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

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Field, Edelle C. and Paul S. G. Stein. Spinal cord coordination of hindlimb movements in the turtle: intralimb temporal relationships during scratching and swimming. J. Neurophysiol. 78: 1394–1403, 1997. Spinal cord neuronal circuits generate motor neuron activity patterns responsible for rhythmic hindlimb behaviors such as scratching and swimming. Kinematic analyses of limb movements generated by this motor neuron output reveal important characteristics of these behaviors. Intralimb kinematics of the turtle hindlimb were characterized during five distinct rhythmic forms of behavior: three forms of scratching and two forms of swimming. In each movement cycle for each form, the angles of the hip and knee joints were measured as well as the timing of a behavioral event, e.g., rub onset in scratching or powerstroke onset in swimming. There were distinct differences between the kinematics of different forms of the same behavior, e.g., rostral scratch versus pocket scratch. In contrast, there were striking similarities between forms of different behaviors, e.g., rostral scratch versus forward swimming. For each form of behavior there was a characteristic angular position of the hip at the onset of each behavioral event (rub or powerstroke). The phase of the onset of knee extension within the hip position cycle occurred while the hip was flexing in the rostral scratch and forward swim and while the hip was extending in the pocket scratch, caudal scratch, and back-paddling forms of swimming. The phase of the onset of the behavioral event was not statistically different between rostral scratch and forward swim; nor was it different between pocket scratch and caudal scratch. These observations of similarities at the movement level support the suggestion that further similarities, such as shared spinal circuitry, may be present at the neural circuitry level as well.

INTRODUCTION

Motor tasks are classified according to their goal. The goal of scratching is to use a limb to generate force against a site on the body surface that has received a stimulus; the goal of locomotion is to move an organism’s center-of-mass from one place to another. Each task may have a number of variations, e.g., forward walking or backward walking (cat: Buford and Smith 1990a,b; Stein and Smith 1997; humans: Thorstensson 1986; Winter et al. 1989). Each variation of a task is a specific movement strategy, a “form” of that task (Stein and Smith 1997; Stein et al. 1986). The turtle hindlimb displays three different forms of scratching (rostral, pocket, or caudal) (Mortin et al. 1985) and two different forms of swimming (forward swimming or back-paddling) (Lennard and Stein 1977; Stein 1978). Previous kinematic analyses of scratching (Mortin et al. 1985; Robertson et al. 1985) and swimming (Davenport et al. 1984; Lennard and Stein 1977; Zug 1971) focused on individual examples of a few cycles of movement. In the present paper we expand these earlier observations and provide quantitative character-
Red-eared turtles (n = 48), Trachemys scripta elegans (formerly Pseudemys scripta elegans; 285–730 gm) were studied. All procedures followed National Institutes of Health guidelines and were approved by the Washington University Animal Care and Use Committee. Detailed analyses of limb movement were performed on a subset of turtles (n = 20). Spinalized turtles (n = 15) were used to study scratching; intact turtles (n = 5) were used to study swimming. In all turtles, bony landmarks of the hip, the knee, and the third toe of both hindlimbs were marked with reflective paint.

The spinalization procedure has been described previously (Mortin et al. 1985). The turtle was placed in crushed ice for 1 h to obtain hypothermic anesthesia (Melby and Altman 1974) and was maintained on ice for the duration of the surgical procedure. A midline channel was drilled in the carapace overlying the upper dorsal segments of the spinal cord. The spinal cord was completely transected between the second (D2) and third (D3) postcervical spinal segments just posterior to the forelimb enlargement. The turtle was removed from the ice and allowed to return to room temperature. Portions of the plastron in the ventral aspect of the pocket shell region were removed to provide better visualization of the hindlimb from below.

**Activation of scratching and swimming**

During experiments that examined scratching behaviors in spinal turtles, each turtle was held in a band clamp that encircled the middle of its body. Scratching was evoked by stimulation in the approximate center of each scratch form’s receptive field. The sites used (Fig. 1) were the rostral scratch receptive field site SP2 (stimulus position 2), pocket scratch receptive field site Femoral 5, and caudal scratch receptive field site Anal 5; for additional descriptions of these sites see Mortin et al. (1985) and Mortin and Stein (1990). One of two methods was used to evoke scratching behaviors. Mechanical stimulation was delivered by means of insect pins inserted into a specific site(s); scratch responses were evoked by touching the pin(s) with a fingertip and gently moving the pin(s) back and forth. Electrical stimulation was delivered via pairs of pin electrodes (interelectrode distance 3 mm) inserted in a specific site(s); electrical pulses of 2–10 V, 1 ms were delivered at 3 Hz for 5–10 s. Stimulus trials were performed in blocks of six in the following order: left stimulation, right stimulation, bilateral stimulation, bilateral stimulation, left stimulation, right stimulation.

Spontaneous swimming was studied in intact turtles. The turtle was held in a band clamp and immersed in an aquarium with the highest point of its carapace just at the water surface. The water level was adjusted to ensure that the turtle’s limbs did not contact the bottom of the aquarium during swimming. Two types of swimming were observed: same-form forward swimming, during which both hindlimbs displayed the forward swimming form with power-stroke during limb retraction; and mixed-form turning swimming, during which one hindlimb displayed the forward swimming form and the contralateral hindlimb displayed the back-paddling form of swimming with powerstroke during limb protraction.

**Data collection**

For scratch trials, the spinal turtle rested on a panel of nonreflective glass. The turtle was viewed from below via a mirror placed below the glass panel at an angle of 45°. When performed on a flat substrate, hindlimb scratching movements were relatively planar; a single camera was therefore adequate for measurements of joint angles. For swim trials, the turtle was also viewed from below via a camera positioned beneath the aquarium. hindlimb movements were videotaped at 60 Hz with a shutter speed of 1/250 s. Data from trials in which the limb movement was not in a plane orthogonal to the optical axis of the camera were not analyzed. This was verified by calculating ratios with the use of measurements obtained from video data: the ratio of the length of the thigh segment to the length of a fixed segment on the shell and the ratio of the length of the shank segment to the length of a fixed segment on the shell. This was compared with the corresponding ratios measured directly on the animal. Trials in which the corresponding measures were within 90% of each other were analyzed.

Video tapes of the behaving animals were replayed and markers were digitized in a Peak Performance Technologies (Englewood, CO) two-dimensional motion measurement system. Each frame was viewed individually; for each alternate frame, the X and Y coordinates of each marker were digitized manually (30 Hz). The definitions of hip joint angle and the knee joint angle (Fig. 1) were according to Mortin et al. (1985). Hip angle was defined as the angle formed by the thigh and the ventral midline of the body. Knee angle was defined as the angle formed by the thigh and the shank. The value of each joint angle increases when the joint is extending and decreases when the joint is flexing.

**Quantitative analyses**

We selected episodes of scratching for analysis that were suitable both for this paper reporting intralimb kinematics and for our companion paper (Field and Stein 1997) reporting interlimb kinematics. The primary focus of the companion paper was on bilateral coupling during absolute (1:1) coordination. For both papers, therefore, we selected for detailed analyses those scratch episodes consisting of at least five cycles from those turtles in which unilateral stimuli produced ipsilateral responses that were robust for both the left and the right stimulus conditions. In addition, we only analyzed groups of episodes in which the cycle period of the left hindlimb in response to a left unilateral stimulus had a value that was near that of the cycle period of the right hindlimb in response to a right unilateral stimulus; in particular, we analyzed only those groups in which the cycle period on the “slow” side was <1.5 times the cycle period on the “fast” side. In addition, for studies
of rostral scratching in both papers, we restricted the data set further: only cycles in which the maximum value of hip extension was >60° were analyzed. This additional criterion was used because cycles with limited hip extension are one of two variations of the rostral scratch termed "omissions" or "deletions" (Robertson et al. 1985). In an omission, the hip flexor burst occurs and is followed by a period of hip flexor quiescence, but hip extensor activity is absent. In a deletion, the hip flexor burst is followed immediately by another hip flexor burst with no intervening hip flexor quiescence and no hip extensor burst. In either case, these cycles differed from the normal rostral scratch kinematically. When they occurred, such variant cycles usually took place within the first one to three cycles of an episode. In addition to the analyses described above, data recorded during specific episodes of stable 2:1 coordination were analyzed separately and are reported in a section of our companion paper (Field and Stein 1997).

**ONSET OF THE BEHAVIORAL EVENT.** The timing of the onset of the behavioral event (rub for scratch, powerstroke for swim) was determined from the video recording. For scratch behaviors, the onset of the rub was defined as the time at which the limb made contact with the stimulated site. For swim behaviors, the onset of the powerstroke was defined as follows: for forward swimming, the time at which the foot began to move in a backward direction; for back-paddling, the time at which the foot began to move in a forward direction. At the onset of powerstroke, the foot was usually aligned in a vertical position. In addition, at this time, the distance between the toes was increasing and the webbing between the toes was spreading out.

**PHASE ANALYSIS.** Phase analyses were performed with the use of custom software. Cycle period was defined as the time from the onset of a hip flexion to the onset of the subsequent hip flexion. Previous investigations have demonstrated that the timing of bursts in hip flexor motor neurons innervating the puboischiofemoralis internus, pars anteroventralis (VP-HP) muscle (Robertson et al. 1985) offers a dependable temporal reference for scratch phase analyses (Berkowitz and Stein 1994b; Stein et al. 1995). The onset of hip flexion is the movement parameter most closely associated with onset of the burst of activity in the VP-HP muscle (Robertson et al. 1985; Robertson et al. 1985). The onset of hip flexion was defined as the point at which the joint angle displacement trace reached a maximum and thereafter reversed direction; the onset of hip extension was defined as the time at which the joint angle displacement trace reached a minimum and thereafter reversed direction. In cycles in which the hip joint angle remained within 10° of the maximum or minimum angle for >333 ms, the midpoint of this period was defined as the time of onset of flexion or extension, respectively. Analogous criteria were applied to define the onsets of knee flexion and extension.

Dual-referent phase analyses were used to normalize both the hip flexion and the hip extension phases of scratching. The relative durations of these two phases can vary during the performance of a single behavior as well as between behaviors. The phase θ of an event that occurred during hip flexion was defined as the latency of the event from the onset of hip flexion divided by twice the duration of hip flexion; the phase θ of an event that occurred during hip extension was defined as the latency of the event from the onset of hip extension, divided by twice the duration of hip extension, plus 0.5. An analogous method has been used to study fictive scratching in the turtle (Berkowitz and Stein 1994b; Stein et al. 1995). Similar dual-reference techniques have been employed by Orlovsky (1972) in characterizing the phase of vestibulospinal neuron activity during locomotion in the cat and by Burns and Usherwood (1979) in the assessment of motoneuron activity during locomotion in locusts and grasshoppers.

The cyclic nature of these data makes them well suited to vector algebra techniques (Batschelet 1981). Each phase θ (0 ≤ θ ≤ 1) was converted to a two-dimensional unit vector with a length of 1 and an angle of 2πθ in radians. These unit vectors were averaged with the use of vector addition techniques. The angle of the mean vector in radians divided by 2π was defined as the mean phase (which varied between 0 and 1). The length of the mean vector (which varied between 0 and 1) represented the "strength" of the preferred phase. The mean vector length was also used to calculate the mean angular deviation, a measure of the dispersion of the phase data (Batschelet 1981). These vector data were suited to the application of circular statistics (Batschelet 1981).

**STATISTICAL METHODS.** Nonparametric statistical methods, both linear and circular, were used to compare movement parameters within behaviors and between behaviors; these statistics were chosen because the variance of the measures of interest differed widely between behaviors and because some parameters were not normally distributed. The Mann-Whitney U test (Hayes 1988; Runyon and Haber 1984), an unpaired, signed-rank test for linear data, was used on pooled data to compare the angle of the hip at the onset of the behavioral event in different behaviors; this test was also used to evaluate differences in hip excursion between scratch forms. The Kruskal-Wallis test (Hayes 1988), a generalized version of the Mann-Whitney U test for multiple-group comparisons, was used to test whether the hip angle at the onset of rub was statistically different between turtles performing the same form of a behavior. The Watson U² test (Batschelet 1981), an unpaired, signed-rank test for circular data, was used to compare the phase data between behaviors.

All statistical tests to analyze between-behavior differences were done in a pairwise fashion; the final P value was corrected to counter increases in the type I error rate due to the multiple pairwise comparisons (Hayes 1988). In multiple pairwise tests, this is corrected by multiplying the final P value by the number of groups being tested. When the three scratch behaviors were tested against one another, the P value was multiplied by 3. When the five scratch and swim behaviors were tested against one another, the P value was multiplied by 5.

In addition, the Rayleigh test for uniformity of circular data was used to evaluate the hypothesis that the distribution of phases (phases of onset of knee extension; phases of onset of the behavioral event) within the hip movement cycle differed significantly from a random distribution (Batschelet 1981).

**RESULTS**

Scratch data from 15 turtles were analyzed. This included rostral scratch data from eight turtles, pocket scratch data from eight turtles, and caudal scratch data from four turtles. In three turtles, both rostral and pocket scratch data were collected; in one turtle, rostral, pocket, and caudal scratch data were collected. A total of 899 scratch cycles comprising 130 episodes (53 rostral, 52 pocket, and 25 caudal episodes) were analyzed. The number of cycles per episode ranged from 5 to 32. Swim data from five turtles were analyzed. A total of 67 swim cycles in eight episodes (3 forward swimming, 5 turning swimming) were analyzed.

**General characteristics of scratch behavior**

The three forms of scratch could be distinguished by the trajectory of the third toe of the hindlimb (Fig. 2) (Mortin et al. 1985). Although this trajectory was similar in the pocket and caudal forms, the toe reached a more caudal position during caudal scratch. In rostral scratch (Fig. 3A), knee extension began during hip flexion and the rub began just before the maximal knee extension. In pocket scratch
All differences between forms in the maximum amount of hip flexion were statistically significant (corrected Mann-Whitney U test, \( P < 0.003 \) for rostral/caudal and pocket/caudal comparison, \( P < 0.03 \) for rostral/pocket comparison). Differences in the maximum amount of hip extension were statistically significant for the rostral/pocket and rostral/caudal comparisons (\( P < 0.003 \)) but not for the pocket/caudal comparison.

**General characteristics of swim behavior**

Spontaneous swimming was examined in intact turtles. Two common swim behaviors were studied: same-form forward swimming and mixed-form turning swimming. Both swim behaviors used all four limbs; in this study, only the hindlimb relationships were analyzed. In same-form forward swimming, each hindlimb displayed the forward swim form (Fig. 5A) and exerted force against the water during hip extension. When forward swimming movements (Lennard and Stein 1977) were performed bilaterally by a freely moving turtle, the animal propelled itself forward with a linear trajectory. In mixed-form turning swimming, one hindlimb displayed the forward swim form; the other hindlimb displayed the back-paddle form of swimming (Fig. 5B). In performance of back-paddling, force is exerted against the water during hip flexion. Intermuslimb coordination during same-form forward swimming and mixed-form turning

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**Fig. 2.** Trajectory of the 3rd toe during 1 cycle of scratch for each of the 3 forms. A: rostral scratch response (stimulation at SP2). B: pocket scratch response (stimulation at Fem 5). C: caudal scratch response (stimulation at Anal 5). In A–C, the position of the left hindlimb indicates the typical posture at the time of rub onset. Portions of the hindlimb that would be obscured by the plastron are marked with dashes. The 3 linked line segments represent, from medial to lateral, the long axis of the thigh, shank, and foot. →, direction of movement of the toe trajectory.

(Fig. 3B), knee extension began abruptly during hip extension; the rub began soon thereafter. In caudal scratch (Fig. 3C), knee extension also began during hip extension, but the knee extended more gradually; the rub began during knee extension near the midpoint of the hip extension phase. Thus the timing of knee extension within the hip movement cycle was similar for pocket and caudal scratch (Fig. 3, B and C).

The excursions of the hip were markedly different among scratch forms (Fig. 4). The hip flexed further in rostral scratch (23.0 ± 3.4°, mean ± SD) than in either pocket (30.0 ± 8.1°) or caudal (85.5 ± 18.9°) scratch. The hip extended further in caudal scratch (149.4 ± 15.5°) than in either rostral (99.8 ± 7.9°) or pocket (142.6 ± 6.3°) scratch.

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**Fig. 3.** Joint angle displacements as a function of time for the hip (•••) and knee (---) during 4 cycles of scratching. A: rostral scratch. B: pocket scratch. C: caudal scratch. ■, onset of the rub phase. Vertical dashed lines at 0.5 s intervals are included to facilitate comparison between traces.
signiﬁcant differences between different turtles performing the same behavior; the Kruskal-Wallis test was used for the hip angle data and the Watson $U^2$ test for the phase data. For each measure, we therefore pooled the data from all turtles performing the same behavior; these data are presented in Table 1.

The hip angle (Table 1A) at the onset of the behavioral event (rub for scratch, powerstroke for swim) was different for each behavior (Mann-Whitney $U$ test, $P < 0.005$) and was therefore a reliable means of discriminating among these behaviors. The different receptive ﬁeld location for each scratch behavior constrained the placement, in body coordinates, of the onset of the behavioral event to a relatively small area for these behaviors. The SD of hip angle at the onset of the behavioral event for each of the scratch forms was $<10^\circ$. The SD of this measure for the forward swim was also small ($3.7^\circ$); in contrast, the SD of this measure for the back-paddle was much larger ($15.6^\circ$). During a back-paddle, powerstroke onset was initiated effectively whenever hip extension was maximal for each cycle; maximal hip extension varied greatly between cycles, from $\sim70^\circ$ to $>100^\circ$.

The mean phase of onset of knee extension (Table 1B) within the dual-referent hip cycle was similar for pocket scratch, caudal scratch, and back-paddle; none of the differences were statistically signiﬁcant (Watson $U^2$ test, not signiﬁcant for each of the pairwise comparisons). As noted previously, in each of these three behaviors the knee extension began just after the onset of hip extension. The mean phase of onset of knee extension within the hip cycle was signiﬁcantly different in all other comparisons between behaviors (Watson $U^2$ test, $P < 0.05$ for rostral scratch vs. forward swim, $P < 0.005$ for all other comparisons).

The mean phase of onset of the behavioral event within the dual-referent hip cycle (Table 1C) was not signiﬁcantly different statistically between rostral scratch and forward swim or between pocket scratch and caudal scratch. In both rostral scratch and forward swim, the rub or powerstroke

Quantitative comparisons between behaviors

We compared three movement variables across all behaviors: 1) the angular position of the hip at the onset of the behavioral event (rub for scratch, powerstroke for swim), 2) the phase of onset of knee extension within the hip cycle, and 3) the phase of onset of the behavioral event within the hip cycle. For each of the three measures, there were no significant differences between different turtles performing the same behavior; the Kruskal-Wallis test was used for the hip angle data and the Watson $U^2$ test for the phase data. For each measure, we therefore pooled the data from all turtles performing the same behavior; these data are presented in Table 1.

The hip angle (Table 1A) at the onset of the behavioral event (rub for scratch, powerstroke for swim) was different for each behavior (Mann-Whitney $U$ test, $P < 0.005$) and was therefore a reliable means of discriminating among these behaviors. The different receptive field location for each scratch behavior constrained the placement, in body coordinates, of the onset of the behavioral event to a relatively small area for these behaviors. The SD of hip angle at the onset of the behavioral event for each of the scratch forms was $<10^\circ$. The SD of this measure for the forward swim was also small ($3.7^\circ$); in contrast, the SD of this measure for the back-paddle was much larger ($15.6^\circ$). During a back-paddle, powerstroke onset was initiated effectively whenever hip extension was maximal for each cycle; maximal hip extension varied greatly between cycles, from $\sim70^\circ$ to $>100^\circ$.

The mean phase of onset of knee extension (Table 1B) within the dual-referent hip cycle was similar for pocket scratch, caudal scratch, and back-paddle; none of the differences were statistically signiﬁcant (Watson $U^2$ test, not signiﬁcant for each of the pairwise comparisons). As noted previously, in each of these three behaviors the knee extension began just after the onset of hip extension. The mean phase of onset of knee extension within the hip cycle was signiﬁcantly different in all other comparisons between behaviors (Watson $U^2$ test, $P < 0.05$ for rostral scratch vs. forward swim, $P < 0.005$ for all other comparisons).

The mean phase of onset of the behavioral event within the dual-referent hip cycle (Table 1C) was not signiﬁcantly different statistically between rostral scratch and forward swim or between pocket scratch and caudal scratch. In both rostral scratch and forward swim, the rub or powerstroke
began soon after the onset of hip extension. The rub began at a very different hip angle in pocket scratch and caudal scratch (Table 1A) but at approximately the same phase of the hip cycle (Table 1C). The phase of onset of the behavioral event was significantly different in all other comparisons between behaviors (Watson U² test, P < 0.05 for pocket scratch vs. forward swim; P < 0.005 for all other comparisons).

For each behavior, the Rayleigh test was used on the pooled data to assess whether the distribution of the phases of onset of knee extension was significantly different from a random distribution; the distribution of these data was significantly different from random in each case (P < 0.001). Similar tests were performed on the pooled data of the phase of the behavioral event for each behavior; the distribution of these data was also significantly different from random in each case (P < 0.001).

### Intralimb performance with bilateral symmetrical stimulation compared with unilateral stimulation

Intralimb characteristics during bilaterally evoked scratching in response to symmetrical sites were qualitatively similar to unilaterally evoked scratching. For each form of scratching, the trajectory of the third toe did not differ between unilaterally evoked and bilaterally evoked scratching. Interlimb phase measurements during bilateral stimulation are presented in the companion article (Field and Stein 1997).

We used the quantitative measures described in the previous section to assess, for each form of scratching, whether intralimb kinematics change when both hindlimbs scratch simultaneously. In most cases there was no difference in the hip angle at which the rub began between unilaterally evoked and bilaterally evoked scratching (Fig. 6). Statistically significant differences in this measure occurred in only 2 of 19 comparisons; both were for bilateral rostral scratching (Fig. 6, asterisks; Mann-Whitney U test, P < 0.001).

The phase of knee extension onset within the hip cycle was not significantly different for unilaterally evoked and bilaterally evoked scratching in the majority of turtles. There was a statistically significant difference in three of the eight turtles analyzed for rostral scratch and in two of the eight turtles analyzed for pocket scratch (Watson U² test, P < 0.01). On some individual cycles of bilaterally evoked scratching, the relative duration of knee flexion (duration of the knee flexion phase divided by the cycle period) was larger than in unilaterally evoked scratching. This contributed to the difference in the mean phase of the onset of knee extension between the unilateral and bilateral conditions in four of the five turtles demonstrating this difference.

The phase of rub onset within the hip cycle was also not significantly different for unilaterally evoked and bilaterally evoked scratching in the majority of turtles. Statistically significant differences in the phase of rub onset occurred in two of the eight turtles analyzed for rostral scratch and for one of the eight analyzed for pocket scratch (Watson U² test, P < 0.01). Only one turtle exhibited significant differences between the bilateral and unilateral conditions in both the phase of knee extension onset and the phase of rub onset.

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**TABLE 1. Summary of pairwise statistical comparisons for pooled data for each of three forms of scratch and two forms of swim**

<table>
<thead>
<tr>
<th>Form and Behavioral Comparisons</th>
<th>A: Hip Angle at Behavioral Event, °</th>
<th>B: Phase of Onset of Knee Extension</th>
<th>C: Phase of Onset of Behavioral Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rostral vs. pocket</td>
<td>3.7 ± 0.4 vs. 2.0 ± 0.4</td>
<td>0.04 ± 0.09 vs. 0.06 ± 0.06</td>
<td>0.62 ± 0.06 vs. 0.76 ± 0.09</td>
</tr>
<tr>
<td>Rostral vs. caudal</td>
<td>6.9 ± 0.4 vs. 2.0 ± 0.4</td>
<td>0.04 ± 0.09 vs. 0.06 ± 0.06</td>
<td>0.62 ± 0.06 vs. 0.77 ± 0.07</td>
</tr>
<tr>
<td>Rostral vs. forward swim</td>
<td>9.0 ± 0.4 vs. 2.0 ± 0.4</td>
<td>0.04 ± 0.09 vs. 0.06 ± 0.06</td>
<td>0.62 ± 0.06 vs. 0.77 ± 0.07</td>
</tr>
<tr>
<td>Rostral vs. back-paddle</td>
<td>9.0 ± 0.4 vs. 2.0 ± 0.4</td>
<td>0.04 ± 0.09 vs. 0.06 ± 0.06</td>
<td>0.62 ± 0.06 vs. 0.77 ± 0.07</td>
</tr>
<tr>
<td>Pocket vs. caudal</td>
<td>15.6 ± 0.4 vs. 2.0 ± 0.4</td>
<td>0.04 ± 0.09 vs. 0.06 ± 0.06</td>
<td>0.62 ± 0.06 vs. 0.77 ± 0.07</td>
</tr>
<tr>
<td>Pocket vs. forward swim</td>
<td>3.4 ± 0.4 vs. 2.0 ± 0.4</td>
<td>0.04 ± 0.09 vs. 0.06 ± 0.06</td>
<td>0.62 ± 0.06 vs. 0.77 ± 0.07</td>
</tr>
<tr>
<td>Pocket vs. back-paddle</td>
<td>3.7 ± 0.4 vs. 2.0 ± 0.4</td>
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</tr>
<tr>
<td>Caudal vs. forward swim</td>
<td>15.6 ± 0.4 vs. 2.0 ± 0.4</td>
<td>0.04 ± 0.09 vs. 0.06 ± 0.06</td>
<td>0.62 ± 0.06 vs. 0.77 ± 0.07</td>
</tr>
<tr>
<td>Caudal vs. back-paddle</td>
<td>3.4 ± 0.4 vs. 2.0 ± 0.4</td>
<td>0.04 ± 0.09 vs. 0.06 ± 0.06</td>
<td>0.62 ± 0.06 vs. 0.77 ± 0.07</td>
</tr>
</tbody>
</table>

Values are means ± SD for the angular data (hip angle at behavioral event) and means ± the mean angular deviation for the phase data (phase of onset of knee extension or behavioral event). Statistical comparisons of angular data were by Mann-Whitney U test; comparisons of phase data were by Watson U² test. * Values are significantly different at P < 0.005. † Values are significantly different at P < 0.05. ** P > 0.05.
**Contralateral limb activity with unilateral stimulation**

In scratch behavior, there was often movement of the limb contralateral to the side of stimulation. In the rostral scratch, the contralateral movement had a limited range of motion and usually involved only hip movement. The one exception to this was a single episode in one turtle in which bilateral rostral scratching was produced in response to a right unilateral stimulation (Fig. 7A). This animal produced seven cycles of rhythmic behavior in the contralateral limb. Analysis of this episode demonstrated that the left limb was directed toward the left rostral scratch receptive field but the left toe did not come in contact with the shell bridge to perform a rub. In this contralateral limb, the phase of the onset of knee extension was slightly later than that observed in the same limb when it responded to stimulation in the ipsilateral rostral scratch receptive field; this difference was statistically significant (Watson $U^2$ test, $P < 0.01$).

Of the eight turtles analyzed for pocket scratch, four had notable movements of a contralateral hindlimb during ipsilateral stimulation. The contralateral knee extended less than in the normal pocket scratch (Fig. 7B). The contralateral knee and hip joint angles were in phase, however, as is characteristic of pocket scratch. The phase of the onset of knee extension within the hip cycle was significantly different in ipsilaterally evoked and contralaterally evoked pocket scratching (Watson $U^2$ test, $P < 0.01$) in five of the six episodes produced by the four turtles with notable contralateral limb movement. In the remaining four turtles, those contralateral limb movements that occurred involved very small excursions with no consistent phase relationships.

During ipsilaterally evoked caudal scratch, by contrast, contralateral hip movements often occurred in a 1:1 relationship with the ipsilateral hip movements. Of the three turtles for which contralateral movements were analyzed during unilaterally evoked caudal scratching, all demonstrated contralateral activity in at least one hindlimb with unilateral stimulation. In two of the three turtles, each hindlimb moved during stimulation of the opposite side. In these two turtles, there was an identifiable rub performed by the limb contralateral to the stimulus (Fig. 7C); this rub was always directed at a site in the caudal scratch receptive field that was a mirror image of the site being stimulated.

![FIG. 6. Angular position of the hip at the onset of the behavioral event (rub for scratch, powerstroke for swim) for each of the 5 behaviors.](image)

DISCUSSION

The major results of this paper are the demonstrations of 1) kinematic similarities between specific forms of one task and specific forms of another task and 2) kinematic differences between one form of a task and another form of the same task. Forward swimming kinematics were similar to rostral scratching kinematics; back-paddling kinematics were similar to both pocket scratching and caudal scratching kinematics. Forward swimming kinematics were different from back-paddling kinematics; rostral scratching kinematics were different from both pocket scratching and caudal scratching kinematics. Not all forms of the same task show major kinematic differences, however; there were similarities in the kinematics of pocket scratching and caudal scratching. The demonstration of kinematic similarities for different behaviors supports the concept that some of these similarities may be the result of shared neuronal circuits for these different behaviors.

An additional important result of this paper is the observation that, for most cases, intralimb kinematic features of unilateral scratching were similar to corresponding features during bilateral scratching. This observation, in the spinal turtle, applied both to same-form bilateral scratching and mixed-form bilateral scratching. This establishes that the spinal cord can appropriately control the kinematics of a hindlimb’s movements while the contralateral hindlimb is displaying a variety of different movements. In addition, in the intact behaving turtle, the kinematics of a hindlimb displaying the forward swimming form were similar during same-form forward swimming and mixed-form turning swimming. These observations in the intact animal emphasize that a mixed-form behavior is part of the turtle’s repertoire of naturally performed motor acts.

Intralimb kinematics

The angular position of the hip at onset of the behavioral event (the rub in scratching, the powerstroke in swimming) differed for each form of scratch and for both forms of swim. The mean value of hip angle at powerstroke onset for back-paddle behavior was between the mean values of hip angle at rub onset for pocket scratch and for caudal scratch. The amount of hip extension varied considerably during back-paddle. In cycles with large hip excursions, the angle of the hip at event onset in back-paddle resembled that of the caudal scratch. In less robust responses, the hip excursion was limited and the angle of the hip at event onset resembled that of pocket scratch.

Phase-based measures revealed both similarities and differences between behaviors. For the rostral scratch and the forward swim, the phase of the onset of knee extension began during hip flexion, but at statistically different phases of the hip cycle. This was attributable to differences in the degree of hip flexion attained in each behavior. In the rostral scratch, the hip must be fully flexed to bring the knee into the pocket and the distal parts of the limb into the appropriate position to achieve an effective rub. The onset of the rub occurred just before full extension of the knee. This requirement was not present for the forward swim: there was no need for the hip to be fully flexed for the powerstroke to be effective. In addition, there was no need for the knee to be fully withdrawn into the pocket and therefore the knee began to extend earlier in the hip cycle. Our observation of a significant difference in the phase of onset of knee extension when rostral scratch is compared with forward swim supports our suggestion that there are differences in the requirements of these behaviors.

In the pocket scratch, caudal scratch, and back-paddle, the knee extension began during hip extension; there were no statistical differences among these three behaviors in the phase of onset of knee extension within the hip cycle. This observation is consistent with the overall similarity of these three behaviors. In each case, the knee was maximally flexed just after the onset of hip extension. In the pocket scratch and the back-paddle, the knee then extended rapidly; in the caudal scratch, the knee extended more gradually.

The phase of the onset of the behavioral event was not statistically different in rostral scratch and forward swim. In both behaviors, the behavioral event began shortly after the onset of hip extension. In forward swim, knee extension began earlier in the hip cycle than in rostral scratch, and the onset of the powerstroke coincided with peak knee extension. There was also no statistically significant difference in the phase of onset of the behavioral event between pocket scratch and caudal scratch. In contrast, the phase of onset of the powerstroke for the back-paddle was significantly different from the phase of onset of the behavioral event in all other behaviors examined. Back-paddle was the only form studied here in which the behavioral event began during hip flexion.

Within a form, the trajectory of the limb was similar among all turtles performing the same form of scratch. We used one stimulus point for each scratch receptive field; however, we would expect slightly different trajectories in response to stimulation of different points within a given form’s receptive field. Although there were individual variations in the excursion of the limb, the overall shape of the trajectory in response to stimulation of a given site was comparable between turtles. This result of similar limb trajectories in response to stimulation of a specific site in turtles differs from the result of more variable limb trajectories observed during scratching in the cat (Kuhta and Smith 1990). In cats, some of the variability may be attributed to differences in body posture (Abraham and Loeb 1985; Kuhta and Smith 1994). In turtles, however, body posture is a constrained parameter because of the rigid nature of the shell. The kinematic differences between the three scratch forms in the turtle may therefore reflect the diverse requirements of the behavioral goals of reaching diverse locations on a rigid body surface.

Stein (1983) suggested that in turtles there are kinematic similarities 1) between forward swim and rostral scratch and 2) between back-paddle and caudal scratch. The present results support those suggestions and in addition demonstrate that back-paddle was similar to both pocket scratch and caudal scratch. These movement observations lead to suggestions about the organization of neuronal circuits that control
these movements. In particular, is there some sharing of circuitry for rostral scratch and forward swim? In addition, is there some sharing among the circuits for pocket scratch, caudal scratch, and back-paddling? Previous work with single-unit recordings supports the concept of shared circuitry among left and right rostral scratch and pocket scratch circuitry (Berkowitz and Stein 1994a,b). Additional work with a hindlimb hemienlargement preparation provides further support for shared circuitry between left and right rostral scratch circuitry (Stein et al. 1995). The present paper provides indications for additional sharing of circuitry controlling hindlimb motor rhythms.

Intralimb phase during bilaterally evoked scratching

For the most part, the scratching performance of an individual limb was not altered when the contralateral limb was also induced to scratch at the same time. In particular, the hip angle at the onset of the rub was similar for 17 of 19 comparisons (Fig. 6). The few instances in which there were differences between the phase of the onset of the rub under the unilateral and bilateral stimulus are most likely due to shortening of the hip excursion that occurred in four of the bilateral trials. It is possible that excitation from contralateral elements resulted in relatively early onset of hip flexion in these episodes. This shortening of the excursion caused the rub to occur relatively later in the cycle period.

Rhythmic behavior in the contralateral limb

In the performance of scratch behavior, there may be tonic muscle activity present in a contralateral limb not engaged in the rub event (Sherrington 1910). The present study demonstrates, however, that there may be rhythmic movement of the hindlimb contralateral to the stimulus. Rhythmic activity during ipsilateral scratching has also been observed in contralateral motor output (Berkowitz and Stein 1994a; Currie and Stein 1989; Deliagina et al. 1981; O’Donovan et al. 1982; Stein et al. 1995) and in contralateral interneurons (Berkowitz and Stein 1994a,b). For most episodes of rostral and pocket scratch in this study, the contralateral hindlimb did not perform a functional rub during these movements. In contrast, for the caudal scratch, the contralateral limb often rubbed a site on that side that was the mirror image of the point being stimulated. This bilateral response for the caudal scratch may be due, in part, to the proximity of the left and the right caudal scratch receptive fields.

Relationships of kinematics to motor patterns

Previous studies of electromyographic (EMG) recordings during the three forms of scratching in spinal turtles have demonstrated rhythmic alternation between hip flexor and hip extensor EMG activities in each movement cycle (Roberson et al. 1985; Stein et al. 1986). Kinematic measurements in the present study, as well as in earlier studies (Mortin et al. 1985), demonstrate rhythmic alternation between hip flexion and hip extension. The present study adds to these observations with the discovery of a specific minimum hip angle for each form and a distinct maximum hip angle for the rostral scratch compared with each of the other forms. These kinematic observations indicate that analyses of the amplitude of hip flexor and extensor motor output may be useful in future studies of motor patterns during turtle scratching.

Comparison of EMG activities during forward swimming and rostral scratching is limited to brief reports (Stein 1981; Stein and Johnstone 1986). For both behaviors, there is similar timing of knee extensor activity in the cycle of hip EMG activities: the offset of knee extensor activity occurs near the offset of hip flexor activity. The present study establishes kinematic similarities between these two behaviors as well.

There are important differences between the timing of kinematic events, e.g., onset of hip extension, and of EMG events, e.g., onset of hip extensor activity. An example of these differences can be revealed for the rostral scratch by examining results from several studies. Kinematic measurements establish that the rub of the rostral scratch takes place after the hip has begun extending (Fig. 3A) (Fig. 5A of Mortin et al. 1985). In contrast, EMG data establish that the rub of the rostral scratch takes place during hip flexor EMG activity and before hip extensor EMG activity (Fig. 1A of Robertson et al. 1985). Future quantitative studies of simultaneous measures of kinematics and motor outputs for the behaviors reported in the present paper are now needed.

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