Example of 2:1 Interlimb Coordination During Fictive Rostral Scratching in a Spinal Turtle

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Stein, Paul S. G. and Margaret L. McCullough. Example of 2:1 interlimb coordination during fictive rostral scratching in a spinal turtle. J. Neurophysiol. 79: 1132–1134, 1998. The usual interlimb coordination pattern during fictive rostral scratching in turtles is 1:1 coordination. We describe an example in a turtle of 2:1 coordination during fictive rostral scratching in which there were two cycles of ipsilateral hip flexor activity during each cycle of contralateral hip extensor activity. During 2:1 coordination, there were fluctuations in the ipsilateral hip flexor cycle period such that a larger ipsilateral hip flexor normalized period, which was associated with the onset of a contralateral hip extensor burst, alternated with a smaller ipsilateral hip flexor normalized period, which was associated with the absence of the onset of a contralateral hip extensor burst. These observations support the concept that contralateral circuitry modulates the timing of ipsilateral motor rhythms and therefore contributes to the production of the ipsilateral motor pattern for rostral scratching.

INTRODUCTION

The usual type of interappendage coordination in animals is 1:1 coordination; motor output to one appendage occurs with the same frequency and a specific phase compared to motor output to another appendage (Kelso 1995; Stein 1976; von Holst 1973). An unusual type of interappendage coordination is 2:1 coordination: motor output to one appendage occurs at twice the frequency of motor output to another appendage and two distinct phases of output to the higher-frequency appendage occur in each cycle of output to the lower-frequency appendage (Field and Stein 1997; Forsberg et al. 1980; Kelso 1995; Kulagin and Shik 1970; Stein 1978; von Holst 1973). 2:1 coordination is a prediction of the mathematics of coupled oscillators (Kelso 1995; Stein 1976). This type of coordination can occur when the intrinsic period of one oscillator is approximately one-half that of the other oscillator.

2:1 interlimb coordination characterizes most responses of fictive rostral scratching in response to unilateral stimulation in a spinal turtle: there is one cycle of ipsilateral hip flexor activity during each cycle of contralateral hip extensor activity (Stein et al. 1995, 1998). This paper reports occurrences of 2:1 interlimb coordination observed during fictive rostral scratching in an individual turtle. In some responses to unilateral stimulation in this spinal turtle, there were two cycles of ipsilateral hip flexor activity during each cycle of contralateral hip extensor activity.

METHODS

We used procedures described previously (Stein et al. 1995, 1998) to obtain bilateral electroneurographic recordings (ENGs) of knee extensor (FT-KE), hip flexor (VP-HP), and hip extensor (HR-KF) nerves in a red-eared turtle (Trachemys scripta elegans) with a complete transection of the spinal cord just posterior to the forelimb enlargement between the D2 and D3 spinal segments. The turtle was immobilized with gallamine (Flaxedil; Rhone-Poulenc Rorer Canada, Montreal, Canada), a neuromuscular blocking agent, at a dosage of 8 mg/kg body wt and maintained on a respirator for the duration of the experiment.

The fictive motor patterns described in the present paper were obtained during a series of control measurements in response to unilateral stimulation in the rostral scratch receptive field that were part of a larger study reported elsewhere (Stein et al. 1998). Stimulus sites on the shell bridge in the anterior and middle portions of the rostral scratch receptive field were used (M7.0 and SP1.5–SP3.0; see Mortin and Stein 1990). The ENGs were amplified (bandpass: 100 Hz–1 kHz), stored on DAT tape, digitized at 2 kHz, full-wave rectified, and integrated; the onset and offset of each burst of integrated full-wave rectified activity were determined (Stein et al. 1995).

We used double-referent phase measurement techniques (Berkowitz and Stein 1994; Stein et al. 1995) to calculate the phases of ipsilateral hip flexor burst onsets in the activity cycle of the contralateral hip extensor during 1:1 coordination and during 2:1 coordination. The phase of the onset of the contralateral hip extensor burst was defined as 0.0 (also 1.0); the phase of the offset of the contralateral hip extensor burst was defined as 0.5. The Watson U² test was used to determine whether or not each distribution of phases was significantly different from random and from the other distribution (Batschelet 1981).

We calculated normalized periods to examine fluctuations in the period of the ipsilateral hip flexor cycle. During every scratch episode, there was a tendency for period to become longer during later times in the episode; we therefore calculated a local mean rather than the mean for the entire episode. We defined the kth normalized period as one-fourth the sum of twice the kth hip flexor period plus the k − 1th hip flexor period and the k + 1th hip flexor period. This method of calculation gave equal weight to odd-numbered periods and to even-numbered periods. We defined N1, the kth normalized period, as the kth hip flexor period divided by the kth weighted mean hip flexor period. During 2:1 coordination, we determined whether the kth ipsilateral hip flexor cycle was associated with the onset of a contralateral hip extensor burst. If the onset of a contralateral hip extensor burst occurred during the kth ipsilateral hip flexor cycle, the kth normalized period was termed N+1. If there was no onset of a contralateral hip extensor during the kth ipsilateral hip flexor cycle, the kth normalized period was termed N−1. We used the Mann-Whitney U test (Siegel 1956) to determine whether or not there was a statistically significant difference between the sets of N+, values and N−, values.

RESULTS

Stimulation of a site in the rostral scratch receptive field in an immobilized turtle elicited fictive rostral scratching. In
played two peaks (Fig. 3B), a peak for $N_{k+}$ values ($1.05 \pm 0.03$) and another peak for $N_{k-}$ values ($0.95 \pm 0.03$). Values of $N_{k+}$ were significantly greater than values of $N_{k-}$ ($P < 0.001$, Mann-Whitney U test; Fig. 3B). Therefore during 2:1 coordination, larger ipsilateral hip flexor normalized periods associated with contralateral hip extensor burst onsets alternated with smaller ipsilateral hip flexor normalized periods associated with no contralateral hip extensor burst onsets.

**DISCUSSION**

2:1 interlimb coordination occurred during fictive rostral scratching in response to unilateral stimulation of a site in a rostral scratch receptive field. A general hypothesis that can explain this type of coordination is that the neuronal network responsible for rostral scratching consists of a bilaterally distributed set of coupled neuronal oscillators with at least one left-side oscillator and at least one right-side oscillator. A more specific version of this hypothesis is that, when a site on one side is stimulated, both the ipsilateral hip flexor module and the contralateral hip extensor module are rhythmogenic (Stein et al. 1995, 1998; Stein and Smith 1997). During the 2:1 coordination observed in the present paper, the period of the contralateral rhythrogenic module was twice that of the ipsilateral rhythmogenic module.
ipsilateral motor rhythm and therefore can contribute to the production of the ipsilateral motor pattern. Our results here add to previous evidence (Berkowitz and Stein 1994; Stein et al. 1995, 1998; Stein and Smith 1997) that demonstrates the critical role of contralateral circuitry in the production of the ipsilateral motor pattern.

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In response to stimulation of a site on one side, alternations between larger and smaller normalized periods of the ipsilateral hip flexor cycle occurred during episodes of 2:1 coordination. The normalized periods of ipsilateral hip flexor cycles associated with the onsets of contralateral hip extensor bursts were larger than the corresponding normalized periods of cycles not associated with onsets of contralateral hip extensor bursts. These data support the concept that contralateral spinal cord circuitry can modulate the timing of the normalized period (Nk) of ipsilateral hip flexor activity during fictive rostral scratching. A: 1:1 coordination. B: 2:1 coordination. In B, Nk+ values are from kth hip flexor cycles in which there was an onset of contralateral hip extensor activity and Nk− values are from kth hip flexor cycles in which there was no onset of contralateral hip extensor activity.