Scratch-Swim Hybrids in the Spinal Turtle: Blending of Rostral Scratch and Forward Swim

GAMMON M. EARHART AND PAUL S. G. STEIN
Department of Biology and Program in Movement Science, Washington University, St. Louis, Missouri 63130

Earhart, Gammon M. and Paul S. G. Stein. Scratch-swim hybrids in the spinal turtle: blending of rostral scratch and forward swim. J. Neurophysiol. 83: 156–165, 2000. Turtles with a complete transection of the spinal cord just posterior to the forelimb enlargement at the D2–D3 segmental border produced coordinated rhythmic hindlimb movements. Ipsilateral stimulation of cutaneous afferents in the midbody shell bridge evoked a rostral scratch. Electrical stimulation of the contralateral dorsolateral funiculus (DLF) at the anterior cut face of the D3 segment activated a forward swim. Simultaneous stimulation of the ipsilateral shell bridge and the contralateral DLF elicited a scratch-swim hybrid: a behavior that blended features of both rostral scratch and forward swim into each cycle of rhythmic movement. This is the first demonstration of a scratch-locomotion hybrid in a spinal vertebrate. The rostral scratch and the forward swim shared some characteristics: alternating hip flexion and extension, similar timing of knee extensor activity within the hip cycle, and a behavioral event during which force was exerted against a substrate. During each cycle, each behavior exhibited three sequential stages, pre-event, event, and post-event. The rostral scratch event was a rub of the foot against the stimulated shell site. The forward swim event was a powerstroke, a hip extension movement with the foot held in a vertical position with toes and webbing spread. The two behaviors differed with respect to several features: amount of hip flexion and extension, electromyogram (EMG) amplitudes, and EMG duty cycles. Scratch-swim hybrids displayed two events, the scratch rub and the swim powerstroke, within each cycle. Hybrid hip flexion excursion, knee extensor EMGs, and hip flexor EMGs were similar to those of the scratch; hybrid hip extension excursion and hip extensor EMGs were similar to those of the swim. The hybrid also had three sequential stages during each cycle: 1) a combined scratch pre-rub and swim post-powerstroke, 2) a scratch rub that also served as a swim pre-powerstroke, and 3) a swim powerstroke that also served as a scratch post-rub. Merging of the rostral scratch with the forward swim was possible because of similarities between the sequential stages of the two forms, making them biomechanically compatible for hybrid formation. Kinematic and myographic similarities between the rostral scratch and the forward swim support the hypothesis that the two behaviors share common neural circuitry. The common features of the sequential stages of each behavior and the production of scratch-swim hybrids provide additional support for the hypothesis of a shared core of spinal cord neurons common to both rostral scratch and forward swim.

INTRODUCTION

A task is a behavior in which an organism achieves a particular goal. Each task may be accomplished in more than one manner. Each different motor strategy used to perform a particular task is called a form of that task (Stein et al. 1986b).

Locomotion is a task where the goal of the organism is to move its center of mass. There are several forms of overground locomotion, e.g., forward walking versus backward walking (Buford and Smith 1990a,b; Grasso et al. 1998; Stein and Smith 1997; Thorstensson 1986; Winter et al. 1989). For some rhythmic behaviors, the features of two forms or tasks are combined into a single behavior such that each cycle expresses features of both forms or tasks. This blended behavior is called a hybrid (Carter and Smith 1986a,b; Mortin et al. 1985; Robertson et al. 1985; Stein et al. 1986a,b).

The turtle spinal cord can produce hindlimb motor outputs for scratch and swim tasks. During scratch, the goal of the turtle is to rub against a stimulated site on the shell; during swim, the goal of the turtle is to generate force against the water and move its center of mass. There are three forms of scratch: rostral, pocket, and caudal; each is used to rub a specific region of the shell (Mortin et al. 1985). There are two forms of swim: forward swim and backpaddle (Field and Stein 1997a,b; Lennard and Stein 1977; Stein 1978). We focus on the rostral scratch and the forward swim in the present paper.

Both the rostral scratch and the forward swim have behavioral events during which force is exerted against a substrate. The rostral scratch event is the rub of the foot against the stimulated site on the midbody shell bridge (Field and Stein 1997a; Mortin et al. 1985). The forward swim event is the powerstroke, a hip extension movement with the foot held vertically and the toes and webbing spread (Davenport et al. 1984; Field and Stein 1997a; Lennard and Stein 1977; Stein 1978; Zug 1971). During the forward swim powerstroke, propulsive force is exerted against the water. In the present study, the turtle’s carapace was restrained; thus there was no center-of-mass movement when the swim powerstroke occurred. The rostral scratch and the forward swim are kinematically similar (Field and Stein 1997a,b; Stein 1983). Their motor patterns are also similar: both have alternating hip flexor and extensor activity and similar timing of monoarticular knee extensor activity within the hip cycle electromyograms (EMGs): Stein and Johnstone 1986; electroneuromyograms (ENGs): Jurank and Currie 1998, 2000). Their motor patterns differ with respect to amplitudes of activity. Jurank and Currie (1998, 2000) have also demonstrated interruption of fictive rostral scratch with fictive forward swim, and vice versa.

The present paper demonstrates a novel interaction between the rostral scratch and the forward swim. We provide kine- matic and electromyographic evidence for a scratch-swim hybrid behavior with combined features of two distinct tasks, rostral scratch and forward swim, in each of several successive cycles of a rhythmic movement. Blending of two forms of the
same task has been demonstrated previously for scratching in the spinal turtle (Mortin et al. 1985; Robertson et al. 1985; Stein et al. 1986a). This is the first demonstration in the spinal turtle of blending of two different tasks to form a hybrid. Our data were presented previously in an abstract (Earhart and Stein 1999).

METHODS

Surgical preparation

Red-eared turtles \( (n = 10) \), Trachemys scripta elegans, were studied. All surgery was performed under hypothermic anesthesia (Melby and Altman 1974). Turtles were placed in crushed ice for at least 1 h before the start of surgery and kept in ice throughout the procedure. For spinalization, a channel was drilled along the midline of the carapace over the second (D2) and third (D3) dorsal segments of the spinal cord. The spinal cord was completely transected between the D2 and D3 segments, a wax well was constructed around the midline channel over the exposed spinal cord, and the well was filled with turtle saline.

After complete transection of the spinal cord, electrodes were implanted in selected hindlimb muscles: a biarticular knee extensor (triceps femoris pars iliobitalis), a monoarticular knee extensor (triceps femoris pars femorotibialis), a hip flexor (puboischiofemoralis internus pars anteroventralis), and a hip extensor (flexor cruris pars flexor tibialis internus) (Robertson et al. 1985). We used bipolar electrodes, each a pair of 100-μm silver wires with enamel coating that were glued together with Permabond 910 (National Starch and Chemical, Englewood, NJ). For hip flexor implantation, a rectangular opening was drilled in the ventral plastron over the pelvic region, providing access to the hip flexor muscle belly. For the knee extensor and hip extensor, a triangular opening was drilled in the dorsal carapace, and muscle bellies were accessed through small incisions of the overlying skin. Electrodes for the knee extensors and hip extensor were threaded under the skin and into the internal cavity exposed by the hole in the carapace. Electrode tips were implanted directly into the muscle bellies and glued in place. Following electrode placement in the hip flexor, the hip flexor electrode was glued to the plastron and the hole in the plastron was sealed with wax. Following electrode placement in the knee extensors and hip extensor, the knee extensor and hip extensor electrodes were secured to the sides of the hole in the carapace, which was then sealed with wax. Skin incisions overlying the implanted knee extensors and hip extensor were closed with glue and covered with Op-Site (Smith and Nephew Medical Unlimited, Hull, UK). The turtle was removed from ice and warmed to room temperature.

Stimulation and recording

Reflective markers were placed over the hip, knee, ankle, and third toe of each turtle. A band clamp that encircled the midbody was used to suspend each turtle in a tank of water. The water level was adjusted so that the turtle’s limbs remained below the water but the turtle could lift its head above the water for breathing. Rostral scratching was evoked using the smooth glass tip of a probe to stimulate mechanically the shell bridge at the SP2 site (Fig. 1) (Mortin et al. 1985). Force was recorded using a Grass FT-03 force transducer (Astromed, West Warwick, RI) attached to the probe. Forward swimming was evoked by electrical stimulation of the dorsolateral funiculus (DLF) at the anterior cut face of the D3 segment of the spinal cord (Fig. 1) (Lennard and Stein 1977). The cut face was accessed in the midline channel drilled for spinalization. Distinctions between gray and white matter were clearly visible on the anterior cut face, allowing for visual identification of the DLF. Electrical stimulation was delivered via the cut ends of a bipolar electrode, consisting of a pair of 75 micrometer silver wires with enamel coating. The stimulating electrode was placed under visual guidance, and DLF stimulation in the ranges of 2–10 V, 30–50 Hz, and 0.4–6 ms pulse durations was delivered. Stimulation of some DLF sites within the ranges specified did not evoke a forward swim. In these cases, the electrode was moved to a new site until stimulation within the specified ranges evoked a forward swim in the hindlimb contralateral to the side of stimulation. Seven of the 10 turtles studied produced scratch-swim hybrids in response to simultaneous stimulation of the ipsilateral shell bridge and contralateral DLF. One of these seven turtles also produced scratch-swim hybrids in response to sequential stimulation in which the termination of ipsilateral shell stimulation was followed immediately by the onset of contralateral DLF stimulation.

Movement was recorded by use of a mirror placed below the tank at an angle of 45°. Hindlimb movements were videotaped at 60 Hz with a shutter speed of 1/250 s. Hindlimb scratching and swimming movements were relatively planar; thus a single camera was sufficient for measurement of joint angles. EMGs from each muscle were amplified, filtered (100–1,000 Hz band-pass), and recorded on digital audio tape (DC-5 kHz band-pass). In all turtles, the monoarticular knee extensor, the hip flexor, and the hip extensor were recorded. In five of the seven turtles that produced scratch-swim hybrids, the biarticular knee extensor was also recorded. A synchronization signal, linked to opening of the camera shutter and generated by the Peak Event Synchronization Unit (Peak Performance Technologies, Englewood, CO), was recorded on the video and the digital audio tapes so that movement data and EMGs could be synchronized for analysis.

Data analysis

Kinematic analyses were performed on a total of 210 cycles, composed of 30 cycles from each of the 7 turtles that produced scratch-swim hybrids. The 30 cycles from each turtle included 10 rostral scratch cycles in response to shell stimulation, 10 forward swim cycles in response to spinal cord stimulation, and 10 scratch-swim hybrid cycles in response to simultaneous stimulation. Episodes were selected for analysis if they contained at least five full cycles of a behavior. Video tape records of selected episodes were replayed, and the X and Y coordinates for each marker manually digitized (30 Hz) using a Peak 5.2 system (Peak Performance Technologies, Engle-
wood, CO). Hip angle was defined as the angle between the thigh and the ventral midline of the body; knee angle was defined as the angle between the thigh and the shank (Fig. 1). Hip and knee angle values increased as the respective joints extended and decreased as the joints flexed. Toe trajectories were obtained by viewing videos frame by frame and tracing the path of the third toe on an acetate sheet placed over the video screen.

The timing of behavioral events was determined from video records. For the rostral scratch, rub was defined as the time during which the foot made contact with the stimulated shell site. For the forward swim, the powerstroke was defined as the time during which the hip was extending and the foot was held in a vertical position with toes and webbing spread.

A total of 150 episodes of EMGs (50 scratch, 50 swim, and 50 scratch-swim hybrids) was analyzed in the 7 turtles that produced scratch-swim hybrids. Each episode of scratch-swim hybrid was matched with a scratch episode and a swim episode from the same turtle. Each episode consisted of at least five cycles. EMGs were digitized at 2 kHz using Cambridge Electronic Design 1401 plus hardware and Spike2 software (Cambridge, UK). EMGs were rectified and averaged so that the mean of 20 successive rectified measurements was calculated, giving 100 data points per second.

For some episodes, only EMGs were analyzed. For other episodes, both EMGs and kinematics were analyzed. For these episodes, software custom written by Dr. Gavin Perry merged kinematic and EMG files, aligning the two data sets using the synchronization signal recorded on each. Onsets and offsets of hip flexion and knee extension movements were determined (Field and Stein 1997a). For all episodes, EMG burst onset and offset times for each muscle were determined. EMG amplitudes were obtained by averaging the activity within each burst, such that the amplitudes for a scratch episode were 100% and amplitudes of the related swim and hybrid episodes expressed as a percentage of the scratch values. Cycle period was defined as the time from the onset of one burst of hip extensor activity to the onset of the next burst of hip extensor activity. Duty cycle, defined as the percentage of cycle period during which a muscle was active, was calculated as burst duration multiplied by 100 and then divided by cycle period.

Phase analyses were used to determine the timing of knee extension onset with respect to hip movement and the timing of monoarticular knee extensor EMG onset with respect to hip muscle activity. Dual-referent phase analyses were used to normalize the hip flexion and hip extension phases of each behavior. Dual-referent analyses are preferred to single-referent techniques in situations where the duty cycle of the referent is variable. Dual-referent methods normalize for active and inactive periods of the referent; thus changes in referent duty cycle will not produce shifts in phase values obtained (see Fig. 2 of Berkowitz and Stein 1994b). Events occurring during the hip flexion portion of the cycle had phase values between 0 and 0.5, whereas those occurring during hip extension had phase values between 0.5 and 1.0.

Kinematic phase analyses were performed using the method described by Field and Stein (1997a). The phase at which knee extension onset occurred was defined as the latency between hip flexion onset and knee extension onset, divided by twice the duration of hip flexion. All knee extension onsets analyzed occurred during hip flexion, so calculations for events occurring during hip extension are not presented.

Motor pattern phase analyses are described in Berkowitz and Stein (1994b). In the present study, the hip extensor rather than the hip flexor was chosen as a referent because the hip flexor had very short burst durations in the forward swim and use of the hip flexor as a referent for the swim gave inconsistent results. Using the hip extensor as a referent, hip extensor offset was given a phase value of 0 and hip extensor onset a phase value of 0.5. The phase of monoarticular knee extensor onset was defined as the latency between hip extensor offset

FIG. 2. Toe trajectories and events of the 3 behaviors. A: rostral scratch. B: forward swim. C: scratch-swim hybrid. Asterisks denote the scratch rub of the foot against the stimulated shell site. Thick dashed lines denote the swim powerstroke. Hindlimb position at the scratch rub is shown in A. Hindlimb position in the middle of the swim powerstroke is shown in B. Two hindlimb positions, one at the scratch rub and one in the middle of the swim powerstroke, are shown for the scratch-swim hybrid in C.
and monoarticular knee extensor onset, divided by twice the duration of hip extensor quiescence. All monoarticular knee extensor onsets analyzed occurred during hip extensor quiescence, so calculations for events occurring during hip extensor activity are not presented.

Because the phase data are cyclic, vector algebra techniques (Batschelet 1981) were used to determine average phase values. Each phase was converted to a two-dimensional unit vector with an angle of $2\pi \phi$ and a length of 1. Unit vectors were averaged using vector addition. The angle of the mean vector, divided by $2\pi$, was the mean phase; it had values between 0 and 1. Mean angular deviation, a measure of phase data dispersion, was also calculated.

**Statistical analyses**

Kinematic and myographic parameters were compared across conditions using nonparametric statistics. Mean minimum and maximum hip angles, mean EMG amplitudes, mean EMG duty cycles, and mean period were compared across behaviors using the Mann-Whitney $U$ test (Hays 1994). Mean phase of knee extension movement onset and monoarticular knee extensor EMG onset were compared across conditions using the Watson $U^2$ test for circular data (Batschelet 1981).

Pair-wise comparisons of scratch to swim, scratch to hybrid, and swim to hybrid were used for all statistical analyses. A Bonferroni correction was used to account for the increase in type I error that resulted from doing multiple tests. Because three separate pair-wise comparisons were performed, the chosen $\alpha$ level of 0.05 was divided by 3. All comparisons were tested at the Bonferroni-adjusted level of 0.0166. Comparisons reported to be statistically significant had values of $P < 0.0166$.

**RESULTS**

Mechanical stimulation of the shell bridge at SP2 evoked rostral scratching movements in the ipsilateral hindlimb. Electrical stimulation of the contralateral DLF at the anterior cut face of the D3 segment evoked forward swimming movements in the ipsilateral hindlimb. In 7 of 10 turtles, simultaneous stimulation of the ipsilateral shell bridge and the contralateral DLF evoked a scratch-swim hybrid, a rhythmic hindlimb behavior in which features of both rostral scratch and forward swim were expressed in each individual cycle of the multicycle response in the ipsilateral hindlimb. In the other three turtles, simultaneous stimulation elicited forward swimming movements only. There were no apparent differences in the scratch or swim behaviors of these three turtles, compared with those of the seven that did produce scratch-swim hybrids. Data from the three turtles that did not produce scratch-swim hybrids were not analyzed.

**Kinematics**

The rostral scratch, forward swim, and scratch-swim hybrid were distinguished from one another based on toe trajectory and behavioral events (Fig. 2). During the rostral scratch and the scratch-swim hybrid, the limb reached toward and the foot rubbed against the stimulated shell site. A rub against the shell did not occur in the forward swim. The scratch rub, which constituted the only event of the rostral scratch and the first of two events of the scratch-swim hybrid, is marked by asterisks in Fig. 2, A and C. For the scratch, the toe reached its most medial position anteriorly at the stimulated site on the shell bridge, SP2. The toe also reached this medial anterior position during the hybrid, but not during the swim.

During the forward swim and the scratch-swim hybrid, the limb performed a swim powerstroke: the foot was held vertically with toes and webbing spread as the hip extended. Spreading of the toes and webbing did not occur in the rostral scratch. The swim powerstroke, which constituted the only event of the swim and the second of two events of the hybrid, is marked by thick dashed lines in Fig. 2, B and C. For the swim, the toe reached its most medial position posteriorly at a location caudal to the rear edge of the carapace. The toe also reached this medial posterior position during the hybrid, but not during the scratch.

Thus the scratch-swim hybrid displayed two events: a scratch rub and a swim powerstroke. The toe trajectory of the hybrid encompassed both the scratch and the swim toe trajectories, merging the two into a single smooth trajectory.

The rostral scratch and the forward swim were also distinguished from one another based on minimum and maximum hip angles (Fig. 3) (see also Field and Stein 1997a). The hip flexed more in the rostral scratch than in the forward swim and extended more in the forward swim than in the rostral scratch. Thus the minimum hip angle was smaller in the scratch than in the swim; the maximum hip angle was larger in the swim than in the scratch. The scratch-swim hybrid had a minimum hip angle similar to that of the scratch and a maximum hip angle similar to that of the swim.

Hip angle versus knee angle plots provided an additional means of distinguishing the rostral scratch from the forward swim. The hip angle versus knee angle plot for the scratch was roughly triangular in shape (Fig. 4A), for the swim was ovoid (Fig. 4B), and for the hybrid combined elements of the two such that the base of the triangle was merged with the upper portions of the oval (Fig. 4C).

For the rostral scratch, the hip angle versus knee angle plot (Fig. 4A) was characterized by a horizontal base, illustrating that the knee extended while the hip remained flexed (Mortin et al. 1985). At the peak of this knee extension, the foot rubbed against the stimulated site on the shell (asterisk, Fig. 4A). A similar scratch rub occurred in the hybrid (asterisk, Fig. 4C), and the hybrid hip angle versus knee angle plot had a horizontal base similar to that of the scratch plot. The horizontal base and occurrence of the scratch rub were not present in the swim, which had a hip angle versus knee angle plot with a rounded base. Scratch minimum knee angle, denoted by the left vertical dashed lines in Fig. 4, was smaller than swim minimum knee angle. Scratch maximum knee angle, denoted by the right vertical dashed lines in Fig. 4, was larger than swim maximum knee angle. The hybrid had minimum and maximum knee angles similar to those of the scratch.

Hip angle versus knee angle plots also illustrated the differences in hip angle minima and maxima. The bottom horizontal dashed lines on each panel of Fig. 4 show the minimum hip

![FIG. 3. Average minimum and maximum hip angles ±SD for the 3 behaviors. Asterisks denote significance at $P = 0.0166$ (Mann-Whitney $U$). NS, not significant.](image)
angle for the scratch; the top horizontal dashed lines show the maximum hip angle for the swim. The hybrid plot spans the area between both of these lines, indicating that the hybrid had hip flexion excursion similar to that of the scratch and hip extension excursion similar to that of the swim.

Mean phase values for the onset of knee extension within the dual-referent hip movement cycle are given in Table 1. The rostral scratch and the forward swim had very similar phasing, with knee extension onset occurring near the middle of the hip flexion phase (Field and Stein 1997a). Hybrid mean phase values were also very similar to those of the scratch and the swim. Differences among the three behaviors were not significant when testing within each turtle or across all turtles (Watson U²).

**EMG**

The rostral scratch and the forward swim motor patterns were distinguished from one another by differences in amplitudes and duty cycles (Juraneck and Currie 1998, 2000; Stein and Johnstone 1986). Figure 5 shows scratch, swim, and hybrid EMGs with the same set of vertical scales (Fig. 5, A, B1, and C, respectively). Figure 5B2 shows the swim data in B1 at 10 times the set of vertical gains of A, B1, and C. This higher gain representation is provided because the monoarticular knee extensor and hip flexor amplitudes are so low in the swim that they are difficult to see when shown with the same set of scales as the scratch and the hybrid, as in Fig. 5B1.

EMG amplitudes differed among the behaviors (Fig. 6). Knee extensor and hip flexor amplitudes were significantly larger for the rostral scratch than for the forward swim.
whereas hip extensor amplitude was significantly larger for the swim than for the scratch (Mann-Whitney U). Knee extensor and hip flexor amplitudes were not significantly different between the scratch and the hybrid. The hybrid had hip extensor amplitudes more similar to those of the swim than those of the scratch. Hybrid hip extensor amplitudes were significantly larger than those of the scratch or the swim (Mann-Whitney U). In summary, the hybrid had knee extensor and hip flexor amplitudes similar to scratch but hip extensor amplitudes similar to swim (compare Fig. 5, A, B1, and C).

Duty cycle was another means of distinguishing among the behaviors (Fig. 7). Knee extensor and hip flexor duty cycles were significantly higher for the rostral scratch than for the forward swim, whereas hip extensor duty cycle was significantly higher for the scratch than for the swim (Mann Whitney U). The hybrid had knee extensor and hip flexor duty cycles intermediate between those of the scratch and those of the swim. Hybrid knee extensor duty cycles were significantly different from those of the scratch and the swim (Mann Whitney U). Hybrid hip flexor and hip extensor duty cycles were not significantly different from those of the swim, but were significantly different from those of the scratch (Mann Whitney U).

Comparisons of cycle period across the three behaviors revealed no significant differences. Mean cycle period for the rostral scratch was 0.89 ± 0.31 (SD) s, for the forward swim was 0.92 ± 0.25 s, and for the hybrid was 1.00 ± 0.25 s. We observed differences in variability of cycle period, however, noting that the swim had a very regular period whereas scratch period was more volatile. The hybrid had a stable period similar to that of the swim. Cycle period standard deviation in the scratch was significantly larger than in the swim or the hybrid (Mann Whitney U). There was no difference in cycle period standard deviation between the swim and the hybrid.

The mean phase values for the onset of the monoarticular knee extensor in the dual-referent hip extensor cycle are given in Table 1. Rostral scratch and forward swim had very similar phasing, with monoarticular knee extensor onset occurring near the middle of the hip flexor phase (Juranek and Currie 1998, 2000). Hybrid mean phase values were also very similar to those of the scratch and the swim. Differences among the three behaviors were not significant when testing within each turtle or across all turtles (Watson U^2).

**Sequential stimulation**

One of the turtles in this study exhibited a substantial scratch afterdischarge (Currie and Stein 1990) in which four to six cycles of scratch were produced following offset of the mechanical shell stimulation. In this turtle, we were able to obtain the scratch-swim hybrid through sequential delivery of me-
Mechanical shell stimulation followed by electrical DLF stimulation. The mechanical shell stimulus was used to evoke rostral scratch and, coincident with the offset of this mechanical shell stimulation, electrical DLF stimulation was initiated. This sequential presentation produced a response that began with rostral scratch, showed several hybrid cycles just after the offset of mechanical stimulation and onset of electrical stimulation, and ended with forward swim (Fig. 8). Thus the onset of electrical DLF stimulation at the offset of scratch stimulation evoked a swim that combined with the scratch afterdischarge to produce the hybrid. The average number of cycles of hybrid obtained with sequential stimulation ($n = 4.8 \pm 0.7$ cycles) was similar to the average number of cycles of afterdischarge obtained in scratch episodes ($n = 4.4 \pm 0.8$ cycles).

The rostral scratch cycles were characterized by greater hip flexion and less hip extension than the forward swim cycles. The scratch also showed higher amplitude monoarticular knee extensor and hip flexor amplitudes and lower hip extensor amplitudes than the swim. The hybrid showed hallmark features of both the scratch and the swim. The hybrid had two events, a scratch rub and a swim powerstroke. The hybrid had a minimum hip angle similar to the scratch and a maximum hip angle similar to the swim. Hybrid monoarticular knee extensor and hip flexor amplitudes were similar to those of the scratch, and hybrid hip extensor amplitudes similar to those of the swim.

**DISCUSSION**

The turtle spinal cord produced blends of the rostral scratch and the forward swim in response to simultaneous mechanical stimulation of the ipsilateral shell bridge and electrical stimulation of the contralateral DLF at the anterior cut face of the D3 segment. The scratch-swim hybrid displayed two events: a scratch rub of the foot against the stimulated shell site and a swim powerstroke during which the hip extended and the foot was held in a vertical position with toes and webbing spread. The hybrid toe trajectory combined the trajectories of the rostral scratch and the forward swim into a single smooth path. This is the first demonstration of a scratch-locomotion hybrid in a spinal vertebrate.

Rhythmic behavior may be characterized as a sequence of stages produced by a pattern generator (Kleinfeld 1986). Each cycle of rhythmic behavior may be represented by a linear chain, i.e., a fixed sequence in which specific stages occur in a particular order (Berridge et al. 1987). The formation of a hybrid of two behaviors depends on the biomechanical compatibility of the stages of the two behaviors. If the stages of two behaviors are very different, hybrid formation may be impossible. However, if the stages of one behavior are similar to those of the other behavior, the two will be biomechanically compatible for formation of a hybrid via merging of the stages of the two behaviors.

Rostral scratch and forward swim are both rhythmic behaviors in which each cycle can be represented by a sequence of stages. Both rostral scratch and forward swim consisted of three stages, pre-event, event, and post-event, performed in sequence during each cycle. For rostral scratch, these stages were prerub, rub, and postrub (Mortin et al. 1985). For forward swim, these stages were pre-powerstroke, powerstroke, and post-powerstroke (Lennard and Stein 1977). The prerub stage of the rostral scratch and the post-powerstroke stage of the forward
swim were similar; both exhibited hip flexion movements during which the foot was held in a horizontal position. The rub stage of the rostral scratch and the prepowerstroke stage of the forward swim were similar; both exhibited knee extension movements that occurred while the hip was flexed. The postrub stage of the rostral scratch and the powerstroke stage of the forward swim were similar; both exhibited hip extension movements, although the toes and webbing were spread during swim powerstroke but not during scratch postrub. We speculate that the similarities of stages in these two behaviors provided biomechanical compatibility that was consistent with the formation of the hybrid. The scratch-swim hybrid, like the individual behaviors, had three stages: 1) a scratch prerub and swim postpowerstroke combination, 2) a scratch rub that also served as a swim prepowerstroke, and 3) a swim powerstroke that also served as a scratch postrub. The similarity of stages between the two behaviors and the merging of stages in the hybrid support the hypothesis that the two behaviors share some pattern-generating circuitry.

Previous work has noted that the minimum and maximum hip angles for the rostral scratch and the forward swim are different (Field and Stein 1997a). We have confirmed this result and expanded on it, demonstrating correspondence of EMG amplitudes and duty cycles with hip angle minima and maxima. Smaller minimum hip angles in the scratch and the hybrid were associated with higher hip flexor amplitude and duty cycle. Greater maximum hip angles in the swim and the hybrid were associated with higher hip extensor amplitude and duty cycle. Higher EMG amplitudes were associated with the behavioral events during which force was exerted against a substrate. Higher knee extensor and hip flexor amplitudes were associated with the scratch rub; higher hip extensor amplitudes were associated with the swim powerstroke.

Thus rostral scratch and forward swim were distinguished from one another by EMG amplitudes. They were not distinguished from one another by phasing of knee movement or monoarticular knee extensor activity within the hip cycle, characteristics that are often excellent discriminators. Rostral scratch and forward swim had similar phasing of movement (knee extension onset during hip flexion) and of motor patterns (monoarticular knee extensor onset near the middle of the hip flexor burst). In contrast, forward swim and backpaddle have very different timings of knee extension onset; knee extension onset occurs near the middle of hip flexion for the forward swim but near the middle of hip extension in the backpaddle (Field and Stein 1997a). The three scratch forms can also be distinguished from one another by phasing of knee activity within the hip cycle. Monoarticular knee extensor onset occurs during the hip flexor burst in rostral scratch, during the hip extensor burst in pocket scratch, and near the offset of the hip extensor burst in caudal scratch (Robertson et al. 1985). In the cat, paw-shake and locomotion can be distinguished from one another by phasing of monoarticular knee extensor activity within the cycle of ankle motor activity. Vastus lateralis activity coincides with ankle flexor activity in paw-shake and with ankle extensor activity during locomotion (Smith et al. 1986).

**Other examples of hybrids**

Hybrids of two different tasks or of two different forms of a task have been demonstrated previously. Carter and Smith (1986a,b) demonstrated hybrids of two different tasks, paw-shake and stepping, in normal and in spinal cats. Cats produced several cycles of paw-shake during the swing phase of each step cycle. Paw-shake and stepping are biomechanically compatible for hybrid formation because the paw-shake can be performed during swing, when the foot is not in contact with the ground, without disrupting the step cycle. Hybrids of two scratch forms in response to two-site mechanical shell stimulation or stimulation within a transition zone have been demonstrated in the turtle. In rostral-pocket, pocket-caudal, and rostral-caudal hybrids, the turtle rubs the shell twice during each cycle (Mortin et al. 1985; Robertson et al. 1985; Stein et al. 1986a,b). Two scratch forms are biomechanically compatible for hybrid formation because each form has different timing of knee extension with the hip cycle to perform the rub. Two scratch rubs of different forms can be performed during each hip cycle to form a hybrid. These studies demonstrate that spinal structures can coordinate hybrids in the absence of supraspinal inputs. The present study adds support to this conclusion.

Hybrids of two forms of a task have also been demonstrated in humans. Horak and Nashner (1986) reported two forms of postural movements: the ankle strategy and the hip strategy. In response to horizontal perturbations, subjects use the ankle strategy if standing on a broad support surface and the hip strategy if standing on a support surface shorter than their feet. When standing on a surface of intermediate length, subjects use a blend of ankle and hip strategies, an ankle-hip hybrid.

Another example of human behavior that illustrates hybrid formation is scratching. A human can scratch some sites on the side of the thorax using either the side of the elbow or the hand. These sites can also be scratched using a hybrid strategy: the site is rubbed with the elbow and then with the hand during each single cycle of movement. This is possible because the two movements are biomechanically compatible. Other human scratch movements are not biomechanically compatible for hybrid formation. For example, a human scratches the upper back using a form with the elbow positioned above the shoulder; a human scratches the lower back using a form with the elbow positioned below the shoulder (Stein et al. 1986b). The below-shoulder and above-shoulder forms require very different upper extremity orientations. Biomechanical constraints prevent the human from reaching the upper back with the below-shoulder form or the lower back with the above-shoulder form. A human can switch between the two forms, performing the above-shoulder form in one cycle and the below-shoulder form in the next cycle, but the two forms cannot be incorporated into a single, smooth hybrid cycle because of their biomechanical incompatibility.

**Shared circuitry**

Our concepts of how pattern generators are organized have changed (Stein et al. 1997). Pattern generators are no longer viewed as static, unshared circuits each exclusive to a single behavior. In *Aplysia*, cerebral interneuron CC5 is known to participate in at least six distinct behaviors (Xin et al. 1996). Evidence from the crustacean stomatogastric system shows that two independent networks can fuse and operate as a single functional unit (Dickinson 1995; Dickinson et al. 1990; Meyrand et al. 1994). Svoboda and Fetcho (1996) demonstrated...
of the swim rhythm by activation of an escape behavior, supporting the concept of shared circuitry for swim and escape in goldfish. Soffe (1993) showed that both swimming and struggling in the *Xenopus* embryo are driven by a common set of premotor and motor neurons. Previous studies in the turtle support sharing between left and right side scratch (rostro, pocket, and caudal) circuitry (Currie and Gonsalves 1997, 1999; Field and Stein 1997b; Stein et al. 1995, 1998a,b). Single-unit recordings in turtle also support the concept of sharing of elements among left and right rostral and pocket scratch circuits (Berkowitz and Stein 1994a,b). Single-unit recordings in cat provide support for sharing of elements for stepping and scratching (Berkinblit et al. 1978). The demonstration in cats of paw-shake and step hybrids also supports the concept of shared circuitry (Carter and Smith 1986a,b; Smith et al. 1986). Thus there is strong evidence from many systems for sharing of circuitry among different behaviors.

Stein (1983) noted kinematic similarities between rostral scratch and forward swim. Quantitative analyses of kinematics confirmed this observation and led to the suggestion that there may be sharing of circuitry between rostral scratch and forward swim networks (Field and Stein 1997a). Motor pattern similarities, such as similar timing of the monourcicular knee extensor within the hip cycle, also support the possibility of shared circuitry (Juranek and Currie 1998, 2000; Stein and Johnstone 1986). Additional support comes from the demonstration of interruption and resetting of an ongoing forward swim by a brief rostral scratch (Juranek and Currie 1998, 2000; Stein 1981).

Differences in rostral scratch and forward swim EMG amplitudes served to discriminate between the two behaviors. Motor pattern amplitude differences between the behaviors may be produced by changes in interneuronal recruitment from classes active during both behaviors. A subset of neurons may be active during each behavior, and additional neurons may be recruited during the behavioral event of each to increase amplitudes during the time when force is exerted against a substrate. These additional neurons may be recruited from unshared populations or from within classes of neurons active during both behaviors. Such recruitment has been demonstrated in *Xenopus*, where additional interneurons not active in low-frequency swimming are recruited during struggling and during high-frequency swimming (Sillard and Roberts 1993; Soffe 1993). The kinematic and myographic similarities between rostral scratch and forward swim, as well as the similarities between the sequentially generated stages of the behaviors, support the hypothesis that network elements are shared between rostral scratch and forward swim circuits. The ability of the spinal cord to blend rostral scratch and forward swim into a single smooth behavior as demonstrated in the present paper provides additional support for this concept. We hypothesize that studies using single-unit recording techniques during rostral scratch and forward swim will reveal spinal interneurons that are active during both behaviors.

We thank A. Berkowitz for editorial assistance and G. Perry for software development.

This work was supported by National Institutes of Health Grants R01-NS-30786 and T32-HD-07434 and by a Promotion of Doctoral Studies Award from the Foundation for Physical Therapy, Inc. to G. M. Earhart.

Address for reprint requests: P.S.G. Stein, Dept. of Biology, Washington University, St. Louis, MO 63130.

Received 23 July 1999; accepted in final form 3 September 1999.

REFERENCES


Currie, S. N. and Gonsalves, G. G. Right-left interactions between rostral scratch circuitry (Berkowitz and Stein 1994a,b). Single-unit recordings in cat provide support for sharing of elements for stepping and scratching (Berkinblit et al. 1978). The demonstration in cats of paw-shake and step hybrids also supports the concept of shared circuitry (Carter and Smith 1986a,b; Smith et al. 1986). Thus there is strong evidence from many systems for sharing of circuitry among different behaviors.

Stein (1983) noted kinematic similarities between rostral scratch and forward swim. Quantitative analyses of kinematics confirmed this observation and led to the suggestion that there may be sharing of circuitry between rostral scratch and forward swim networks (Field and Stein 1997a). Motor pattern similarities, such as similar timing of the monourcicular knee extensor within the hip cycle, also support the possibility of shared circuitry (Juranek and Currie 1998, 2000; Stein and Johnstone 1986). Additional support comes from the demonstration of interruption and resetting of an ongoing forward swim by a brief rostral scratch (Juranek and Currie 1998, 2000; Stein 1981).

Differences in rostral scratch and forward swim EMG amplitudes served to discriminate between the two behaviors. Motor pattern amplitude differences between the behaviors may be produced by changes in interneuronal recruitment from classes active during both behaviors. A subset of neurons may be active during each behavior, and additional neurons may be recruited during the behavioral event of each to increase amplitudes during the time when force is exerted against a substrate. These additional neurons may be recruited from unshared populations or from within classes of neurons active during both behaviors. Such recruitment has been demonstrated in *Xenopus*, where additional interneurons not active in low-frequency swimming are recruited during struggling and during high-frequency swimming (Sillard and Roberts 1993; Soffe 1993). The kinematic and myographic similarities between rostral scratch and forward swim, as well as the similarities between the sequentially generated stages of the behaviors, support the hypothesis that network elements are shared between rostral scratch and forward swim circuits. The ability of the spinal cord to blend rostral scratch and forward swim into a single smooth behavior as demonstrated in the present paper provides additional support for this concept. We hypothesize that studies using single-unit recording techniques during rostral scratch and forward swim will reveal spinal interneurons that are active during both behaviors.

We thank A. Berkowitz for editorial assistance and G. Perry for software development.

This work was supported by National Institutes of Health Grants R01-NS-30786 and T32-HD-07434 and by a Promotion of Doctoral Studies Award from the Foundation for Physical Therapy, Inc. to G. M. Earhart.

Address for reprint requests: P.S.G. Stein, Dept. of Biology, Washington University, St. Louis, MO 63130.

Received 23 July 1999; accepted in final form 3 September 1999.


