SENSORY-EVOKED TURNING LOCOMOTION IN RED-EARED TURTLES

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Introduction

Successful goal-directed locomotion in a varying environment requires frequent steering adjustments and abrupt turns, yet the biomechanical and neural mechanisms that mediate turning in locomotion are infrequently studied and poorly understood compared to rectilinear (straight-forward) locomotion. However, there have been several interesting exceptions, including studies of visually guided turning in jumping spiders (Land 1972), kinematics and EMGs that underlie walking and turning in the cockroach (Ma and Ritzmann 2005), fictive and actual turning in lampreys (McClellan 1984, McClellan and Hagvik 1997, Saitoh et al. 2007), turning produced by asymmetric paddling strokes of the right and left forelimbs during swimming in sea-turtles (Renous and Bels 1993, Lohmann et al. 1995) and walking circular paths in humans (Courtine and Schieppati 2003, Orendurff et al. 2006). Some previous work has also been done on straight swimming vs. turning in fresh-water turtles. Rivera et al. (2006) described the pattern of limb movements during lateral turns in free-swimming turtles in a study that investigated the dynamics of turning performance rather than the specifics of limb motor patterns and inter-limb coordination. The bilateral movements and EMG patterns of turtle hindlimbs were also described for spontaneous turning in band-clamped turtles (Field and Stein 1997, Earhart and Stein 2000). In the present study, we examined the kinematics and EMG motor patterns of hindlimbs and forelimbs that underlie prolonged episodes of sensory-evoked turn-swimming in red-eared turtles.

1 Methods

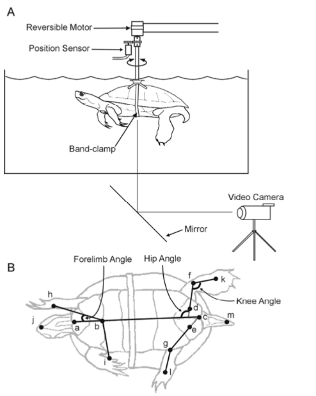

Figure 1. Apparatus used to record turn-swimming and rectilinear swimming in carapace-restrained turtles. **A.** Animals were held by a band-clamp around the shell, just beneath the water-surface in a clear tank. Digital videos were recorded from below in a 45° mirror. Slow rotation of the animal to the right or left, via a variable-speed, geared motor attached to the band-clamp, evoked turn-swimming in the opposite direction. In the figures shown, rotation was at 90°/sec. Episodes of rectilinear (straight, bilaterally symmetric) swimming could be elicited by many visual and tactile stimuli. **B.** Markers on the plastron (ventral shell), limb joints, and chin and tail (a-m) permitted us to monitor forelimb, hip, knee, head and tail angles as a function of time, using motion capture and analysis software (Run Technologies) and synchronize those measurements with EMG recordings from selected hindlimb or forelimb muscles.

MUSCLE IDENTITIES:
Forelimb: Shoulder retractor (SR) = pectoralis; shoulder protractor (SP) = deltoideus; elbow extensor (EE) = triceps brachii.
Hindlimb: Hip retractor-knee flexor (HR) = flexor tibialis internus; hip protractor (HP) = puboischiofemoralis internus; knee extensor (KE) = triceps femoris pars femorotibialis.

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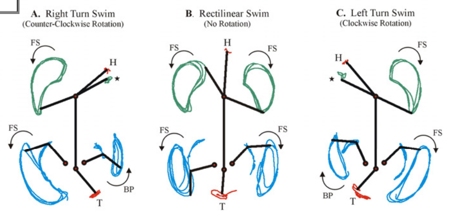

Figure 2. Limb trajectories compared for right and left turn-swimming and rectilinear swimming in the same animal (D24). Right limbs shown on right side of stick figures. FS = forward swim; BP = back-paddle; H = head; T = tail. In A. and C., we digitally stabilized the ventral mid-line of rotating stick figures (line b-c in Fig. 1B) via the kinematic analysis software so that the trajectories of limb markers could be observed relative to a stationary body axis. Stars indicate braking forelimb.

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Figure 3. Average min and max limb angles during left (A) and right (B) turn-swimming evoked by rotation. Error bars = std dev. Statistical comparisons were made between corresponding min angles (e.g., right forelimb) and between corresponding max angles during left and right turns, using the Mann-Whitney U test. *p<0.0005 and p>0.05, respectively.

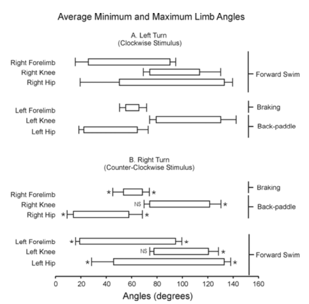

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Figure 4. Intralimb (knee-hip) phase relationships for the forward swimming hindlimb **(A)** on the outer side of the turn and the back-paddling hindlimb **(B)** on the inner side of the turn during right turn-swimming episodes. Circular histograms indicate phase values pooled from 5 turtles for the onset of knee extension within the hip protraction cycle. Vector angle indicates mean phase; vector length indicates the strength of intralimb coupling (r) on a scale of 0 (innermost circle) to 1 (outermost). Representative kinematic sequences are shown on right from turtle D19.

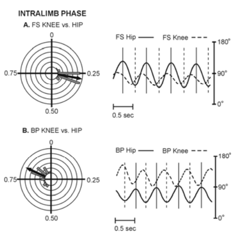

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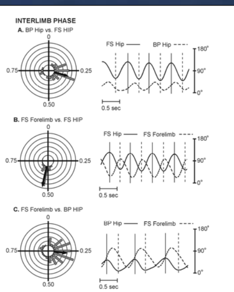
Figure 5. Interlimb phase relationships during right turn-swimming episodes. Circular histograms indicate phase values pooled from 5 turtles. **A:** Phase relationship of BP hip protraction onsets within the contralateral FS hip protraction cycle. **B:** Phase of FS forelimb protraction onsets within the ipsilateral FS hip protraction cycle. **C:** Phase of FS forelimb protraction onsets within the contralateral BP hip protraction cycle. Vector angle indicates mean phase; vector length indicates the strength of intralimb coupling (r) on a scale of 0 (innermost circle) to 1 (outermost). Representative kinematic sequences are shown on right from turtle D19.



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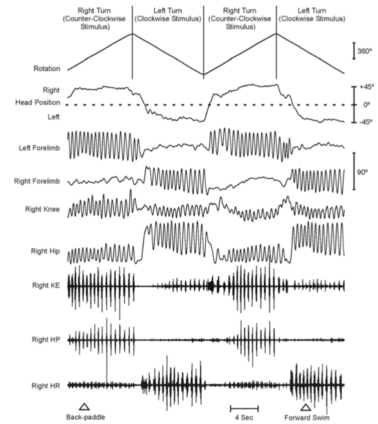

Figure 6. Synchronized kinematic and EMG recordings of right and left turn-swimming in response to abrupt switches in the direction of rotation (90°/sec) from turtle D21. *Top trace*: output of rotational position sensor. *Second from top trace*: head position, with the dashed line (0°) indicating that the head is pointed straight forward. *Middle 4 traces*: kinematic recordings of left and right forelimb angles and right knee and hip angles. *Bottom 3 traces*: EMG recordings from right KE (knee extensor), HP (hip protractor) and HR (hip retractor-knee flexor) muscles. Triangles below bottom trace indicate onsets of time-expanded sequences shown in Figure 7.

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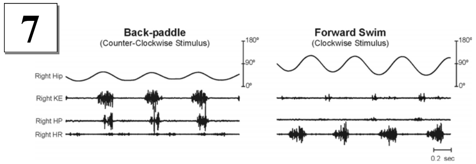

Figure 7. Hip angle (upper trace) and EMG recordings (lower 3 traces) from the right hindlimb of turtle D21 during 2-sec back-paddle and forward swim sequences, taken from Figure 6. Note that the BP motor pattern was dominated by large-amplitude HP and KE EMG bursts (with KE onsets preceding HP onsets), while the forward swim motor pattern was dominated by large-amplitude HR bursts (with KE onsets occurring during the latter part of each HP burst). These features are characteristic of BP and FS motor patterns, as previously described for spontaneous turning episodes (Earhart and Stein, 2000).

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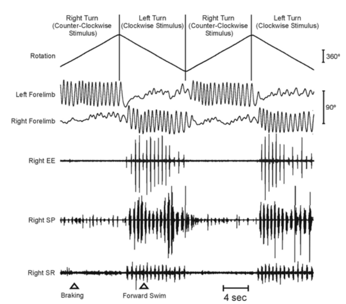

Figure 8. Kinematic and EMG recordings of right and left turn-swimming in response to switches in the direction of rotation (90°/sec) from turtle D20, focusing on forelimb activity. *Top trace*: output of rotational position sensor. *Second and third traces from top*: kinematic recordings of left and right forelimb angles. *Bottom 3 traces*: EMG recordings from right EE (elbow extensor), SP (shoulder protractor) and SR (shoulder retractor) muscles.

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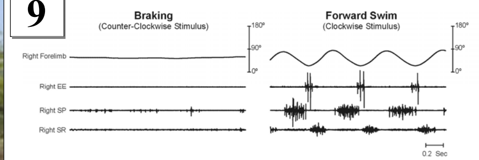

Figure 9. Forelimb angle (upper trace) and EMG recordings (lower 3 traces) from the right forelimb of turtle D20 during 2-sec braking and forward swim sequences, taken from Figure 8 and shown with expanded time-bases. During braking, the largely stationary forelimb exhibited only weak rhythmic discharge in the SP muscle, while EE and SR were silent. In contrast, forward swimming was characterized by large-amplitude bursting EMG discharge in EE, SP and SR muscles that was correlated with cyclic forelimb movements. The timing of EE burst-onsets just before each SR burst is similar to that described previously for forelimb forward swimming evoked by spinal cord stimulation (Stein, 1978).

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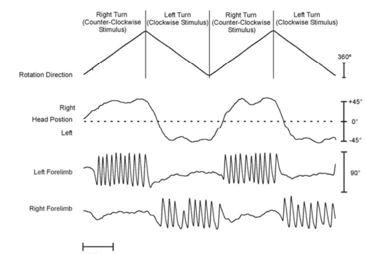

Figure 10. Rotation still elicited robust turn-swimming responses to the right and left when the animal (D20) was suspended in the air (to abolish proprioceptive sensations caused by water currents) and blind-folded with opaque goggles (to prevent movement-related visual stimuli), suggesting that the turning response may be driven primarily by vestibular inputs (n = 3 turtles). Hindlimb movements not shown.

Summary

Rotation-evoked turning exhibited a highly stereotyped pattern of [1] coordinated forward swimming in the hindlimb and forelimb on the outer side of the turn, [2] back-paddling in the hindlimb on the inner side of the turn, [3] a largely stationary, "braking" forelimb on the inner side of the turn, and [4] neck bending toward the direction of the turn. Reversing the direction of rotation caused animals to rapidly switch the direction of the turn and the pattern of right and left limb activities. Turtles still performed rotation-evoked turning while blindfolded (without vision) in the air (without water currents), suggesting that vestibular inputs were sufficient to drive the behavior. Sensory-evoked turning locomotion may provide a useful experimental platform in which to examine the descending brainstem commands and spinal neural networks that activate and switch between different locomotor forms in right and left-side limbs.