Blends of Rostral and Caudal Scratch Reflex Motor Patterns Elicited by Simultaneous Stimulation of Two Sites in the Spinal Turtle

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Simultaneous tactile stimulation of 2 sites on the body surface of a spinal turtle elicits complex blends of the scratch forms and motor patterns associated with each site. Our previous work has utilized 1-site stimulation to elicit distinct forms of the scratch reflex in the spinal turtle (Mortin et al., 1985; Robertson et al., 1985). Using this paradigm, stimulation of a site on the shell bridge anterior to the hindlimb elicits a rostral scratch reflex in which the dorsum of the foot rubs against the stimulated site; stimulation of a site near the tail elicits a caudal scratch reflex in which the heel or side of the foot rubs against the stimulated site (Mortin et al., 1985). During each scratch cycle, the monoarticular knee extensor muscle is active when the limb rubs against the stimulated site, and there is rhythmic alternation between hip protractor and hip retractor muscle activity (Robertson et al., 1985). In a rostral scratch, the monoarticular knee extensor muscle is active during the latter portion of hip protractor muscle activity; in a caudal scratch, the monoarticular knee extensor muscle is active near the end of hip retractor muscle activity. Pure-form motor patterns that are similar to those recorded from these muscles during movement can be recorded from the corresponding nerves in a spinal turtle immobilized with a neuromuscular blocking agent (Robertson et al., 1985).

In this paper, we describe blend responses to simultaneous stimulation of 2 sites, one in the rostral scratch and the other in the caudal scratch receptive field. During these blends, the responding hindlimb rubs against both stimulated sites in one continuous movement sequence. The rostral site always is rubbed by the dorsum of the foot; the caudal site always is rubbed by the heel or the side of the foot. A blend can be either a "switch" or a "hybrid." In a switch, the hindlimb rubs against one site in one cycle and the other site in the following cycle. In a hybrid, the hindlimb rubs against both sites in each of several successive cycles. During all blends, the monoarticular knee extensor muscle is active when the limb rubs against each of the stimulated sites, and there is rhythmic alternation between hip protractor and hip retractor muscle activity. During a switch, the monoarticular knee extensor muscle displays a timing relationship with respect to hip muscle activation that is characteristic of one scratch form in one cycle and a timing relationship that is characteristic of the other scratch form in the next cycle. During a hybrid, the monoarticular knee extensor muscle is active 2 times in each cycle; one activity burst is characteristic of the rostral scratch form and the other activity burst is characteristic of the caudal scratch form. Motor patterns of switch responses

and hybrid responses that are similar to those recorded from muscles in the spinal turtle with a moving limb can be recorded from the corresponding nerves in the spinal turtle immobilized with a neuromuscular blocking agent. Thus, the turtle spinal cord has the adaptive ability to blend pure-form motor patterns in response to 2-site stimulation in the absence of both supraspinal input and movement-related feedback.

A motor task is classified according to the goal of the movement. Locomotion is one motor task; its goal is to move the body from one location to another. Grasping food is another motor task; its goal is to hold food prior to feeding. Several motor tasks can be produced during the same movement sequence (Bellman, 1979; Bellman and Krasne, 1983; Carter and Smith, 1984, 1986; Smith et al., 1986; Stein et al., 1986). A crayfish can grasp a small piece of food during escape swimming (Bellman and Krasne, 1983). The term *blend* is utilized to describe such a movement sequence during which several motor tasks are performed. In addition, an organism can use each of several movement strategies to perform a given motor task. Each specific strategy used to perform a task is termed a *form* of that motor task (Mortin et al., 1985; Stein, 1983; Stein et al., 1986). A turtle with a complete transection of the spinal cord, termed a *spinal turtle*, generates a rostral scratch form in response to tactile stimulation of a site on its shell bridge, a pocket scratch form in response to stimulation of a site in the pocket region just anterior to its hip, and a caudal scratch form in response to stimulation of a site near the base of its tail (Mortin et al., 1985). The spinal turtle also generates (1) rostral–pocket scratch blends in response to stimulation of a site in the narrow transition zone located between the rostral scratch receptive field and the pocket scratch receptive field and (2) caudal–pocket scratch blends in response to stimulation of a site in the narrow transition zone located between the pocket scratch receptive field and the caudal scratch receptive field (Mortin et al., 1985). In this example, the term *blend* is utilized to describe a movement sequence that displays a combination of several strategies or forms of a single motor task.

Motor pattern analysis is a useful technique for the recognition of motor blends. These analyses are performed using either electromyographic (EMG) recordings from selected muscles in a preparation with movement or with electroneurographic (ENG) recordings from the nerves that innervate these muscles in a preparation immobilized with neuromuscular blockade (Robertson et al., 1985). Each pure form of the turtle scratch has a distinct motor pattern, characterized by the timing of knee extensor muscle activation within each cycle of hip muscle activation. Stimulation of a single site in a transition zone between 2 receptive fields elicits a scratch response whose motor pattern displays a blend of 2 distinct timings of knee extensor muscle activation (Robertson et al., 1985). These EMG motor pattern blends in the spinal turtle are produced without descending neural input from supraspinal structures. The types of motor pattern blends produced in the spinal turtle with a moving limb are also produced in the immobilized spinal turtle (Robertson
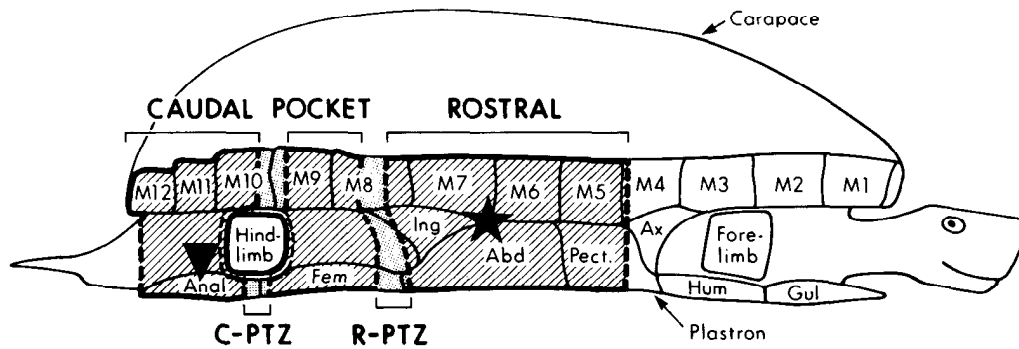
Figure 1. Receptive fields for the 3 forms of the turtle scratch reflex: rostral scratch, pocket scratch, and caudal scratch. The caudal–pocket transition zone (*C–PTZ*) and the rostral–pocket transition zone (*R–PTZ*) are labeled with *stippling*. In this sketch of the right side of the turtle, the shields of the shell have been unfolded and flattened to scale. Stimulated sites were assigned to the rostral scratch receptive field if the hindlimb rubbed against the stimulated site with the dorsum of the foot. A representative site in the rostral scratch receptive field, SP 2, is marked with a *star*. Stimulated sites were assigned to the pocket scratch receptive field if the hindlimb rubbed against the stimulated site with the side of the thigh, knee, and/or shank. Stimulated sites were assigned to the caudal scratch receptive field if the hindlimb rubbed against the stimulated site with the heel or the side of the foot. A representative site in the caudal scratch receptive field, *Anal 5*, is marked with an *inverted triangle*. (Modified Fig. 2 of Mortin et al., 1985. The Methods section of that paper describes the turtle shell and the complete names of the markings on the shell.)

et al., 1985). Thus, movement-related feedback from peripheral structures is not required for motor blend formation. The turtle spinal cord has the neuronal circuitry sufficient for the production of motor blends.

The ability of the spinal turtle to generate motor blends in response to stimulation of a single site in the transition zone led us to examine the response to simultaneous stimulation of 2 distinct sites along the receptive surface for the scratch reflex. Stimulation of 2 sites, one anterior to the hindlimb in the rostral scratch receptive field and the other posterior to the hindlimb in the caudal scratch receptive field, produces complex and potentially conflicting sensory input to challenge the behavioral¹ adaptability of the spinal cord's control of the hindlimb. An adaptive response to 2-site stimulation requires a "decision" by the spinal cord: The limb can produce a motor pattern appropriate for either the anterior site, the posterior site, or both sites. The spinal turtle has the ability to produce each of these options. In this paper, we focus on those episodes in which the motor patterns appropriate for both stimulated sites are exhibited during simultaneous 2-site stimulation. A brief description of these data has been presented in an abstract (Stein et al., 1984).

Materials and Methods

Adult turtles (*n* = 12), *Pseudemys scripta elegans,* carapace length 10–20 cm, were placed in crushed ice for 1 hr prior to surgery to obtain hypothermic anesthesia (Maxwell, 1979; Melby and Altman, 1974; Mortin et al., 1985). These turtles were maintained on crushed ice for the duration of all surgical procedures. Each turtle was spinalized by a complete transection of the spinal cord just caudal to the forelimb enlargement, at the junction of the second dorsal (D2 = second post-cervical) and third dorsal (D3 = third postcervical) spinal segments. After surgery was completed, each turtle was allowed to warm up to room temperature prior to testing. Each turtle was tested to determine if it could produce a site-specific scratch in response to gentle mechanical stimulation of a site in the rostral scratch receptive field and a site in the caudal scratch receptive field (Fig. 1; see also Mortin et al., 1985). Pocket scratch receptive field stimulation was not used in the present study.

Two different preparations were used to record the motor output patterns produced during the scratch reflex. First, a preparation in which the limbs were free to move was used to record EMG patterns from selected muscles of the hindlimb (*n* = 6). Second, a preparation in which the limbs were immobilized via a neuromuscular blocking agent was used to record ENG patterns from the nerves innervating the selected muscles of the hindlimb (*n* = 6). In each of these turtles, we monitored 3 channels of electrical recordings and observed both a rostral scratch and a caudal scratch.

Stimulation procedures

The turtle scratch reflex can be elicited by gentle mechanical stimulation applied to specific sites on the shell or skin with the smooth, fire-polished end of a glass rod. Maintained stimulation was used to elicit responses consisting of as many as 25 scratch cycles. The sites used in this study and the terminology assigned to them have been described by Mortin et al. (1985). A sketch of the scratch receptive fields is presented in Figure 1. Sites in the rostral scratch receptive field were located on the shell bridge anterior to the hindlimb; the shell bridge connects the dorsal carapace with the ventral plastron. The star in Figure 1 indicates the location of SP 2, a site on the shell bridge. Stimulation of SP 2 elicits a rostral scratch. Sites in the caudal scratch receptive field were located on the shell and skin posterior to the hindlimb and anterior to the tail. The triangle in Figure 1 indicates the location of Anal 5, a site on the shell posterior to the hindlimb. Stimulation of Anal 5 elicits a caudal scratch.

In this study, 2 stimulation procedures were used: (1) 1-site stimulation, as described by Mortin et al. (1985), and (2) 2-site stimulation, in which there is simultaneous maintained stimulation of a site in the rostral scratch receptive field and a site in the caudal scratch receptive field. Usually one investigator stimulated one site, a second investigator stimulated the other site, and a third investigator viewed the oscilloscope displaying the motor patterns and indicated the form displayed in each cycle of the response. The most common response to 2-site stimulation was a rub directed against either one or the other site. In many cases, the site that was rubbed was the site that received the most intense stimulation (intensity not quantified). In other cases, one site was much more sensitive than the other site; in these cases, the limb rubbed against the more sensitive site even when it was the site that received the lowest pressure stimulation.

We used a balanced 2-site stimulation procedure to elicit responses in which the limb rubbed against both sites. In this procedure, each investigator continually stimulated a particular site. If the turtle responded with a motor pattern appropriate to only one site for more than one cycle, the experimenter stimulating that site applied slightly less pressure while the experimenter stimulating the other site applied slightly more pressure. If the turtle responded with a motor pattern that combined characteristics of motor patterns directed at both sites, each experimenter continued stimulating with the same pressure, respectively. Thus, feedback concerning the turtle's motor pattern was used on a cycle-by-cycle basis to adjust the relative strength of stimulation applied to each of the 2 sites. In preparations with limb movement, the investigators had the additional cue of viewing the locations on the body surface against which the limb rubbed to determine the appropriate intensity of the pressure applied to each site. As long as the preparation responded well to each of the sites during 1-site stimulation, we were always able to elicit blends of motor patterns with the balanced 2-site stimulation procedure.
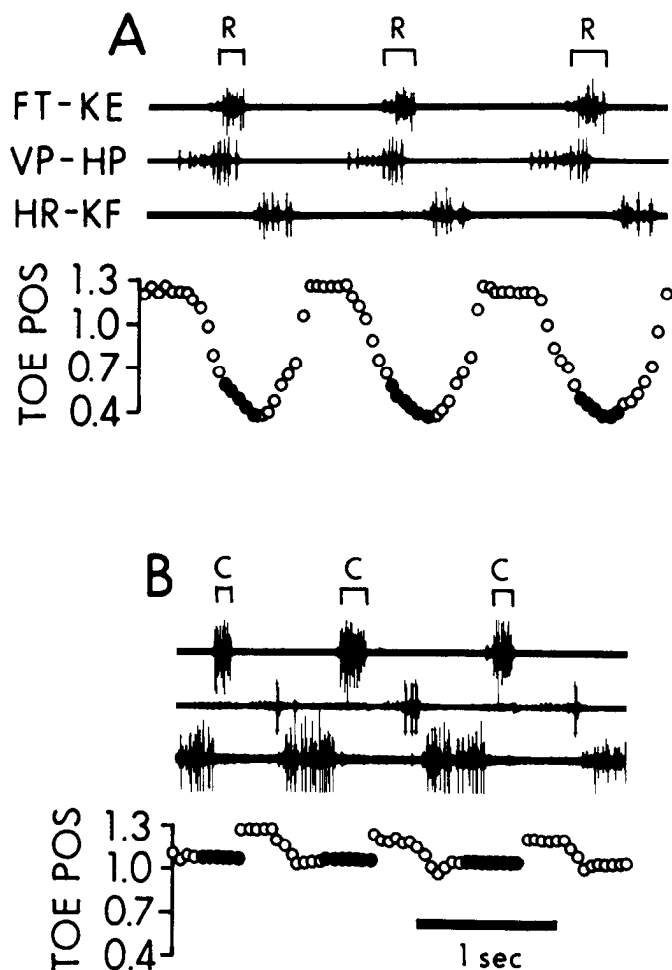
Figure 2. Pure-form motor patterns recorded from 3 muscles of the hindlimb in a spinal turtle during a rostral scratch (*A*) and a caudal scratch (*B*). The *first trace* in each episode is a recording from the FT-KE muscle, a knee extensor; the *second trace* is a recording from the VP-HP muscle, a hip protractor; the *third trace* is a recording from the HR-KF muscle, a hip retractor. Below each set of muscle recordings is a plot labeled *TOE POS* that displays a simultaneous measure of the anterior–posterior movement of the middle toe, normalized to the carapace length of the turtle. In this plot, a value of 1.0 corresponds to the posterior edge of the carapace; a value of 0.0 corresponds to its anterior edge; a value of 0.5 corresponds to the middle of the carapace along the anterior–posterior axis. Each value in the toe position plot in which the foot rubs against a stimulated site is indicated with *filled circles*. The rostral scratch pattern in *A* was elicited by stimulation of SP 3; the caudal scratch pattern in *B* was elicited by stimulation of Anal 5. Brackets mark the activation of FT-KE, the knee extensor muscle. Note that FT-KE is active during each rub phase for both forms of the scratch. In the rostral scratch, FT-KE (brackets marked *R*) is active during the latter portion of VP-HP activity. In the caudal scratch, FT-KE (brackets marked *C*) is active near the end of HR-KF activity.

EMG recordings and movement analysis

Three muscles in the turtle hindlimb were prepared for EMG recordings: (1) FT-KE, triceps femoris, pars femorotibialis, a monoarticular knee extensor muscle; (2) VP-HP, puboischiofemoralis internus, pars antero-ventralis, a hip protractor and femoral rotator muscle; and (3) HR-KF, flexor cruris, pars flexor tibialis internus, a hip retractor and knee flexor muscle (Robertson et al., 1985; Walker, 1973). Robertson et al. (1985) give a complete description of the implantation and recording procedures. The data from all experiments were recorded on an FM tape recorder for later analysis and filming. The turtles used for EMG recordings were also simultaneously videotaped from a lateral view. Mortin et al. (1985) describe the video recording procedure, and Robertson

et al. (1985) describe the synchronization of the video images and the EMG signals. The videotapes were analyzed frame by frame, and the position of the middle toe of the responding hindlimb was measured relative to the anteroposterior extent of the carapace. We converted the toe position measure to a normalized measure: A normalized value of 0.0 corresponded to the anterior edge of the carapace and 1.0 corresponded to the posterior edge of the carapace (see Fig. 5D of Mortin et al., 1985). This measure was used to compare the position of the foot with the EMG recordings. We also determined those frames of the video recording in which the foot was rubbing against a stimulated site.

ENG recordings

Three peripheral nerves were surgically dissected from the hindlimb for ENG recordings. Two of these nerves, VP-HP and FT-KE, each innervate a single muscle. The third nerve, HR-KF, innervates a hip adductor muscle and several bifunctional muscles that retract the hip and flex the knee. The procedures used in recording from these nerves were described previously (Robertson et al., 1985; Stein et al., 1982).After completion of the surgical procedures, each turtle used for ENG recording was immobilized with 6 mg gallamine triethiodide/kg body weight. The data from these experiments were recorded on an FM tape recorder for later analysis and filming. The ENG motor patterns produced in these immobilized preparations are termed "fictive" motor patterns, since they occur in the absence of an actual movement (Stein, 1983, 1984).

Results

Limb movements and EMG patterns

EMG recordings: Stimulation of a single site

Stimulation of a single site in the rostral scratch receptive field in a spinal turtle elicits a scratch response in which the dorsum of the foot rubs against the stimulated site (Bakker and Crowe, 1982; Mortin et al., 1985; Robertson et al., 1985; Stein and Grossman, 1980). The rostral scratch receptive field is located on the shell bridge of the turtle; the site in this field termed SP 2 is marked with a star in Figure 1 (see Mortin et al., 1985, for a complete description of the turtle shell and the convention for naming sites). Stimulation of a single site in the caudal scratch receptive field elicits a scratch response in which the heel or side of the foot rubs against the stimulated site (Mortin et al., 1985; Robertson et al., 1985). The caudal scratch receptive field is located on the shell and skin posterior to the hindlimb; the site in this field termed Anal 5 is marked with a triangle in Figure 1.

A simultaneous record of both muscle activity and limb position during each pure-form scratch is shown in Figure 2. The motor patterns during both a rostral scratch (Fig. 2*A*) and a caudal scratch (Fig. 2*B*) consist of rhythmic alternation of activity between the VP-HP and HR-KF muscles. In the rostral scratch, activation of the FT-KE muscle occurs during the latter portion of the VP-HP activity burst and is indicated with a bracket marked R in Figure 2*A*. In the caudal scratch, FT-KE muscle activation begins near the end of HR-KF muscle activation and is indicated with a bracket marked C in Figure 2*B*. The position of the middle toe during a rostral scratch (Fig. 2*A*) rhythmically alternates between a protracted position with toe position value near 0.5 and a retracted position with toe position value greater than 1.0. The rostral scratch rub occurs when the value of the toe position is near 0.5 (filled circles in Fig. 2*A*). The position of the middle toe varies rhythmically during the caudal scratch (Fig. 2*B*) but to a lesser extent than during the rostral scratch. The caudal scratch rub occurs when the value of the toe position is near 1.0 (filled circles in Fig. 2*B*). For both forms of the scratch, the rub occurs when FT-KE is active. Similar observations on the motor pattern, toe position, and rub phase of the rostral and the caudal scratches were reported previously (Fig. 1 of Robertson et al., 1985). These data are presented here for comparison to aid in the identification of the pure-form elements within each blend response.
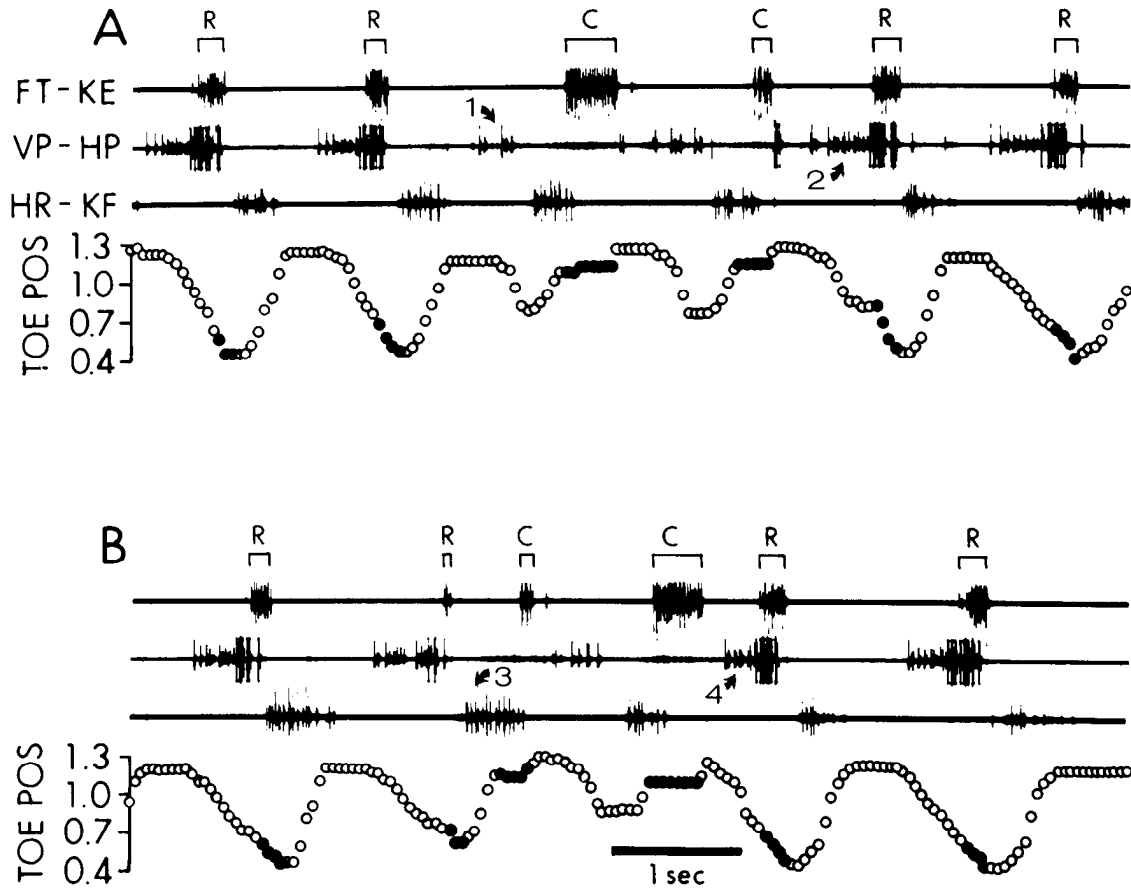
Figure 3. Switch motor pattern in response to simultaneous stimulation of a rostral site (SP 3) and a caudal site (Anal 6) recorded from 3 muscles of the hindlimb in a spinal turtle. The labeling of EMG recordings and toe position values is the same as in Figure 2. The response in *B* is a continuation of *A*. The brackets marked *R* indicate FT-KE activity during the latter portion of VP-HP activity, characteristic of the rostral scratch. In each of these cycles, the *filled circles* with toe position values near 0.5 indicate a rub against the rostral site on the shell bridge. The brackets marked *C* indicate FT-KE activity near the end of HR-KF activity, characteristic of the caudal scratch. In each of these cycles, the *filled circles* with toe position values near 1.0 indicate a rub against the caudal site near the tail. The complete response contains: in *A*, 2 rostral FT-KE bursts, followed by 2 caudal, and 2 rostral bursts; and in *B*, 2 more rostral, 2 caudal, and finally 2 rostral FT-KE bursts. The *curved arrows* mark the activity bursts during which a change from one scratch pattern to the other scratch pattern takes place. *Arrows 1* and *3* indicate the timing of a rostral-to-caudal switch. *Arrow 1* indicates that the first rostral-to-caudal switch in the episode occurs during a VP-HP burst; *arrow 3* indicates that the other rostral-to-caudal switch in the episode occurs during an HR-KF burst. *Arrows 2* and *4* indicate the timing of caudal-to-rostral switches that takes place during VP-HP activity.

EMG recordings: Simultaneous stimulation of 2 sites

When tactile stimulation is applied simultaneously to 2 sites, one in the rostral scratch receptive field and the other in the caudal scratch receptive field, the spinal turtle displays 2 types of scratch responses: pure forms and blends. During each pure-form response, only one of the sites is rubbed by the turtle's hindlimb. In the rostral pure form, the limb rubs against the rostral site; in the caudal pure form, the limb rubs against the caudal site. These pure-form responses to 2-site stimulation are similar to the pure-form responses to 1-site stimulation described above in Figure 2. Two types of blend responses are seen in response to 2-site stimulation: switches and hybrids. In both types of blends, the limb moves smoothly in a coordinated manner and rubs both sites during the behavioral response. In a switch, the limb rubs against one site during one cycle of the response and against the other site during the next cycle of the response. In a hybrid, the limb rubs against one and then the other site in each of several successive cycles. These blend responses are observed when balanced stimulation is applied simultaneously to the 2 sites (see Materials and Methods for a description of the balanced stimulation technique). The next

section describes a switch response and the subsequent section describes a hybrid response.

Switch responses. The EMG motor pattern and limb position during 12 cycles in a switch response are shown in Figure 3. The figure shows data recorded during two rostral rubs, followed by 2 caudal rubs, 4 rostral rubs (2 in *A* and 2 in *B*), 2 caudal rubs, and finally 2 rostral rubs. During the entire episode, there is rhythmic alternation between VP-HP and HR-KF activation, and the position of the toe rhythmically changes between an anterior and a posterior position. The frames in which the limb rubs against the stimulated site are marked with filled circles in the toe position trace: Rubs against the rostral site occur when the value of toe position is near 0.5; rubs against the caudal site occur when the value of toe position is near 1.0. During rostral rubs, FT-KE is active in the latter portion of the VP-HP activity burst (brackets marked R); during caudal rubs, FT-KE is active just after the HR-KF activity burst (brackets marked C).

Each individual cycle of a switch response is similar to an individual cycle of a pure form of the scratch. In a response in which there is only a pure-form motor pattern (e.g., in Fig. 2), each cycle is similar to the preceding cycle. In a switch response, the motor pattern expressed in one cycle may differ from that
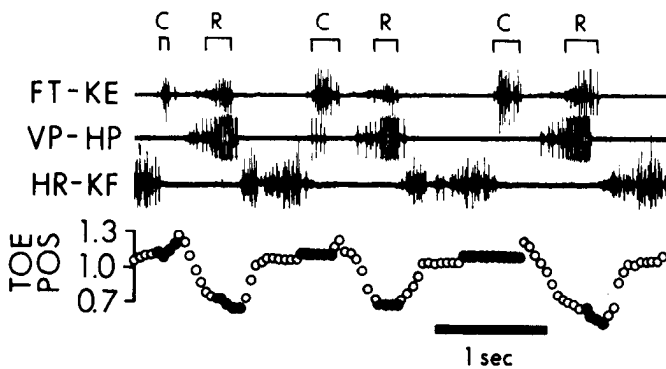
Figure 4. Hybrid motor pattern in response to simultaneous stimulation of a rostral site (midway between SP 1 and SP 2) and a caudal site (Anal 5) recorded from 3 muscles of the hindlimb in a spinal turtle. The labeling of EMG recordings and toe position values is the same as in Figure 2. In each cycle, the brackets marked *R* indicate FT-KE activity during VP-HP activity, characteristic of the rostral scratch; the brackets marked *C* indicate FT-KE activity near the end of HR-KF activity, characteristic of the caudal scratch. In each cycle, the *filled circles* with toe position values near 0.5 indicate a rub against the rostral site; those values near 1.0 indicate a rub against the caudal site. Note that there are 2 activity bursts of FT-KE in each cycle. These 2 bursts correspond to 2 rubs, 1 against each stimulated site in each of the 3 cycles of this response.

expressed in the preceding cycle. In these switch responses, the change from the timing of muscle activation expressed in one cycle to that expressed in the next cycle is discrete. Within each cycle, either one timing is observed or the other timing is observed; intermediate values were not seen. Similarly, we observed no responses in which the limb rubbed against a site located between the 2 stimulated sites.

The timing in the scratch cycle when the switch occurs is of special interest, since it reveals the flexible characteristics of the spinal motor apparatus controlling the limb. There are 2 rostral-to-caudal switches illustrated in Figure 3, one in part *A* (arrow 1) and the other in part *B* (arrow 3). The rostral-to-caudal switch in Figure 3*A* is more complex than the other switches in this episode. There are 3 bursts of hip muscle activation between the rub against the rostral site and the rub against the caudal site: a first burst of HR-KF activity, a burst of VP-HP activity (arrow 1), and a second burst of HR-KF activity. We infer that the switch between the rostral pattern and the caudal pattern occurred during the VP-HP burst. Our reasoning underlying this inference is as follows: The first burst of HR-KF activity in this interval must be part of a rostral pattern, since it is preceded by a FT-KE burst (marked R); if the first HR-KF burst were also part of a caudal pattern, additional FT-KE activity would occur near the end of this HR-KF burst; since a FT-KE burst did not occur at this time, the first HR-KF burst can only be part of a rostral pattern. In addition, the second burst of HR-KF activity in this interval must be part of a caudal pattern, since it is followed by FT-KE activity (marked C); if the second HR-KF burst were also part of a rostral pattern, additional FT-KE activity would precede it; since a FT-KE burst did not occur at that time, the second HR-KF burst must be part of a caudal pattern only. Therefore, since there was a rostral pattern prior to the VP-HP burst indicated with arrow 1 and a caudal pattern following that VP-HP burst, we infer that the rostral-to-caudal switch occurred during that burst. In the rostral-to-caudal switch illustrated in Figure 3*B*, there is a single HR-KF activity burst (arrow 3) between the rub against the rostral site and the rub against the caudal site. Thus, we infer that the switch in the pattern from the rostral program to the caudal program occurred during this HR-KF activation.
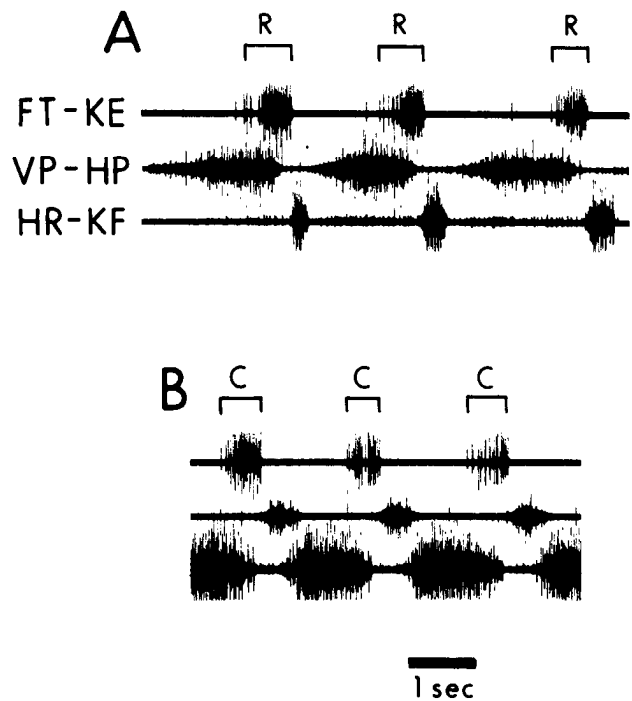

Figure 5. Pure-form motor patterns recorded from 3 nerves of the hindlimb during a fictive rostral scratch (*A*) and a fictive caudal scratch (*B*) in a spinal turtle immobilized with a neuromuscular blocking agent. The 3-cycle fictive rostral scratch was elicited by stimulation of SP 2; the 3-cycle fictive caudal scratch was elicited by stimulation of Anal 3. The *first trace* is an ENG recording from the FT-KE nerve, a knee extensor; the *second trace* is a recording from the VP-HP nerve, a hip protractor; the *third trace* is a recording from the HR-KF nerve, a hip retractor. The brackets mark the timing of FT-KE activation. FT-KE is active during the latter portion of VP-HP activity in the fictive rostral scratch. FT-KE is active near the end of HR-KF activity in the fictive caudal scratch. Each of these fictive motor patterns has timing characteristics similar to the corresponding motor patterns recorded in the preparation with movement shown in Figure 2.

There are 2 caudal-to-rostral switches illustrated in Figure 3, one in part *A* (arrow 2) and the other in part *B* (arrow 4). In each of these examples, there is a single VP-HP activity burst between the rub against the caudal site and the rub against the rostral site. Thus, we infer that the switch in the pattern from the caudal program to the rostral program occurred during each of these VP-HP activity bursts. The only switch type not observed during this episode was a caudal-to-rostral switch during an HR-KF activity burst; we never observed this switch type in the preparation with limb movement.

Hybrid responses. The EMG motor pattern and limb position during 3 cycles of a hybrid response are shown in Figure 4. During each cycle of this episode, the limb first reaches back and rubs against the caudal site and then reaches forward and rubs against the rostral site in a smooth and continuous movement. During the episode, there is rhythmic alternation between HR-KF and VP-HP activation, and the location of the toe rhythmically changes between posterior and anterior positions. FT-KE is active twice in each cycle: There is one FT-KE burst during each of the rubs in every cycle. FT-KE activation is indicated during a rub against the caudal site with a bracket marked C and during a rub against the rostral site with a bracket marked R. FT-KE activation during each caudal rub occurs near the end of HR-KF activation; FT-KE activation during each rostral rub occurs during the latter portion of VP-HP activation. Thus, the motor pattern for the hybrid response displays char-
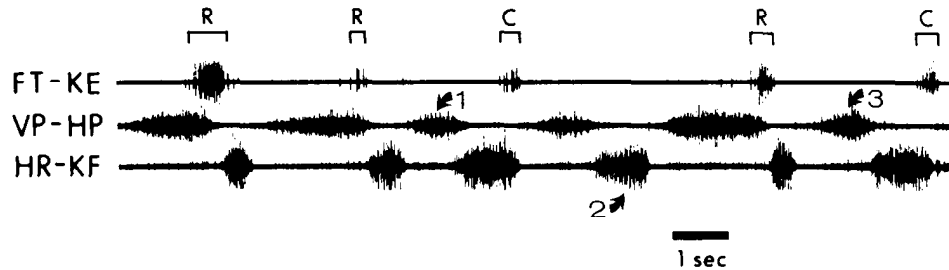
Figure 6. Switch motor pattern in response to simultaneous stimulation of a rostral site (SP 2) and a caudal site (Anal 3) recorded from 3 nerves of the hindlimb in a spinal immobilized turtle. The labeling of ENG recording traces is the same as in Figure 5. The brackets marked *R* indicate cycles in which FT-KE activity occurs during VP-HP, characteristic of the fictive rostral scratch pattern. The brackets marked *C* indicate cycles in which FT-KE activity occurs near the offset of HR-KF activity, characteristic of the fictive caudal scratch pattern. The response contains 2 rostral FT-KE bursts, followed by a caudal, a rostral, and a final caudal FT-KE burst. *Arrows 1* and *3* mark the timing of fictive rostral-to-caudal switches; these switches occur during VP-HP activation. *Arrow 2* marks the timing of a fictive caudal-to-rostral switch that occurs during HR-KF activation.

acteristics of both forms in each of the 3 successive cycles of this episode.

ENG patterns in the immobilized turtle

ENG recordings: Stimulation of a single site

In the spinal turtle immobilized with a neuromuscular blocking agent, stimulation of a site in the rostral scratch receptive field elicits a fictive rostral scratch (Fig. 5*A*) (Robertson et al., 1985; Stein and Grossman, 1980). During the fictive rostral scratch there is rhythmic alternation between VP-HP nerve activation and HR-KF nerve activation. The activation of the FT-KE nerve (brackets marked R) occurs during the latter portion of VP-HP activation. Stimulation of a site in the caudal scratch receptive field elicits a fictive caudal scratch (Fig. 5*B*) (Robertson et al., 1985). During the fictive caudal scratch there is rhythmic alternation between the activation of the VP-HP nerve and the HR-KF nerve. The activation of the FT-KE nerve (brackets marked C) occurs near the offset of HR-KF activation. Thus, in response to stimulation of each site, the timing of activation of these nerves in the immobilized preparation is an excellent replica of the timing of the corresponding muscles in the preparation with movement. Similar observations were presented previously (Fig. 4 of Robertson et al., 1985). These fictive scratch responses are presented in this paper to assist in the identification of the pure-form components of the fictive blend responses.

ENG recordings: Simultaneous stimulation of 2 sites

In the immobilized spinal turtle, when a site in the rostral scratch receptive field is stimulated simultaneously with a site in the caudal scratch receptive field, we observe 2 types of fictive motor patterns: pure-form patterns and blend patterns. Two types of pure-form patterns are seen: either a fictive rostral scratch pattern or a fictive caudal scratch pattern. These pure-form patterns in response to 2-site stimulation are similar to the pure-form patterns elicited by 1-site stimulation described above in Figure 5. We observe blends of the fictive rostral scratch pattern and the fictive caudal scratch pattern in the immobilized spinal turtle when the balanced stimulation procedure is applied simultaneously to both sites. Two types of blend patterns are seen in response to 2-site stimulation: switches and hybrids. In a switch, a fictive pattern characteristic of one form in one cycle is followed by a fictive pattern characteristic of the other form in the next cycle. In a hybrid, each cycle contains characteristics of the motor patterns of both scratch forms.

It is more difficult to elicit a blend in the immobilized preparation than in the preparation with movement. In the immobilized preparation, the limb cannot move and does not rub either site. Thus, the only cue that each investigator could use

to select the intensity of stimulation was the motor pattern displayed on the oscilloscope. In addition, motor pattern blending may be enhanced by movement-related feedback, and, thus, it may be more difficult for the turtle spinal cord to generate a motor pattern blend in the absence of movement. The next section describes switches between fictive motor patterns and the subsequent section describes hybrids of fictive motor patterns.

Switches in fictive motor patterns. The motor pattern during a fictive switch response is shown in Figure 6. In each cycle of this response, there is rhythmic alternation between the VP-HP nerve activity and the HR-KF nerve activity. The first, second, and fourth FT-KE activation bursts (brackets marked R) of this response occur during the latter portion of VP-HP activity. These bursts of FT-KE activity display the characteristic timing of the fictive rostral scratch. The third and fifth FT-KE activation bursts (brackets marked C) of this response occur near the offset of HR-KF activity. These activity bursts display the characteristic timing of the fictive caudal scratch. Thus, this response contains some cycles displaying a fictive rostral pattern and other cycles displaying a fictive caudal pattern.

There are 2 rostral-to-caudal switches in this episode: (1) a switch (arrow 1) from the rostral pattern displayed by the second FT-KE burst to the caudal pattern displayed by the third FT-KE burst and (2) a switch (arrow 3) from the rostral pattern displayed by the fourth FT-KE burst to the caudal pattern displayed by the fifth FT-KE burst. In each case, there are 3 hip activity bursts between the FT-KE burst marked R and the FT-KE burst marked C: An HR-KF hip retractor burst, a VP-HP hip protractor burst, and a second HR-KF hip retractor burst. The first HR-KF burst in each interval is associated with the rostral scratch pattern since it follows a FT-KE burst and is not immediately followed by a FT-KE burst. The second HR-KF burst in each interval is associated with the caudal scratch pattern since it is followed by a FT-KE burst and is not immediately preceded by a FT-KE burst. Thus, we infer that the switch from the rostral pattern to the caudal pattern occurred during the intervening VP-HP burst in each interval. This type of switch was also observed in the preparation with movement (arrow 1 in Fig. 3*A*).

There is 1 caudal-to-rostral switch in this episode: a switch (arrow 2) from the caudal pattern displayed by the third FT-KE burst to the rostral pattern displayed by the fourth FT-KE burst. There are 3 hip activity bursts between the FT-KE burst marked C and the FT-KE burst marked R: a VP-HP burst, an HR-KF burst, and a second VP-HP burst. The first VP-HP burst is part of a caudal pattern since it follows immediately after FT-KE activity and there is no FT-KE activity during the latter portion of this VP-HP burst. The second VP-HP burst is part of a rostral pattern since there is FT-KE activity during the
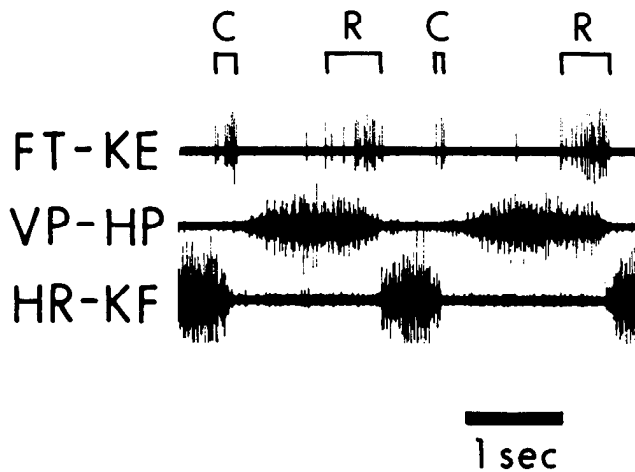
C   R   C   R

FT-KE

VP-HP

HR-KF

1 sec

Figure 7. Hybrid motor pattern in response to simultaneous stimulation of a rostral site (SP 2) and a caudal site (Anal 3) recorded from 3 nerves of the hindlimb in a spinal immobilized turtle. The labeling of ENG recording traces is the same as in Figure 5. In each cycle, the brackets marked *R* indicate FT-KE activation during VP-HP, characteristic of the fictive rostral scratch; the brackets marked *C* indicate FT-KE activation near the offset of HR-KF, characteristic of the fictive caudal scratch. Note that there are 2 activity bursts of FT-KE in each of the 2 cycles of this response.

latter portion of the VP-HP burst and there is no FT-KE activity just prior to the VP-HP burst. We infer, therefore, that the switch between the caudal pattern and the rostral pattern occurred during the HR-KF burst marked by arrow 2. We did not observe this type of switch in the preparation with limb movement. We also observed rostral-to-caudal fictive switches that occurred during an HR-KF burst and caudal-to-rostral fictive switches that occurred during a VP-HP burst (data not shown). These switch types were observed in the preparation with movement.

Hybrid fictive motor patterns. Two cycles of a hybrid fictive motor pattern in response to 2-site stimulation are shown in Figure 7. In both cycles of this response, there is rhythmic alternation between the HR-KF nerve activation and the VP-HP nerve activation. In each cycle, there are 2 activity bursts of FT-KE. The FT-KE burst (marked C) that occurs just after HR-KF nerve activation is characteristic of the caudal motor pattern. The FT-KE burst (marked R) that occurs during the latter portion of VP-HP nerve activation is characteristic of the rostral motor pattern. This response is a hybrid motor pattern since it displays characteristics of both the fictive rostral motor pattern and the fictive caudal motor pattern in each of the 2 successive cycles.

Discussion

The spinal turtle can produce adaptive blends of scratch motor output in response to simultaneous stimulation of 2 sites on the body surface. During these blends, the limb rubs against both sites within the same behavioral response. These blends are produced in the spinal turtle with limb movement and in the spinal turtle immobilized with a neuromuscular blocking agent. Therefore, the motor circuitry of the turtle spinal cord can generate blends of motor patterns in response to 2-site stimulation without the assistance of movement-related sensory feedback and descending input from supraspinal structures.

Human postural control is another example of the blending of 2 forms of the same task (Horak and Nashner, 1983, 1986; Horak et al., 1984). A human with a normal CNS uses an ankle strategy (or form) when balancing on a broad support surface and a hip strategy when balancing on a narrow support surface.

When the size of the support surface is changed, the normal subject produces adaptive blends of both strategies during the set of responses immediately following the change. After a number of trials, the subject uses the pure-form strategy appropriate for the new size of the support. Patients with Parkinson's disease produce each of the 2 postural forms, but are unable to produce the appropriate form in response to a given support surface. In addition, the patients attempt to produce blends that lack postural stability. Such unstable blends are not seen in normal subjects. An inference resulting from these observations is that Parkinson's patients have neural circuitry available for the production of pure-form postural responses but have suffered damage to neural circuitry required for the production of adaptive postural blends.

Our work with the spinal turtle demonstrates that a vertebrate with a complete transection of the spinal cord can produce adaptive motor blends of 2 forms of the same task using neural structures located caudal to the level of the transection. In addition, Carter and Smith (1984, 1986) have shown that a spinal vertebrate can blend 2 different tasks into a unified motor behavior. A cat with a complete transection of the thoracic spinal cord can be induced to step with its hindlimbs on a moving treadmill; such a spinal cat will also shake its hindlimb to remove an object attached to its paw. The spinal cat can blend paw-shaking with stepping; several cycles of the paw-shake are generated during the swing phase of each step cycle. Thus, supraspinal neural structures are not required for the blending of different motor tasks.

The 2-point stimulation procedure used here is an example of behavioral choice. In a behavioral-choice paradigm, 2 stimuli are presented simultaneously. The term *behavioral hierarchy* has been used to describe the priorities within the set of responses by an organism in a choice paradigm (Davis et al., 1974a, b). If the animal responds selectively to only 1 of the 2 stimuli, the behavior that is exhibited is termed *dominant* over the behavior that is not expressed. If the animal responds by combining both behavioral responses, the result is a "blend" of the 2 responses (also termed *merging* by Bellman, 1979, and Bellman and Krasne, 1983). When selected, the blend of 2 behaviors may have a greater adaptive value than if only 1 behavior were expressed. During choice behavior, therefore, an organism may exhibit only one of the possible responses, or it may blend together both responses. The present paper has shown that the spinal cord of the turtle displays both selection and blending. We have emphasized the coordination of motor output during the blend to demonstrate the motor capabilities of the spinal cord.

One of the most impressive features of the blending of the rostral and caudal scratch motor patterns revealed here is the smoothness of the observed changes between one motor pattern and the other. We also observed smooth changes during motor pattern blends in response to 1-site stimulation within a transition zone (Robertson et al., 1985). We proposed a hypothesis for the interneuronal mechanism underlying transition-zone blends: There is an interneuronal hip control center responsible for the rhythmic movement of the hip musculature and an interneuronal knee extensor control center responsible for knee extensor activity; the synaptic drive between the hip control center and the knee extensor center is modified according to which form is expressed at each moment of the blend response. The motor pattern blends in response to balanced 2-site stimulation described here provide additional data supporting this modifiable synaptic drive hypothesis.

The turtle spinal cord responds to stimulation of a single site within a receptive field with a pure-form scratch response. More complex tactile stimuli are probably more representative of natural environmental conditions such as an obstacle in the turtle's path or a predator. Such multisite stimuli may elicit responses

that blend the pure forms in a coordinated manner. Blending extends the adaptive behavioral repertoire of an organism. We suggest that the pure scratch forms constitute the basic elements of this repertoire; the neural networks underlying each scratch form interact to produce blends that provide the organism with additional adaptive responses to natural selective pressures.

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