while contralateral limbs display backward stepping (Graham 1985; Land 1972). During turning swimming movements in red-eared turtles, one hindlimb displays forward swimming while the other hindlimb displays back-paddling (Field and Stein 1997; Lennard and Stein 1977; Stein 1978). The present paper describes interlimb kinematics during the symmetrical same-form behavior of bilateral forward swimming and the asymmetric mixed-form behavior of turning swimming.

Scratching is usually regarded as a unilateral behavior; most studies of scratching have emphasized the responses of a limb ipsilateral to a tactile stimulus (Stein 1983). A few studies have described rhythmic contralateral motor output as well; interlimb phase during rhythmic scratching has not been studied extensively, however. Rhythmic contralateral motor output occurs during fictive scratching in the mesencephalic cat (Deliagina et al. 1981) and the spinal turtle (Berkowitz and Stein 1994a,b; Currie and Stein 1989; Stein et al. 1995); the contralateral motor output is out of phase with the ipsilateral motor output. In the spinal turtle,
bilateral fictive rostral scratching can be elicited by simultaneous stimulation of mirror-image sites in the left and the right rostral scratch receptive fields (Stein et al. 1995); left hindlimb fictive rostral scratching is out of phase with right hindlimb fictive rostral scratching.

Before the present study, it was not known what type of interlimb coordination occurs during actual bilateral scratching in spinal turtles in response to simultaneous stimulation of sites in the left and the right scratch receptive fields. Bilateral scratching is a novel behavior in response to the two-point stimulation paradigm. The phase relationships between the hindlimbs that occur during this novel behavior reveal important information about the underlying neural organization of the spinal cord. The present paper describes interlimb phase relationships during each of several types of actual bilateral scratching in the spinal turtle. We present results from stimulation of mirror-image sites in each of three distinct receptive fields. In addition, we present results from two-site asymmetric stimulation of an ipsilateral site in the rostral scratch receptive field and a contralateral site in the pocket scratch receptive field. Some of the results of this article have previously been presented as an abstract (Field and Stein 1994); in addition, these results have been described in a doctoral thesis (Field 1995).

METHODS

Data collection

We investigated interlimb relationships in red-eared turtles during six different combinations of bilateral rhythmic hindlimb movements: rostral/rostral scratch, pocket/pocket scratch, caudal/caudal scratch, rostral/pocket scratch, forward swim/forward swim, and forward swim/back-paddle (swimming). For the scratch behaviors, a site in the center of each scratch form’s receptive field was stimulated. The sites used were: SP2 (stimulus position 2) for rostral scratch, Femoral 5 for pocket scratch, and Anal 5 for caudal scratch (Field and Stein 1997; Mortin and Stein 1990; Mortin et al. 1985). For the bilateral scratch trials, simultaneous stimulation was delivered to a site in a left receptive field and a site in a right receptive field. For symmetrical stimulation, the site on the ipsilateral side was the mirror image of the site on the contralateral side. For asymmetric stimulation, the site in the ipsilateral rostral scratch receptive field and the site in the contralateral pocket scratch receptive field were stimulated simultaneously. For the swimming behaviors, spontaneous movements of intact animals were observed. Details of animal preparation, stimulation, videography, definitions of joint angles, and phase analysis are presented in the companion paper (Field and Stein 1997).

Statistical methods

Interlimb phase was measured with respect to a dual-referent hip cycle, as was done for intralimb phase in the companion paper (Field and Stein 1997). For interlimb phase measurements, one limb, the “ipsilateral” limb, was selected as the referent limb. Each onset of hip flexion in the ipsilateral limb marked the beginning (0.0 phase) of a referent cycle; the subsequent onset of hip flexion in that limb marked the end (1.0 phase) of that cycle. The onset of hip extension in the ipsilateral limb was defined as the 0.5 phase of the cycle. If the onset of contralateral hip flexion occurred during ipsilateral hip flexion, then interlimb phase was defined as the latency of contralateral hip flexion onset from ipsilateral hip flexion onset divided by 2 times the duration of ipsilateral hip flexion. If the onset of contralateral hip flexion occurred during ipsilateral hip extension, then interlimb phase was defined as 0.5 plus the following: the latency of contralateral hip flexion onset from ipsilateral hip extension onset divided by 2 times the duration of ipsilateral hip extension. Thus both the flexion phase and the extension phase of the referent hip cycle were normalized.

Mean phase and mean angular deviation were calculated with the use of vector techniques (Batschelet 1981; Field and Stein 1997). For each hindlimb and for each of the six combinations of left and right movements, the interlimb phases from all movement cycles selected for analyses of absolute coordination were pooled; see Field and Stein (1997) for criteria for inclusion of cycles for analyses.

The Rayleigh test, a goodness-of-fit test for uniformity of circular data (Batschelet 1981), was used to test the hypothesis that the distribution of phases of onset of contralateral hip flexion within the dual-referent cycle of the ipsilateral hip was significantly different from random. The Watson U² test, a goodness-of-fit test for unimodal and multimodal samples of circular data, was used to test the distribution of phases of onset of contralateral hip flexion in episodes displaying 2:1 coordination in which the mean period of the test limb was approximately half that of the referent limb (Batschelet 1981).

RESULTS

Coordinated movements of the hindlimbs were observed during both bilateral scratching movements and bilateral swimming movements. In most cases, the movements of one hindlimb were out of phase with the movements of the contralateral partner; for some episodes of bilateral caudal scratching, however, the hindlimbs moved in phase with each other. In 15 spinal turtles analyzed for bilateral scratching, our main focus was on 1:1 (absolute) coordination (von Holst 1973). Each referent cycle began and ended with the onset of ipsilateral hip flexion; during 1:1 coordination, there was a single onset of contralateral hip flexion during each referent cycle. In addition, five intact turtles were analyzed for coordination between the hindlimbs during swimming behaviors that displayed 1:1 coordination.

Interlimb coordination during symmetrical behaviors—general observations

SAME-FORM BILATERAL SCRATCHING. Simultaneous stimulation of mirror-image sites in left and right scratch receptive fields produced site-specific rostral/rostral (Fig. 1A) or pocket/pocket (Fig. 1B) scratching. In these same-form rostral and same-form pocket bilateral responses, movements of the left and right hips were usually out of phase (Fig. 2, A and B, ——). Caudal/caudal bilateral scratching, however, involved out-of-phase hip movements in some turtles (Figs. 3A and 4A) and in-phase hip movements in others (Figs. 3B and 4B).

SAME-FORM BILATERAL FORWARD SWIMMING. Intact turtles spontaneously performed forward-swimming behavior in which both hindlimbs generated force against the water as each hindlimb retracted during the powerstroke (Fig. 5). During bilateral forward swimming, the movements of the left and right hips were usually out of phase.

Interlimb relationships during same-form bilateral behaviors—quantitative analyses

Quantitative analyses confirmed that hip movements of the two hindlimbs were out of phase, i.e., near 0.5, during
phase relationship in one animal (Fig. 6C) and an in-phase relationship in two other animals (Fig. 6D). For the data illustrated in Fig. 6C, the mean interlimb phase was 0.52 ± 0.11 with the left hip as referent and 0.54 ± 0.14 with the right hip as referent. In contrast, for the data illustrated in Fig. 6D, the mean interlimb phase was 0.01 ± 0.12 with the left hip as referent and 0.99 ± 0.11 with the right hip as referent. Thus, for these turtles, the onset of flexion in one hip was coincident with the onset of flexion in the other hip. In each turtle tested for bilateral caudal scratch behavior, the interlimb phase relationship, whether in phase or out of phase, was significantly different from random (Rayleigh test, $P < 0.001$).

In bilateral forward same-form swim behavior, the distribution of interlimb phases demonstrated an out-of-phase relationship (Fig. 6E). Mean interlimb phase was 0.56 ± 0.06 with the left hip as referent and 0.55 ± 0.06 with the right hip as referent. For each turtle in which forward-swim behavior was tested, the distribution of phases was significantly different from random (Rayleigh test, $P < 0.001$).

During bilateral caudal same-form scratching evoked by simultaneous stimulation of mirror-image sites in the left and the right caudal scratch receptive fields, in contrast, the distribution of interlimb phases demonstrated an out-of-phase relationship in one animal (Fig. 6C) and an in-phase relationship in two other animals (Fig. 6D). For the data illustrated in Fig. 6C, the mean interlimb phase was 0.52 ± 0.11 with the left hip as referent and 0.54 ± 0.14 with the right hip as referent. In contrast, for the data illustrated in Fig. 6D, the mean interlimb phase was 0.01 ± 0.12 with the left hip as referent and 0.99 ± 0.11 with the right hip as referent. Thus, for these turtles, the onset of flexion in one hip was coincident with the onset of flexion in the other hip. In each turtle tested for bilateral caudal scratch behavior, the interlimb phase relationship, whether in phase or out of phase, was significantly different from random (Rayleigh test, $P < 0.001$).

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**Fig. 1.** Trajectory of the 3rd toe of each hindlimb during 1 cycle of scratching in response to simultaneous stimulation of mirror-image sites in the left and the right scratch receptive fields. A: bilateral rostral scratch. B: bilateral pocket scratch. Dashes: portions of the hindlimb obscured by the plastron. The 3 linked line segments represent, from medial to lateral, the long axis of the thigh, shank, and foot. $\rightarrow$, direction of the toe trajectory. In A and B, the position of the left hindlimb indicates the typical posture at the time of rub onset. The position of the right hindlimb at the time of left hindlimb rub onset is indicated; note that the direction of movement at that time for the right hindlimb is opposite that of the left hindlimb. ●, position of the left toe at rub onset; ○, position of the right toe at the same moment.

**Fig. 2.** Joint angles as a function of time during (A) bilateral rostral scratch and (B) bilateral pocket scratch. ---, hip angle; ---, knee angle. A and B, top: left hindlimb. A and B, bottom: right hindlimb. ■, onset of each rub. Vertical dashed lines at 0.5-s intervals are included to facilitate comparison between traces. Value of each joint angle increases when the joint is extending and decreases when the joint is flexing; see Field and Stein (1997) for definitions of hip angle and knee angle.
Asymmetric modes of bilateral coordination—general observations

MIXED-FORM BILATERAL SCRATCHING. Simultaneous stimulation of asymmetric sites, the ipsilateral rostral scratch receptive field site and the contralateral pocket scratch receptive field site, produced bilateral scratch responses that were asymmetric (Fig. 7). Each hindlimb’s responses were site specific: each displayed a scratch form appropriate to the ipsilateral stimulus. In this “mixed-form” bilateral response, the interlimb relationship was one in which the right and left hip movements were out of phase with each other (Fig. 8). This is not a simple bilateral task to coordinate. In the rostral scratch, the foot passes closest to the body while the hip is flexing; in the pocket scratch, the foot passes closest to the body while the hip is extending. Stimulation of a caudal receptive field site in combination with a rostral site or a pocket site on the contralateral side produced a response that appeared erratic for the first few cycles and then settled into what appeared to be a bilateral caudal response (data not shown).

2:1 COORDINATION DURING BILATERAL SCRATCHING. In four turtles, episodes of 2:1 interlimb coordination were observed. In three of these turtles, this atypical pattern occurred during bilateral rostral/rostral stimulation; in one turtle, it
occurred during bilateral pocket/pocket stimulation. In such episodes, the animal exhibited periods during which the hindlimb on one side of the body, the ‘‘fast’’ side, performed two scratch cycles during each single cycle produced on the contralateral side, the ‘‘slow’’ side (Fig. 9). The intralimb pattern of cycles on the fast side was such that there was a longer and a shorter cycle that occurred in alternation with each other. During the longer cycles on the fast side, hip flexion on the two sides was approximately out of phase; during the shorter cycles on the fast side, hip flexion on the two sides was approximately in phase.

**Mixed-Form Bilateral Turning Swimming.** Intact turtles also generate a mixed-form behavior during spontaneous episodes of turning swimming. In this behavior, the animal performs a turning maneuver by swimming forward with the forelimb and hindlimb on one side of the body while simultaneously back-paddling with the contralateral forelimb and hindlimb. The forward-swimming limbs exerted force against the water during hip extension; the back-paddling limbs exerted force against the water during hip flexion. In this behavior, there was an out-of-phase relationship between the left and right hip angles (Fig. 10). This out-of-phase relationship was present despite the fact that in most episodes the excursion of the forward-swimming limb was greater than that of the back-paddling limb.

**Interlimb Relationships in Mixed-Form Bilateral Behaviors—Quantitative Analyses**

Quantitative analysis confirmed that hip movements of the two hindlimbs were out of phase during bilateral rostral/pocket mixed-form scratching episodes (Fig. 11A). The mean interlimb phase was $0.50 \pm 0.11$ with the rostral scratch hip as referent and $0.49 \pm 0.10$ with the pocket scratch hip as referent. These values were statistically different from random for each turtle with the use of either the rostral scratch hip as the referent or with the use of the pocket scratch hip as the referent (Rayleigh test, $P < 0.001$).

Similarly, the interlimb phase relationship during mixed-form turning swimming was also out of phase (Fig. 11B). The mean interlimb phase was $0.48 \pm 0.10$ with the forward-swimming hip as referent and $0.48 \pm 0.08$ with the backward-swimming hip referent. Each distribution of phases was significantly different from random (Rayleigh test, $P < 0.001$).

Quantitative analysis demonstrated that both out-of-phase and approximately in-phase interlimb coordination relationships occurred during episodes of 2:1 coordination. With the hip of the slow limb as the referent, there was a bimodal distribution of phases of onset of hip flexion of the fast limb (Fig. 12). Some cycles occurred at a phase of ~0.5; others
Interlimb relationships during scratching and swimming

Figure 8. Joint angles as a function of time for bilateral mixed-form scratching. Top: left hindlimb with rostral scratch response. Bottom: right hindlimb with pocket scratch response. Note the out-of-phase relationship between the hip angle values.

Interlimb relationships in response to unilateral stimulation

In many instances, bilateral limb movements occurred in response to unilateral stimulation (Field and Stein 1997). In some cases, these movements had a stable interlimb phase relationship. Of the eight turtles tested with a unilateral pocket scratch stimulus, four had bilateral activity in the presence of unilateral stimulation. In these turtles, movements of the two hindlimbs were out of phase; in three of these turtles, this relationship was significantly different from random (Rayleigh test, $P < 0.001$ for each).

All three turtles tested with a unilateral caudal scratch stimulus demonstrated movement of the contralateral limb. In two turtles, this movement exhibited intralimb relationships typically associated with caudal scratch. The interlimb relationships were out of phase in one animal and in phase in the other; in each case, the interlimb relationship was similar to that observed during bilateral caudal stimulation in the same animal. In the turtle exhibiting an out-of-phase relationship between the hindlimbs, the distribution of phases was significantly different from random for left hindlimb movement in response to unilateral right caudal stimulation and for right hindlimb movement in response to unilateral left caudal stimulation.

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FIG. 12. Distribution of phase relationships during bilateral scratching with 2:1 interlimb coordination. ■, phases of onset of hip flexion on the fast side within the hip cycle of the slow side. Note that the distribution is bimodal.

DISCUSSION

The first major result of this paper was that hip movements of the two hindlimbs were consistently out of phase during symmetrical behaviors in which both hindlimbs displayed the same movement strategy (e.g., same-form forward swimming, bilateral same-form rostral/pocket scratching, and bilateral same-form pocket/pocket scratching) as well as during asymmetric behaviors in which the movement strategy of the left hindlimb was different from that of the right hindlimb (e.g., mixed-form turning swimming and bilateral mixed-form rostral/pocket scratching). Out-of-phase interlimb coordination occurred during swimming behaviors in intact turtles as well as during scratching behaviors in spinal turtles. Out-of-phase interlimb coordination also occurs during fictive bilateral scratching (Stein et al. 1995); thus proper regulation of interlimb phase during bilateral rostral scratching does not depend on movement-related sensory input. These demonstrations of interlimb phase control during bilateral scratching in spinal turtles and previous demonstrations of interlimb phase control during locomotion in spinal vertebrates (Forssberg et al. 1980; Grillner 1981; Lenard and Stein 1977; Stein 1978, 1984) establish that the spinal cord contains sufficient circuitry to control interlimb phase in the absence of supraspinal influences. Note especially that this circuitry can control interlimb phase even when the behavior is a novel bilateral task such as bilateral mixed-form scratching.

Our observations of out-of-phase hip movements during...
both symmetrical and asymmetric behaviors support the concept that neuronal signals related to the hip play a key role in establishing the timing of motor output responsible for rhythmic movements of each limb. During a symmetrical behavior, the phase of the left knee in the left hip cycle is the same as the phase of the right knee in the right hip cycle; therefore, when the hip movements were out of phase with each other, then the knee movements were also out of phase with each other. During an asymmetric behavior, however, the phase of the left knee in the left hip cycle is different from the phase of the right knee in the right hip cycle (Table 1 of Field and Stein 1997); thus, while the hip movements remained out of phase with each other, left and right knee movements were no longer out of phase with each other. The simplest hypothesis consistent with these data is that, for a given movement strategy: 1) the timing signals for out-of-phase interlimb control result from the interaction of neuronal signals related mainly to the hip; 2) the pacemaker of each limb’s rhythm is related to the control of that limb’s hip; and 3) the phasing of each distal joint of a limb is controlled relative to that limb’s hip. Previous support for this hypothesis was obtained by analyses of movements and motor patterns in a single hindlimb during blends of two scratch forms. Blends are produced during the transition zone between two scratch forms’ receptive fields (Mortin et al. 1985; Robertson et al. 1985) and in response to simultaneous stimulation of two ipsilateral sites, each in the receptive field of a different scratch form (Stein et al. 1986). Additional support for this hypothesis was obtained by analyses of phase shifts in ongoing fictive scratch motor patterns when a flexion reflex was evoked (Currie and Stein 1989). Consistent with this hypothesis is the prediction that the rhythmic activity of each member of a population of spinal cord commissural interneurons is best related to a hip’s motor rhythm; future experiments with single-unit recordings of commissural axons during several forms of fictive scratching can test this prediction.

Fictive scratching evoked by unilateral tactile stimulation involves bilateral rhythmic motor output; contralateral motor output is out of phase with ipsilateral motor output during fictive rostral scratching and fictive pocket scratching (Berkowitz and Stein 1994a; Currie and Stein 1989; Stein et al. 1995). Descending propriospinal interneurons are also active bilaterally (Berkowitz and Stein 1994a,b). In a related set of experiments, Stein et al. (1995) removed the contralateral half of the hindlimb enlargement; in this preparation, unilateral stimulation in the rostral scratch receptive field activates an altered ipsilateral motor pattern. These authors suggested that, in a preparation with an intact hindlimb enlargement, bilateral activity may play an important role in generating the proper ipsilateral rostral scratch motor output, i.e., contralateral spinal circuitry may interact with ipsilateral spinal circuitry to generate normal ipsilateral rostral scratching in response to stimulation of an ipsilateral site. This suggestion led to the proposal of the existence of a “bilateral shared core” of hip-related interneurons for rostral scratching (Stein et al. 1995). The present observations of out-of-phase hip movements of the two hindlimbs during bilateral rostral, bilateral pocket, and mixed-form rostral/pocket scratching, combined with the results of Berkowitz and Stein (1994a,b), support the suggestion that there may be a bilateral shared core of hip-related interneurons that contribute to the generation of both rostral scratch and pocket scratch motor patterns. If such interneurons are involved specifically in the timing of hip movements, then they will produce the same phase relationship between the two hips during bilateral same-form scratching (Fig. 6, A and B) and bilateral mixed-form scratching (Fig. 11A). There is also bilateral motor output and bilateral interneuronal activity during cat scratching elicited by a unilateral stimulus (Barajon et al. 1992; Deliagina et al. 1981; O’Donovan et al. 1982); further work with other vertebrates is now required to test the generality of the bilateral shared core hypothesis.

A second major result of this paper was that either of two preferred interlimb phase relationships occurs during bilateral caudal/caudal same-form scratching in spinal turtles. In some cases, the preferred phase was near 0.5, i.e., out of phase; in other cases, the preferred phase was near 0.0, i.e., in phase. Either of two preferred interlimb phase relationships is also observed during locomotion of spinal kittens on a treadmill; out-of-phase interlimb coordination (walk, trot) occurs at low treadmill speeds and in-phase interlimb coordination (gallop) occurs at high treadmill speeds (Forsberg et al. 1980). Humans initiate stepping with in-phase dorsiflexion of the ankles (Herman et al. 1973), but subsequent stepping movements involve out-of-phase ankle movements. Freshwater turtles initiate escape behavior with an in-phase movement that is followed rapidly by out-of-phase swimming (Davenport et al. 1984). Bilateral fictive rostral/rostral same-form scratching in the turtle begins with an in-phase hip flexor motor output that is followed rapidly by out-of-phase hip flexor motor output (Stein et al. 1995); similar observations were obtained in spinal turtles during swimming movements evoked by electrical stimulation of the spinal cord (Stein 1978). Thus the spinal cord contains sufficient circuitry to coordinate more than one preferred phase.

The neuronal mechanisms responsible for selection of a particular interlimb phase relationship in a vertebrate are currently not well understood. The demonstration of two distinct phase relationships for bilateral caudal/caudal same-form scratching in the present paper invites future experiments with spinal turtles to reveal underlying mechanisms responsible for selection of a particular interlimb phase in a vertebrate. In-phase and out-of-phase interlimb control may rely on crossed excitatory and crossed inhibitory pathways, respectively. Crossed glycinergic inhibition in the spinal cord plays a major role in the production of left/right out-of-phase motor output; blockade of these receptors by strychnine reveals left/right in-phase coordination that most likely is generated by crossed excitatory pathways (Cohen and Harris-Warrick 1984; Cowley and Schmidt 1995; Currie and Lee 1996; Kudo et al. 1991). Further experiments are required to understand how the spinal cord selectively controls the relative strength of crossed inhibition and crossed excitation.

A third major result of this paper was the observation that, under some conditions, stable 2:1 interlimb coordination occurs in the spinal turtle during bilateral same-form scratching. Two-to-one coordination is a result predicted by coupled oscillator theory (Stein 1976; von Holst 1973). Such coordination has been demonstrated for cats...
and humans stepping on a split-belt treadmill (Forssberg et al. 1980; Kulagin and Shik 1970; Thelan et al. 1987) and for spinal turtles displaying swimming movements (Stein 1978). The simplest hypothesis consistent with these results is that there is a neural oscillator within a hemiernargement with circuitry sufficient to generate a motor rhythm for the limb innervated by that hemiernargement. According to coupled oscillator theory, 2:1 coupling occurs when the intrinsic period of one oscillator is approximately twice the intrinsic period of the other oscillator (Stein 1976). Stein et al. (1995) recently demonstrated that the turtle hindlimb hemiernargement contains a neuronal oscillator, termed the hip flexor module, with sufficient circuitry to generate a rostral scratch motor rhythm with rhythmic bursts of hip flexor activity and with no hip extensor activity. Further work that characterizes motor patterns and interneuronal activity patterns during 2:1 bilateral scratching is now required to reveal the neural mechanisms responsible for such coordination.

Interlimb coordination is a fundamental feature of multilimb behavior (Stein 1976). In the crayfish, evidence copy "coordinating neurons" carry information required for interlimb phase control during rhythmic swimmeret motor output (Stein 1971, 1976). The present demonstration of interlimb phase control in a spinal turtle during bilateral scratching indicates that future experiments in which the turtle is used may provide more specific insights into the neuronal signals, e.g., those related to hip motor output, that are responsible for interlimb phase control in a vertebrate.

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