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Sensory-Motor Integration and Control

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Neuroscience

by

Dan B. Welch

December 2011

Dissertation Committee:
Dr. Aaron R. Seitz, Chairperson
Dr. Scott N. Currie
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The Dissertation of Dan B. Welch is approved:

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ABSTRACT OF THE DISSERTATION

Sensory-Motor Integration and Control

by

Dan B. Welch

Doctor of Philosophy, Graduate Program in Neuroscience
University of California, Riverside, December 2011
Dr. Aaron R. Seitz, Chairperson

Two leading vertebrate animal models were used in studying sensory motor integration and control: [1] Red eared turtles-Trachemys scripta elegans, (Locomotion) and [2] Humans- Homo sapiens (Cognition). [1] Locomotion: Survival depends on locomotor circuitry being driven by a variety of sensory inputs, such that movements can be adapted dynamically to survive against life threatening changes in the environment. With the first study, an examination of the forelimb/hindlimb kinematics and electromyographic (EMG) motor patterns that underlie aquatic lateral turning behavior in red-eared turtles was made.

Rotation-evoked turning provides a convenient experimental platform in which to investigate the brainstem commands that underlie locomotor form selection (e.g., forward swimming vs. back-paddling) in a limbed vertebrate. [2] Cognition: Many vertebrates are also capable of cognitively driven fine motor movements. Humans for example, use their hands to manipulate objects as a result of a complex blend of sensory-motor control mechanisms. A second study was conducted in order to determine how intentional cognitive processes might be strengthened and/or automatic responses may be weakened using the Simon task (Simon et al., 1973). The results support the conclusion that the reduction of the latency in responding to incongruent stimuli from training might be due to route suppression/gating of irrelevant location information. Fine motor movements can work separately, synergistically, or in parallel with locomotor production. Future studies can expand our current perspective by learning how these sub-systems function together.

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CHAPTER 1

LOCOMOTION

VERTEBRATE LOCOMOTOR SYSTEMS

For many animals, locomotion is essential for survival. We know that early non-limbed vertebrate species depended on axial muscles to bend the body to produce slow swimming movements as well as very rapid bending associated with fast swimming or escape responses (Fetcho, 1987). Premotor neuronal networks that produce swimming are composed of descending interneurons that provide excitation of ipsilateral motoneurons and other interneurons, as well as inhibitory commissural interneurons that inhibit contralateral activity (Grillner, 2006). However, if this basic locomotor circuitry simply produced rigidly fixed motor patterns, vertebrates would behave as a kind of mindless mechanical apparatus. Survival depends on locomotor circuitry being driven by a variety of sensory inputs, such that movements can be adapted dynamically to survive against life threatening changes in the environment (Grillner, 2006).

Locomotor command systems

The mesencephalic and the diencephalic locomotor regions are two major command systems that link the sensory systems in the head to the premotor networks in the spinal cord. The mesencephalic locomotor region influences spinal networks via projections to the reticular formation (Grillner et al., 2008). The diencephalic locomotor region corresponds to groups of neurons with descending connections that make up the ventral thalamus in the lamprey. These two areas have independent monosynaptic projections to the reticulospinal neurons in the middle and posterior reticulospinal nuclei which, in turn, activate the spinal central pattern generator circuitry that generate locomotor activity.

From the mesencephalic locomotor region a monosynaptic cholinergic projection acts on nicotinic receptors for reticulospinal neurons (Grillner et al., 2008).

Reticulospinal neurons are important for initiation of rhythmic swimming and turning movements. The reticulospinal cells partially produce their effects through monosynaptic connections with motoneurons and premotor interneurons (Grillner et al., 2008). Locomotor activity can be produced with brainstem stimulation, and in an isolated spinal cord with glutamate agonists in order to simulate a supraspinal drive (*lamprey:* Grillner and Wallén, 2002). Electrical stimulation of the dorsal lateral funiculus (thought to be reticulospinal) in the spinal cord will also produce a wide variety of movements such as those seen during forward swimming and back-paddling (*turtle:* Lennard and Stein, 1977). Electrical stimulation of the rhombencephalon in decerebrate animals can also induce cyclic coordinated limb movements (*turtle:* Kazennikov et al., 1981).

For all vertebrates, locomotor descending command pathways travel through the spinal cord. The spinal cord is a complex system that subserves sensory, and motor functions. The spinal cord also contains the primary neuronal circuitry that produces and coordinates locomotor activity (Grillner, 1985). There are three major categories of neuronal pathways in the spinal cord. First, there are axons that originate from sensory afferents in the dorsal root ganglia, as well as the fiber systems that transmit descending motor commands from the brain. For most vertebrates, the outermost portion of the spinal cord contains myelinated axons (white matter) from spinal and supraspinal neurons that have tracts that ascend and descend along its length.

Second, there are axons that exit the cord to either innervate skeletal muscle fibers, or function as autonomic ganglia. The inner gray matter contains the cell bodies of spinal neurons and most of the synaptic neuropil. Third, there are spinal axons that terminate entirely within the central nervous system as interneurons or tract cells (Shepherd and Burke, 2003).

Spinal central pattern generators

After a locomotor command is produced, "central pattern generator" (CPG) networks within the spinal cord produce the proper rhythmic timing of motor output to the appropriate sequence of muscle groups. The intermixing of numerous different types of interneurons within the spinal gray mater has made it difficult to identify the organization of specific functional circuits (Shepherd and Burke, 2003). However, some interneurons have been characterized to a certain degree (Grillner, 1981). Berkowitz et al. (2006; 2008) recently obtained intracellular recordings from the gray matter on the right side of the hindlimb enlargement (D8, D9, D10, S1, and S2 segments) from the turtle spinal cord. Their data indicated that locomotion and scratching might be produced by a combination of shared and dedicated interneurons. A similar characterization of recruitment patterns, both within and between different neuron classes, has been studied for several different types of motor patterns in other species (*tadpole:* Li et al., 2007; Soffe, 1993; *fish:* Kimura et al., 2006; mice: Lieske et al., 2000).

Interneurons that form the central pattern generator circuits produce the proper rhythmic timings and some are probably composed of circuits dedicated to flexion or extension of a joint (Grillner, 1981).

These units might be interconnected, so that conditions would allow for two portions of a circuit to mutually excite each other while other conditions allow the same two units to inhibit each other. Evidence for this is supported by studies where knee extensors and hip extensors are out of phase during swimming (*turtle:* Earhart and Stein, 2000; Juranek and Currie, 2000) but coactive during turtle pocket scratch (*turtle:* Earhart and Stein, 2000). In addition, it has been suggested that these circuits could be divided into "modules" distinguished by whether they were producing paw shake movements or locomotion (*cat:* Koshland and Smith, 1989). Another example of a rhythm-generating module is the hip flexor module during rostral scratching, since rhythmic hip flexor activity occurs when no rhythmic hip extensor activity is present (*turtle:* Currie and Gonsalves, 1999). There is culminating evidence that turtle spinal cord neuronal networks that generate locomotion and scratching have significant shared components, or robust interactions between them (*turtle:* Hao et al., in press).

In addition, some progress has been made in identifying the anatomical location of different types of interneurons. For example, flexion reflex-selective neurons have only been identified within the dorsal horn (Berkowitz et al., 2010). Multifunctional interneurons activated during scratching and swimming, seem to be most frequently found in the intermediate zone and ventral horn (Berkowitz et al., 2010).

Interlimb coordinating mechanisms

An animal's survival can depend on the coordination of their limb movements during rhythmic behaviors, so that effective movements can be produced. In red-eared turtles, the limbs can be coordinated into out-of-phase movements such as during forward swimming, where a limb's movements alternates with the contralateral one (Samara and Currie, 2007). The limbs can also be coordinated into in-phase movements such as during the initial backward-directed portion of escape swimming, when the movements of a pair of limbs occur nearly at the same time (Zug, 1971).

Commissural and propriospinal projections

There are commissural projections in the spinal cord used to help coordinate the limbs. Locomotor-related commissural projections seem to be redundantly distributed along a bi-directional gradient that centers on the thoracolumbar junction (*neonatal rat:* Cowley et al., 2009). This commissural system both provides a left-right coordinating mechanism but also supports locomotor rhythm generation in response to brain stem stimulation. Descending propriospinal (forelimb–hindlimb) and crossed commissural (hindlimb–hindlimb) spinal cord pathways function together as type of redundant pathway used to sustain right–left hindlimb alternation (*turtle:* Samara and Currie, 2007).

An anatomical characterization of the propriospinal axons in red-eared turtle spinal cord has been made (Berkowitz and Stein, 1994). First, descending propriospinal axons have been identified in all regions of the spinal white matter. Second, neurons in each region of the gray matter have been demonstrated to rise in a different distribution of descending, funicular axons.

Some of these distributions overlap widely. Separate funicular axon distributions might be associated with different sets of synaptic contacts with the white-matter dendrites of spinal neurons (Berkowitz and Stein, 1994).

Telencephalon

The telencephalic areas may also play a role in modulating interlimb coordination. However, comprehensive physiological studies of cortical cell properties and intrinsic synaptic circuitry have been largely restricted to mammals (for a review see Jones and Peters, 1984). For example, lesions of the right sensory cortex was made in dogs, and limb movements as well as interlimb coordination were significantly altered. Both limbs contralateral to the lesion showed a proprioceptive deficit and the limbs were more flexed during locomotion. Due to this proprioceptive deficit, the dogs did not have the necessary control over the position of the distal portion of the forelimb, which caused frequent stumbling and falling (Błaszczyk and Dobrzecka, 1995).

Conclusion

All of the subsystems that have been characterized so far, are important for understanding the underlying neurological substrates used for sensory motor integration and control during locomotion. Throughout vertebrate history, survival depended on the intimate relationship between these locomotor circuits. These circuits are driven by a variety of sensory inputs, such that movements can be dynamically produced. Command systems drive the various locomotor behaviors. They descend through the spinal cord and activate the appropriate central pattern generator modules.

These central pattern generators produce the rhythmic alternating patterns of activation which stimulate the motoneruons. The extrafusal motor units cause the muscles to contract and the intrafusal fibers send feedback to the system.

In chapter 2, this dissertation will describe a new study that was conducted to evaluate the forelimb and hindlimb kinematics and motor patterns that underlie sensory-evoked turning locomotion in red-eared turtles. This study was designed to extend our knowledge gained from the lamprey studies and apply it to limbed vertebrates.
In order to do this, a method for reliably evoking locomotion with intact and surgically reduced preparations is required.

Several methods for reliably evoking locomotion with intact and surgically reduced preparations has been previously been accomplished with lamprey. As a result of this accomplishment, we have learned a tremendous amount from these limbless animals. For example, in lamprey we know that the deviation of the head towards the left or right will generate asymmetric reticulospinal neuron activations, which will in turn, produce an automatic correction of body orientation (Deliagina and Orlovsky, 2002). Another lamprey study found that an asymmetric light stimulus applied to one eye would cause a bias body position so that the dorsum of the body becomes oriented towards the light (Ullén et al., 1995). So far, we know that the vestibular system is the primary input for postural control for fish and for the orientation of the head in higher vertebrates, in which the correction of body position is also modified by proprioceptive input from the limbs (Grillner et al., 2008).

Evoking locomotion in turtles with a rotational stimulus will allows us to observe responses that are more “natural” than those found with electrical stimulation alone (e.g. Kazennikov et al., 1981).

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CHAPTER 2

ROTATION-EVOKED TURNING LOCOMOTION IN RED-EARED TURTLES

ABSTRACT

We examined the forelimb and hindlimb kinematics and motor patterns that underlie sensory-evoked turning locomotion in red-eared turtles. Intact animals were held by a band-clamp in a water-filled tank. Robust lateral turn-swimming was evoked by slowly rotating the turtle to the right or left via a motor connected to the shaft of the band-clamp. During such evoked responses, animals executed forward turn-swimming against the direction of the imposed rotation in an attempt to stabilize their yaw orientation. We recorded digital video of rotation-evoked turn-swimming and straight forward swimming from below and computer-analyzed limb and head movements. In a subset of turtles, we also recorded electromyogram (EMG) motor patterns from identified hindlimb or forelimb muscles. We found that rotation-evoked turning exhibited a stereotyped pattern of [1] forward swimming in the hindlimb and forelimb on the outer side of the turn, [2] backpaddling in the hindlimb on the inner side of the turn, [3] a stationary and extended forelimb on the inner side of the turn, and [4] neck bending in the direction of the turn. Reversing the direction of rotation caused the animal to rapidly switch the direction of its 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). This suggests that vestibular inputs were sufficient to drive the behavior. Sensory-evoked turning may provide a useful experimental platform in which to examine the brainstem commands and spinal neural networks that underlie switching between different locomotor forms.

INTRODUCTION

We characterized limb kinematics and the electromyographic (EMG) motor patterns that underlie aquatic lateral turning behavior in red-eared turtles, *Trachemys scripta elegans.* In a complex natural environment, locomotion is seldom steady state (e.g. running on a treadmill). Many studies on locomotion use rectilinear conditions since they lend themselves well to laboratory measurements. Studies of rectilinear locomotion have revealed general patterns of locomotion dynamics (e.g. Altshuler and Dudley, 2003; Landberg et al., 2003; Mori et al., 1977; Samara and Currie, 2008b; Swallow et al., 1998), however the mechanics and control of dynamic locomotion (e.g. during perturbations) have not been well characterized.

Red-eared turtles often live in lakes with muddy bottoms or near streams that have lateral flow shears, whirlpools, and backflows that can impose disruptive movements. Being able to offset imposed movements is important, especially, when the visual features of the environment are difficult or impossible to perceive. For example, hatchling sea turtles can detect wave direction while swimming under water at night in complete darkness (Lohmann et al., 1995). Experimentally, these hatchlings were suspended in the air and subjected to mechanically imposed movements that simulated waves. When the waves approached from their right sides, they attempted to turn right. Movements that simulated waves from the left elicited left-turning behavior. However, a detailed joint-angle phase analyses and electromyograms (EMGs) were not done. (Lohmann et al., 1995).

To determine how freshwater turtles compensate under some dynamic conditions, we constructed a rotation evoked behavioral assay to compare the kinematics (movement analyses) and motor patterns electromyography (EMGs) of the limbs that underlie lateral swim turning. We have found that turtles execute yaw-turns to counter these imposed rotations.

Hindlimb movements and EMG patterns have been described for spontaneous turning behavior in stationary shell-restrained freshwater turtles (i.e. in a steady state condition) (Earhart and Stein 2000; Field and Stein 1997). Generally, freshwater turtles display highly coordinated movements during swimming (Walker, 1973; Zug, 1971). When red-eared turtles exhibit swim turning, the outer hindlimb can display forward swimming while the inner hindlimb displays back-paddling (Field and Stein, 1997; Earhart & Stein, 2000). Similar motor patterns have also been demonstrated in low-spinal (Lennard and Stein, 1977) and high-spinal (Stein 1978) preparations. The hindlimb is often viewed as the primary propulsive apparatus during aquatic locomotion (Walker, 1973; Zug, 1971). In most freshwater turtles the webbing is much more extensive between the toes of the hindfeet than the toes of the forefeet (Walker, 1973). As a result, the hindfoot can form a broad paddle believed to serve as the predominant source of thrust during swimming (Pace et al., 2001; Zug, 1971).

Red-eared sliders use their forelimbs primarily for balance and orientation during aquatic locomotion. In habitats with vegetative or other debris, the claws of the red-eared slider forelimbs could assist in propulsion by facilitating the use of aquatic plants as a substratum (Pace et al., 2001).

Painted turtles, *Chrysemys picta,* while exhibiting predatory behavior (e.g. chasing fish), will conduct turns by extending the forelimb on the inside of the turn and hold it stationary into the water flow while continuing to move the contralateral forelimb and both hindlimbs with forward swimming (Rivera et al., 2006). Although the overall pattern of these limb movements during turning behavior have been described for freely behaving turtles, a detailed joint-angle phase analyses and electromyograms (EMGs) were not done (Rivera et al., 2006). Since both hindlimbs and forelimbs serve important roles, we characterized both the kinematic and the EMG motor patterns of each. However, in order to study locomotion in these animals, the shell must also be taken into consideration.

Turtles are a lineage of vertebrates that rely almost exclusively on coordinated movements of their limbs for locomotion due to how the vertebral skeleton is fused to the shell, excluding the neck and tail. The shell armor on most fresh water turtles consists of a large dorsal shield of plates fused to the axial skeleton connected laterally between the forelimbs and hindlimbs to large ventral scutes (Zug, 1971). Since red-eared slider turtles have this rigid shell and a non-propulsive tail, only the fore- and hindlimbs can be used to produce aquatic thrust (Pace et al., 2001). These qualities make turtles an excellent simplified model for studies of interlimb coordination (Field & Stein, 1997; Samara & Currie, 2007; Samara & Currie, 2008a). Another obvious mechanical limitation imposed by the turtle shell is a restriction in the degrees of freedom of the limbs. How rigid bodies limit maneuverability across a wide range of phyla remains largely unresolved despite thorough discussions (Walker, 2000).

METHODS

All procedures were performed according to protocols approved by the UC Riverside Institutional Animal Care and Use Committee in accordance with federal guidelines. A total of 16 turtles *Trachemys scripta elegans,* were used in this study. The turtle weight ranged from 492 to 707 g and the plastron lengths were from 13 to 15.5 cm. Nine of those animals were also used for EMG experiments. At the conclusion of each physiology experiment, the turtles were euthanized by a lethal dose of greater than 390 mg of sodium pentobarbital (Beuthanasia-D Special: Schering – Plough Animal Health, Wim de Körverstraatm, The Netherlands) per kg body weight. They were injected with a 20 gauge injection needle into the pleuroperitoneal cavity and monitored at room temperature for an hour after the injection. Afterwards, the turtles were placed into the freezer and quickly frozen.

Kinematics

We held the turtles suspended just below the surface in a water-filled Plexiglas tank [40 X 35 X 16 cm (length X width X height)] by a band clamp placed around the shell positioned just posterior to the pectoral scute. We rotated the turtles in the horizontal (yaw) plane with an attached reversible geared (250:1) DC motor that was attached to a clamp shaft that encircled the animal's shell. A sufficient high torque (0.73 N·m) motor driven by a variable DC power supply was used to counter act the forces produced by the turtle's vigorous turning movements in the opposite direction. The rotational velocity was varied from 45°, 90° and 120°/s by adjusting the driving voltage on the power supply.

The direction of the motor rotation was reversed via a polarity switch. The duration, delay, and interval parameters for the stimuli were accurately controlled with a Master-8 (A.M.P.I , Jerusalem, Israel) programmable pulse generator. The rotation speed was monitored with a calibrated variable resistor, and recorded simultaneously with Datapac 5 (Run Technologies, Mission Viejo, CA).

Rotation evoked swimming movements were recorded from below in these shell-restrained animals with a horizontally mounted digital video camera (Canon Optura 20 mini-DV), which was aimed at a 45° mirror beneath the clear bottom of the tank (Fig. 1). Brightly colored markers (3-mm beads) were attached to the skin at the wrists (h and i in Fig.1), knees (f and g), and ankles (k and l) on both sides. The position of the markers on the plastron for the right and left hip joints (d and e) positions were made (Samara and Currie, 2008a). We tracked the movement of these markers relative to fixed reference points on the plastron marked by high contrast markers or painted with white correction fluid (a–e).

Swim episodes were videotaped at a 30-Hz frame rate and 1/250 s shutter speed, and digitized directly to the computer hardrive. Datapac 5 was used to de-interlace the video frames, yielding a virtual 60 “fields” per second resolution from the AVI file. Marker positions for the plastron were digitized using an auto tracking feature and the limbs were manually tracked every other frame using Datapac 5 software. Linear interpolation was used to calculate the equidistant points along the line of best fit for the manually tracked markers.

A circular calibration object (diameter of 12.2 cm) was held at the same distance from the camera as the turtle plastron to calibrate the dimensions of the X and Y axes. Datapac 5 was used to measure changes in forelimb, hip, and knee angles over time and the Datapac 5 scientific spreadsheet module was used to calculate maximum and minimum limb angles, interlimb phase, and cycle frequency from these swim episodes. A detailed description of the angle measurements of the limbs has been described previously (Samara and Currie, 2007). In brief, hip angle was defined as the angle between the thigh line (d–f on the right or e–g on the left in Fig. 2-1) and a line parallel to the ventral midline (a–c) with its origin at the hip joint. Forelimb angle was defined as ∠abh on the right and ∠abj on the left, and was measured relative to a stationary marker on the plastron midline (b). Head angle was defined as ∠abj, where an angle of 0° indicated that the head was pointed straight rostrally. When the head moved to the right, the head angle was recorded as a positive value, and when the head moved to the left a negative value. Digitized images of the turtle's ventral mid-line (line b-c) were stabilized, using customized Datapac 5 kinematic software developed by Youan Chang at Run Technologies, so that the bilaterally asymmetric limb movements that occurred during rotation-evoked turning could be viewed relative to a stationary body axis (Fig. 2).

We calculated the cycle frequency of the forward swimming hip using Datapac 5. We assessed how the rate of rotation and time effects cycle frequency. In order to assess the effect of time, we placed the cycles into three distinct eight second time bins.

The onset of each cycle that was initiated during 0.0 to 8.0 seconds were placed in the first time bin, 8.1 to 16.0 in the second time bin, and 16.1 to 24 in the third time bin for comparison.

We calculated dual-referent phase values to assess interlimb coordination. The dual-referent phase of an event was used to normalize the flexion and extension phases of the locomotor patterns. During locomotion, the relative duration of phase can diverge during the presentation of a single behavior as well as between behaviors. The phase θ of an event that occurs during hip flexion is defined as the latency of the event from the onset of hip flexion divided by twice the duration of hip flexion; the phase θ of an event that occurred during hip extension is defined as the latency of the event from the onset of hip extension, divided by twice the duration of hip extension, plus 0.5. The phase values for the onset of knee extension (target) movement and onset of forelimb flexion (target) were both taken within the respective hip flexion cycle (referent).

Electromyography

The implantation of the electrodes into hindlimb muscles has been described previously (Lennard and Stein, 1977). Prior to surgery the turtles (n =9) with plastron lengths from 13 to 15.5 cm, were placed in crushed ice for 2 hours or longer to induce hypothermic anesthesia. During all surgical procedures, turtles remained partially submerged in ice.

Electromyograms (EMGs) were recorded with bipolar 0.004-in. silver wire (California Fine Wire Company, Grover City, CA) electrodes.

Each electrode consisted of two silver wires glued together with Permabond 910 adhesive (National Starch and Chemical, Bridgewater, NJ). EMGs were amplified, filtered (30 – 1,000 Hz) with a Grass P5 series A.C. preamplifier (Astro-Med West Warwick, RI) and digitized using Datapac 5 (Run Technologies, Laguna Hills, CA) computer software. A remote video synchronization unit (Peak Performance Technologies (Vicon), Los Angeles, CA) was used to synchronize the EMG recordings with the kinematic video data. We used Datapac 5 to digitally record the electromyograms (EMGs), and the video with a record that contained a synchronization landmark. A light emitting diode (LED) was used to create a flash of light in the video while simultaneously recording the electrical pulse by the data acquisition system.

In the current study, three hindlimb muscles, m. flexor cruris, pars flexor tibialis internus, a hip retractor and knee flexor (HR) (n=5), and m. triceps femoris, pars femorotibialis, vastus medialis, a knee extensor (KE) (n=4), and m. puboischio-femoralis internus, par anteroventralis, a hip protractor (HP) (n=4) were utilized. Forelimb EMG patterns have been described for forward swimming in a high spinal preparation (Stein, 1978). In the current study, three forelimb muscles, m. pectoralis, a pectoral girdle retractor and a shoulder retractor (SR) (n=3), and m. triceps brachii, humeral head, an elbow extensor (EE) (n=2), and m. deltoideus, abductor and protractor of the upper forelimb (FP) (n=1) were also implanted (Walker, 1973). We conducted a post mortem analysis to verify correct electrode placements. Recordings from electrodes that were not properly placed in the correct muscle were excluded from our counts.

Data analysis

We used dual-referent phase analysis to assess interlimb coordination (Berkowitz and Stein, 1994; Field and Stein, 1997; Samara and Currie, 2007); phase values were calculated with Datapac 5. One limb was selected as "referent" (RH or LH) and the other as "target" (LF or RH). Phase data were imported into Oriana 3.0 (Kovach Computing Services, Anglesey, Wales, UK) to obtain circular statistics (Batschelet, 1981; Mardia and Jupp, 2000; Zar, 1999). Vector algebra (Batschelet, 1981) was used with the cyclic data. Each phase θ was calculated as a two-dimensional unit vector with a length of 1 and an angle of $2\pi\ \theta$ in radians. Angle of the mean vector in radians was calculated using vector addition, divided by 2π and defined as the mean phase, which has a range of 0 to 1. The angle of the mean vector (μ) represents the average length of the mean vector, while (r) indicates the directional concentration of data points around the mean vector angle (strength of the preferred phase), which also has a range of 0 to 1. We also calculated the mean angular deviation used to indicate the dispersion of the phase data. Since these data are not normally distributed, we used the Mann-Witney U2 test (Samara and Currie, 2007) to compare locomotor patterns within and between each of the respective behaviors.

We used the Rayleigh test to discriminate between uniform and unimodal-clustered distributions. A statistical comparison between referent and target angles were made with the Watson U2 test. Cycle period was calculated for left forward swim hips, using Datapac 5 software, by measuring the time between consecutive flexion onsets in kinematic recordings.

Analysis of Variance (ANOVA) was used to assess how rotation speed and time differed in its effects on cycle frequency. Cycle frequency data was imported into SYSTAT 11 (Systat Software, Inc. Chicago, IL ,USA) for analysis. Post hoc t-tests with Bonferroni adjusted p-values were used to account for the increase chance in type I error due to multiple tests.

RESULTS

Kinematics

Rotation elicits a highly stereotyped pattern of forward swimming (FS) motor patterns in the hindlimbs on the outside of the turn, and back-paddling (BP) motor patterns on the inner side of the turn. The ankle trajectories for the forward swim and back-paddle movements are indicated by the arrows in Fig. 2-2, and the movements were made in the opposite direction for the two locomotor forms. The posterior extent of the back-paddle ankle trajectory was more variable from cycle to cycle verses the other trajectories (Fig. 2-2), congruent with previous findings during spontaneous turning behavior (Earhart and Stein, 2000; Field and Stein, 1997).

Rotation also elicits a highly stereotyped pattern of forward swimming (FS) motor patterns in the forelimb on the outside of the turn and a stationary and extended forelimb on the inner side of the turn (Fig. 2-2). The forelimb angles were used to examine the coordination of limb movements as observed from the ventral view of the turtle with the video camera. The apex for the forelimb angle was defined as the point along the ventral midline of the plastron between the border of the humeral and pectoral scutes.

The forelimb forward swim cycle was defined as the onset of limb extension towards the head of the turtle and ending at the start of the next forelimb extension cycle (Fig. 2-2). As such, the forelimb forward swim is initiated at end of the flexion phase of the locomotor cycle (Fig. 2-2).

In the center trace (Fig. 2-2), a comparison with forward swimming is made. Voluntary forward swimming in freshwater turtles typically consists of 1:1 out-of-phase movement of contralateral limbs (right–left forelimbs: RF–LF; and right–left hindlimbs: RH– LH) and of ipsilateral limbs (RF–RH and LF–LH), and 1:1 nearly in-phase movement of diagonal limbs (RF–LH and LF–RH) (Field and Stein, 1997; Samara and Currie, 2007). The average minimum and maximum limb angles (degrees) ± SDs for all four limbs during clockwise and counter-clockwise rotations (n=5 Turtles) are presented in Fig. 2-3. The overall symmetry of the limb movements can be observed when you compare the contralateral limb ranges when they are engaged in the same locomotor form (e.g. FS or BP).

In order to calculate the minimum and maximum limb angle of the relatively stationary (non-swimming) extended forelimb, we used the onsets and offsets of the contralateral forward swim forelimb to sample the angle position of the protracted forelimb at the same rate. In this way, we were able to provide an objective method for being able to compare the two forelimb ranges with the same number of samples. We also measured the intralimb phase relationships between the hip and knee during both FS and back-paddle as a form discriminator.

We investigated differences in turning behavior due to different imposed rotation velocities in order to determine the optimum rotation rate. The cycle frequency increases with the rate of rotation. A run-down of the behavior is exhibited over the 24-second duration of the stimulus. There were no significant effects of rundown between the last two time bins 8-16 s verses 16-24 s for all three rotation speeds, which suggests that most of the run-down occurred during the first 8 seconds of rotation (Fig. 2-4). The optimum rotation rate used for further experiments was determined to be 90°/s, since we were able to elicit a consistent and robust motor response at that speed, with no apparent benefit at higher speeds.

Since the forward swim and back-paddle patterns produce different kinds of effective thrust through the water, we expected to find a quantitative difference in the phase relationships between them. Quantitative analysis confirmed that intralimb hip and knee phase relationships were different from one another during FS verses BP (Fig. 2-5). A statistical comparison of knee extension onset within the hip cycle between FS and BP was made with the Watson U2 test. As was expected, the phase values for FS and BP were found to be statistically different $P<0.01$.

Intralimb phase relationships are important as form discriminators. Circular histograms indicate phase values for the onset of knee extension (target) movement within the ipsilateral hip flexion cycle (referent). Values close to 0.5 indicate an out-of-phase intralimb relationship; values close to 0.0 or 1.0 indicate an in-phase intralimb relationship.

The direction of the vector arrows indicates the mean phase, and the length indicates the strength of intralimb coupling (r) on a scale of 0.0 to 1.0. (Fig. 3- 4a): The "outer" forward swimming (FS) knee and hip (127 cycles). Mean intralimb phase = 0.28, r = 0.97, P <0.01 (Rayleigh test). The "inner" back-paddling (BP) knee and hip (110 cycles) are presented in (Fig. 2-5b). The mean intralimb phase = 0.82, r = 0.839, P <0.01 (Rayleigh test).

We also quantified the interlimb relationships for both FS and BP for each of the limbs producing swimming movements (i.e. not the stationary extended forelimb) in order to examine the degree of coordination between them. Distributions of interlimb phase relationships between the hip(s) and/or forelimb during mixed form bilateral turn (n=5 turtles) (Fig. 2-6). In Fig. 2-6a, the phase values (110 cycles) for the onset of back-paddle (BP) hip flexion (target) movement within the contralateral foreword swim (FS) hip flexion cycle (referent) were compared. Mean intralimb phase = 0.29, r = 0.67, P <0.01 (Rayleigh test). The results for the phase values for the FS forelimb and hip were similar to the phase values found in previous studies of shell restrained turtles (Field and Stein, 1997; Samara and Currie, 2007).

We also examined the coordination of the limbs diagonally during the rotation evoked swim. We found phase values (123 cycles) for the onset of FS forelimb flexion (target) movement within the ipsilateral FS hip flexion cycle (referent) (Fig. 2-6b). Mean intralimb phase = 0.54, r = 0.94, P <0.01 (Rayleigh test). Distribution of interlimb phase relationship between the BP hip and the contralateral FS forelimb during mixed form bilateral swim (turning) (n=5 turtles) was assessed.

Phase values (109 cycles) for the onset of forward swim (FS) forelimb flexion (target) movement within the contralateral back-paddle (BP) hip flexion cycle (referent). Mean intralimb phase = 0.27, r = 0.603, P <0.01 (Rayleigh test) (Fig. 2-6c). These results indicate that the two limbs were not as tightly coupled to one another.

Motor Patterns

We made a comparison of counter-clockwise and clockwise Rotations at 90°/s. Abruptly changing the direction of rotation causes the animal to rapidly switch the direction of its turning behavior and the pattern of right and left limb activities. Kinematic data show an alternation of forelimb and hindlimb locomotive forms. In addition, EMGs were recorded from a selection of muscles that demonstrate how these hindlimb movements correspond with the knee extensor (KE), hip flexor (HF), and hip extensor (HE) activity respectively (Fig. 2-7). A selection of 2 seconds of rotation evoked turning for counter-clockwise rotation BP and clockwise rotation FS can be seen in Figure 8. A single KE burst occurred during each swim cycle. The onset of the KE burst occurred during the hip flexor burst for forward swim, but before the onset of the hip flexor burst in the back-paddle. The forward swim powerstroke occurred with hip extension and high-amplitude hip extensor activity. The back-paddle powerstroke occurred with hip flexion movement and high-amplitude hip flexor activity and knee extensor activity. These data confirm previous findings in stationary band clamp turtles that swam spontaneously (Earhart and Stein, 2000).

We also characterized the motor patterns for the forelimbs. A comparison was made with counter-clockwise and clockwise rotations at 90°/s.

EMGs were recorded that demonstrate how these forelimb movements correspond with the EE, SF, and SR activity respectively (Fig. 2-9). A selection of 2 seconds of forelimb cycles of rotation evoked turning for back-paddle and forward swim was compared (Fig. 2-10). Activity of the forelimb muscle EE serves to extend the distal portion of its limb and is active during the late extention portion of the movement cycle in its limb. The activity of the forelimb muscle SR serves to retract its limb and is active during the retraction portion of the movement cycle of its limb. These data confirm previous findings in forward swimming movements observed in a turtle high spinal preparation (Stein, 1978). When the forelimb is in a protracted position, a low amplitude (nearly abolished) rhythmic activity can be observed in SF. SF server as the abductor and protractor of the upper forelimb and shoulder retractor. The start of the power stroke of the forelimb forward swim is indicated by the onset of forelimb flexion, which occurs after the limb is positioned in its furthest anterior position (Rivera et al., 2006). As such, we find that the SF muscle activation is in antiphase with EE and SR muscles during forward swim.

Sensory Activation

We make a comparison of counter-clockwise and clockwise rotations at 90°/s with a turtle that was blindfolded and with all of the water removed from the tank (n=2). We observe the same motor patterns with water and without blindfold (see Fig. 2-7 through 2-9). We observed a similar rotation evoked turning response, as seen previously (see Fig. 2-7 through 2-10). These results suggest that the rotation evoked turning response can be evoked without visual cues or water present (Fig. 2-11).

DISCUSSION

The major result of this study is the demonstration that stereotyped lateral turn swimming can be evoked with imposed mechanical rotations.

The red-eared sliders responded to these imposed perturbations of motion, by generating a highly coordinated production of forces with its limbs (Fig. 2-7 and 2-8). A second major result of this paper is that the rotation evoked turning response can be evoked without visual cues or water present (Fig. 2-11).

In a previous study, sea turtles were shown to be capable of responding to wave direction by using simulated waves (Lohmann et al., 1995). As such, similar mechanisms may be widespread among many other aquatic animals. Additional examples include other open-sea migrants such as fish and cetaceans that have the ability to detect wave direction without surfacing (Lohmann et al., 1995). Voluntary turning behavior is 'self-generated' perturbations of motion that also requires a highly coordinated production of forces. Voluntary turning requires an asymmetry in forces between the limbs on the inside and outside of a turn.

Voluntary turning can be produced via several different motor patterns, and have been characterized with an established simplified descriptive framework by Rivera et al., 2006. Within this framework each individual limb might show one of four basic locomotor forms: (1) forward swimming, (2) modified forward swimming, (3) fold along the body to stop contributing to propulsion, but minimize additional drag, or (4) stationary protracted limb from the body to increase drag and act as a pivot.

Missing from this descriptive framework is (5) the hindlimb back-paddle form (Earhart & Stein, 2000;Field and Stein, 1997) where stationary band clamped turtles have one hindlimb that can display back-paddling while the contralateral hindlimb displays forward swimming.

In the present study, we also observed the head bend in the opposite direction of the imposed turn. We believe that this was active verses passive neck bending for two reasons. The most compelling evidence for active neck bending was that it occurred just as robustly in air (without water resistance) at slow rotation speeds. This finding would be insufficient to explain passive head movement driven primarily by inertia (see Fig 2-7, head position trace), which suggests a muscular response. In the Rivera et al., 2006 study, their data demonstrated that, during voluntary forward turns, painted turtles consistently combine patterns 4 and 1, extending the forelimb on the inside of the turn and holding it stationary into the flow, while continuing to move the contralateral forelimb and both hindlimbs with a forward swimming motor pattern. In the present study, we demonstrated a consistent combination of patterns 5 and 1, which is consistent with other band clamp restrained turtles form (Earhart & Stein, 2000; Field and Stein, 1997). One interesting distinction between the band clamp restrained turtles and the current study is the observed phase value difference found in the BP verses the FS hip angles. In stationary band clamp turtles (Field and Stein, 1997; (Earhart & Stein, 2000), a consistent mean phase value of 0.5 was observed between the FS hip and BP hip, while in the current study, a consistent mean phase value of 0.29 was observed (Fig. 2-6).

In the stationary band clamp studies (Earhart & Stein, 2000; Field and Stein, 1997) they were held stationary and did not receive many of the sensory cues that they would have during the rotation evoked turn such as in the current study. Voluntary turning may involve the integration of proprioceptive afferents, efference copy signals, and vestibular cues that allows for more accurate estimation of displacement than does use of vestibular cues alone during external perturbations (Stevens & Earhart, 2006). This suggests that voluntary verses external perturbations may have different underlying mechanisms that modulate these motor patterns. Support for this kind of difference was observed in a study with humans that where found to be less accurate at estimating displacements when they were exposed to external perturbations than when they actively turned themselves (Jürgens et al., 2003).

Unfortunately, Rivera et al., (2006), making any further comparison difficult, did not report phase values for the two hips. We may find that the control mechanisms of body orientation following maneuvers may use similar general stabilization strategies common to those used in rejecting external perturbations (e.g. imposed lateral movements). The slight modifications found in these locomotor forms suggest that there may be sharing of circuitry that produces them.

Possible shared neural control circuitry

Since the freely swimming turtles exhibit a consistent motor pattern (Rivera et al., 2006) that is distinct from the stationary (Field and Stein 1997, Earhart and Stein 2000) and rotation evoked turtles in the current study, it is possible that the underlying neuro-substates might be different.

The combinations of limb movements during turns are modest modifications of each of the respective locomotor forms, which indicates some possible shared neural control circuitry might be used, as found with other related behaviors (Macpherson, 1991; Earhart and Stein, 2000). Pattern generators are dynamic, shared structures that can be modulated to produce different motor outputs (Dickinson et al., 2000). For example, some evidence from turtle studies support sharing between left and right side circuitry controlling three scratch reflex forms (Berkowitz and Stein 1994; Currie and Gonsalves 1999; Field and Stein 1997). There is also evidence for sharing of circuitry between rostral scratch and forward swim (Earhart and Stein 2000; Field and Stein 1997; Juranek and Currie 2000). In a more recent experiment using both electrophysiological and histological techniques, interneurons that were found to be rhythmically active during both swimming and scratching had axon terminal arborizations in the ventral horn of the hindlimb enlargement, indicating a contribution of hindlimb motor patterns for both behaviors (Berkowitz, 2008). In a similarly reduced preparation, it may be possible to identify shared circuitry between forward swim and back-paddle motor patterns as well.

Knee extension during forward swim versus back-paddle

A selection of cycles of counter clockwise rotation (A) and clockwise rotation (B) evoked swimming can be seen in Fig. 2-8. During back-paddle, knee extension begins during hip extension and power stroke occurs during hip flexion. During forward swim, knee extension begins during hip flexion and power stroke occurs during hip extension.

These results are consistent with hindlimb movements and EMG patterns that have been described for spontaneous turning in band-clamped turtles (Earhart and Stein, 2000; Field and Stein, 1997). This asymmetric motor pattern is one way an animal is able to produce lateral turns.

Lateral Turns

It is obvious that the ability of the turtle to control its direction is required in order for it to reach different locations in its environment. A good example of direction control has been demonstrated experimentally with turtles when they capture prey (Rivera et al., 2006). In order for an animal to be a successful at capturing prey, it does depend significantly on its own ability to perform turns. However, motor responses are also utilized for recovering from imposed perturbations during locomotion in order to maintain stability, as in the current study. These responses manifest themselves as coordinated forelimb and hindlimb motor patterns. This interlimb coordination is possibly maintained via a combination of propriospinal pathways, central pattern generators (cervical and lumbar), as well as other sensory input (e.g. vestibular) that facilitates this stereotyped swimming motor pattern.

In the present study, we blindfolded a subset of turtles and placed them in a tank with the water removed. We found that the rotation stimulus was sufficient to evoke a turn swim (Fig. 2-11) and head position changes when compared to turtles with visual and water cues are present (Fig. 2-7). This suggests that the vestibular sense likely plays a major role in evoking this behavior.

This finding is more significant when we appreciate the fact that these red-eared turtles are also quadrupeds capable of traveling on land. In terrestrial quadrupeds (e.g. cat, rabbit), the postural system can under certain specific conditions dissociate into the sub-systems controlling independently the head and the trunk (Barberini and Macpherson, 1998; Beloozerova et al., 2005). These sub-systems are driven by sensory signals of different modalities: the head orientation is stabilized mainly on the basis of vestibular and visual information; for trunk stabilization, somatosensory inputs from limbs are most important (Beloozerova et al., 2003; Deliagina et al., 2000). In this respect, terrestrial animals strongly differ from aquatic ones, whose postural mechanisms are driven primarily by vestibular input (Deliagina et al., 2008). In standing quadrupeds, each of the four limbs can participate in supporting the body. When the animal's posture is perturbed, each of the limbs contributes to the generation of a corrective motor response (Beloozerova et al., 2003; Jacobs and Macpherson, 1996).

In some aquatic animals such as the lamprey, the turning ‘commands’ have been studied in both intact and reduced preparations (e.g. Fagerstedt et al., 2001; McClellan, 1984; McClellan & Hagevik, 1997; and Kozlov et al., 2002). An in vitro lamprey nervous system preparation was developed which consisted of the head and exposed brainstem attached to an isolated spinal cord (McClellan, 1984). It was found that mechanical or electrical stimulation of the snout elicits motor activity in ventral roots, which underlies a turning response (head withdrawal) away from the stimulus followed by escape swimming.

Direct stimulation of the sensory division of the trigeminal nerve activates these patterns, and cutting this nerve abolishes ventral root activity elicited by stimulation of the snout (McClellan, 1984). One general principle that was demonstrated in studies with this kind of preparation is that asymmetric activity between the two respective reticulospinal populations on each side of the brainstem will result in the production of turning motor patterns (for review see Grillner et al., 2008). In computer model simulations of lamprey spinal cord, when brief excitatory descending inputs were applied to one oscillator and the contralateral oscillator received inhibition, it produced changes in the rhythmic output patterns that were similar to those observed during turning motor activity in whole animals (McClellan & Hagevik, 1997). In future studies, we hope to develop reduced preparations and computer models of the turtle spinal cord that can generate similar turn motor patterns as found in the lamprey. We believe that rotation-evoked turning may provide a convenient experimental platform in which to investigate the brainstem commands that underlie locomotor form selection (e.g., forward swimming vs. back-paddling) in a limbed vertebrate.

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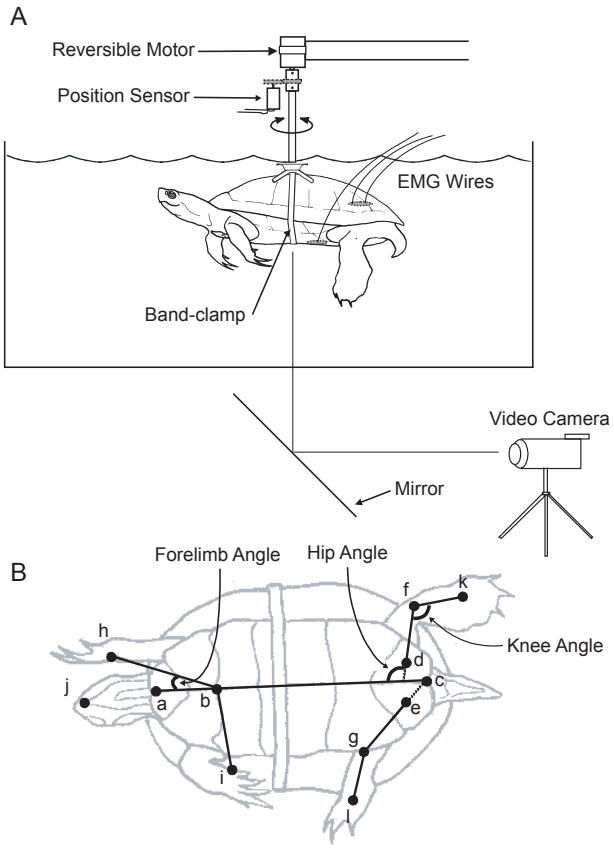


Figure 2-1. Apparatus used to elicit and record turn-swimming and rectilinear swimming in restrained turtles. A. Animals were held by a band-clamp that wrapped around the plastron and carapace, just beneath the water-surface in a transparent plastic tank. Digital videos were recorded from below reflected off a 45° mirror. Slow rotation of the animal to the right or left, via a reversible variable-speed motor attached to the band-clamp, reliably evoked robust turning behavior in the opposite direction. Forward swimming could be elicited by using various stimuli, including movement within the animal's visual field, and touching the caudal body surface. B. Markers on the plastron (ventral shell), limb joints, chin and tail (a-m) permitted us to monitor forelimb, hip, knee, head and tail angles as a function of time, using video motion capture and analysis software (Datapac 5, Run Technologies) and synchronized those measurements with EMG recordings from selected hindlimb or forelimb muscles.

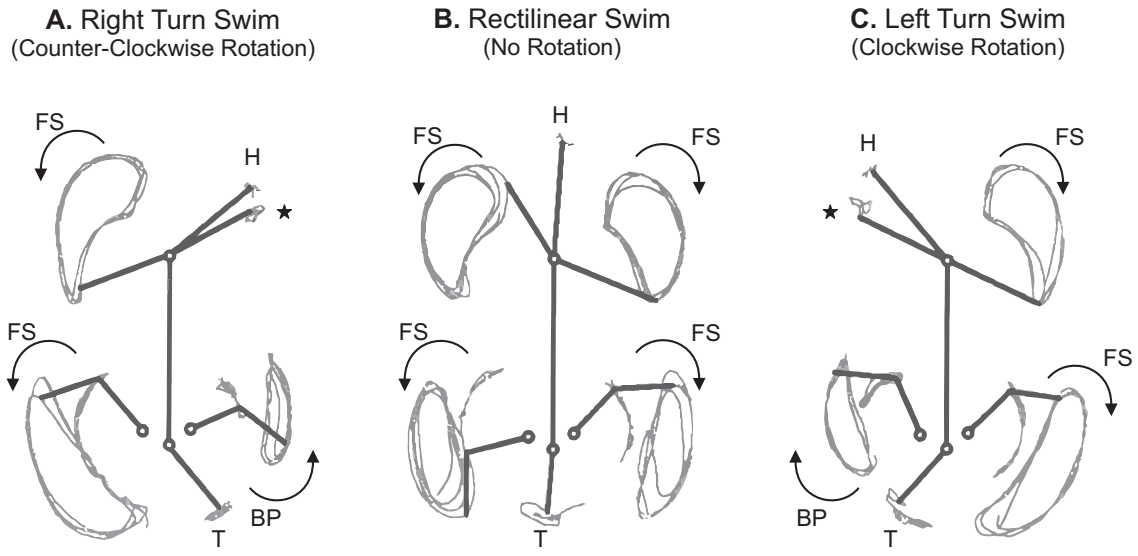


Figure 2-2. Limb trajectories compared for right and left turn swimming and rectilinear swimming in the same animal (experiment D24). Right limbs are shown on the right and left limbs on the left. Stick figures show the trajectories of the left and right wrists, knees, ankles, head (H; indicating a painted dot on the chin) and tail (T: indicating a pigmented spot near the tip) for 2-second episodes of turn swimming (elicited by 90°/sec counter-clockwise and clockwise rotations, respectively) and voluntary rectilinear swimming. During turn swimming (A and C), the "outer" forelimb and hindlimb exhibited out-of-phase forward swimming (FS), the "inner" hindlimb exhibited back-paddling (BP), the "inner" forelimb (star) was held motionless in a protracted position, and both the head and tail were strongly bent toward the direction of the turn. During rectilinear swimming (B), right and left forelimbs and hindlimbs all exhibited bilaterally symmetrical forward swim movements, and both the head and tail were kept nearly straight (close to the center midline), although the tail oscillated slightly to the right and left. In order to visualize the overlapping limb trajectories of the rotating animal in A and C, we digitally stabilized the ventral mid-line of stick figures (line b-c in Fig. 2-1B) via the kinematic analysis software (see Methods: Kinematics).

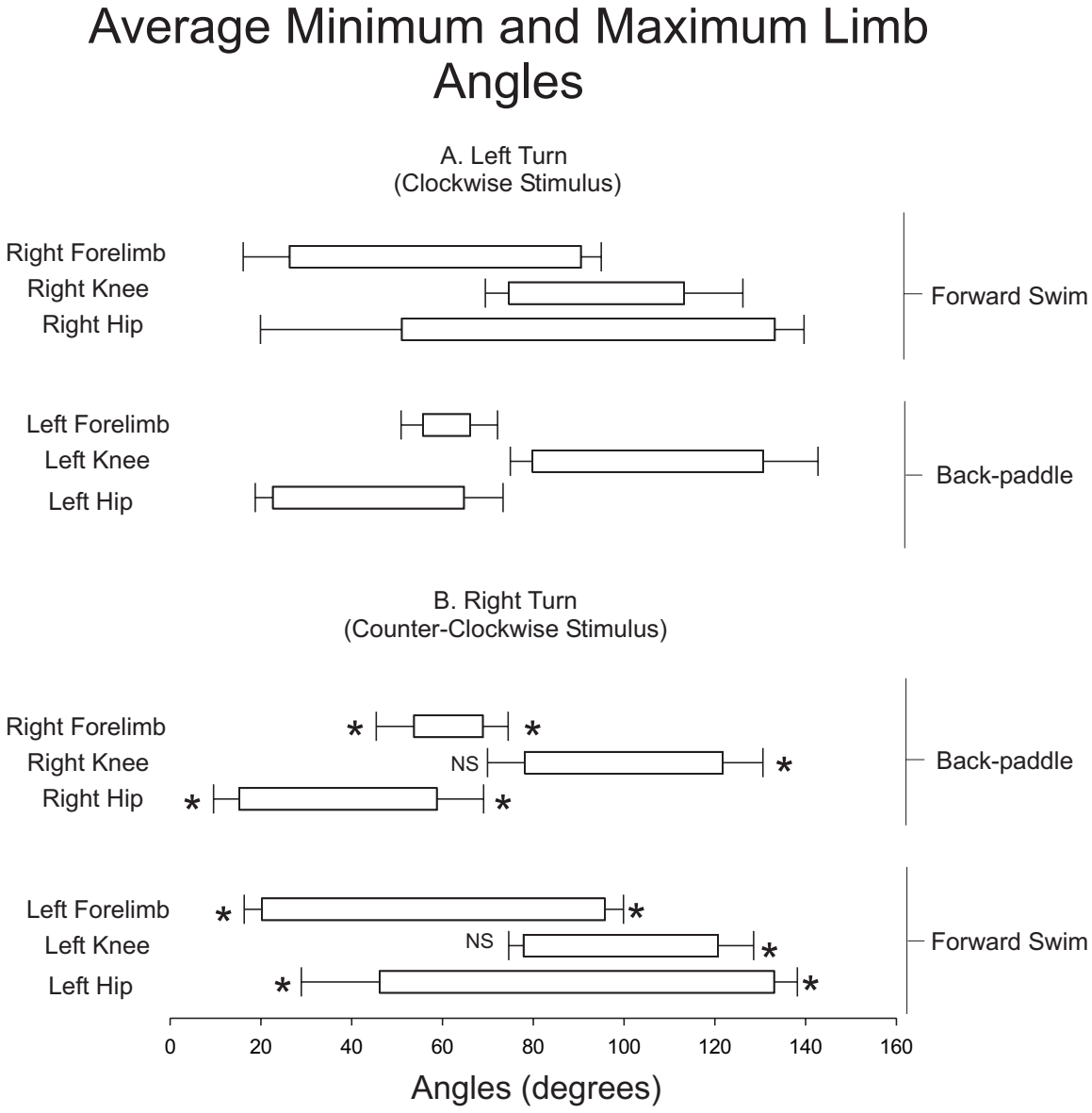


Figure 2-3. Average minimum and maximum forelimb, knee, hip angles on the right and left sides during left turn-swimming elicited by clockwise rotations (A) and right turn-swimming elicited by counter-clockwise rotations (B) (n=5 turtles; 108-148 cycles per sample). Left and right edges of the rectangles represent average minimum and maximum angles, respectively. Error bars= standard deviations. Statistical comparisons were made between corresponding minimum angles (e.g. right forelimb) and between corresponding maximum angles during left and right turns, using the Mann-Whitney U test (Siegal, 1956). * $p < 0.0005$ and NS $p > 0.05$, respectively.

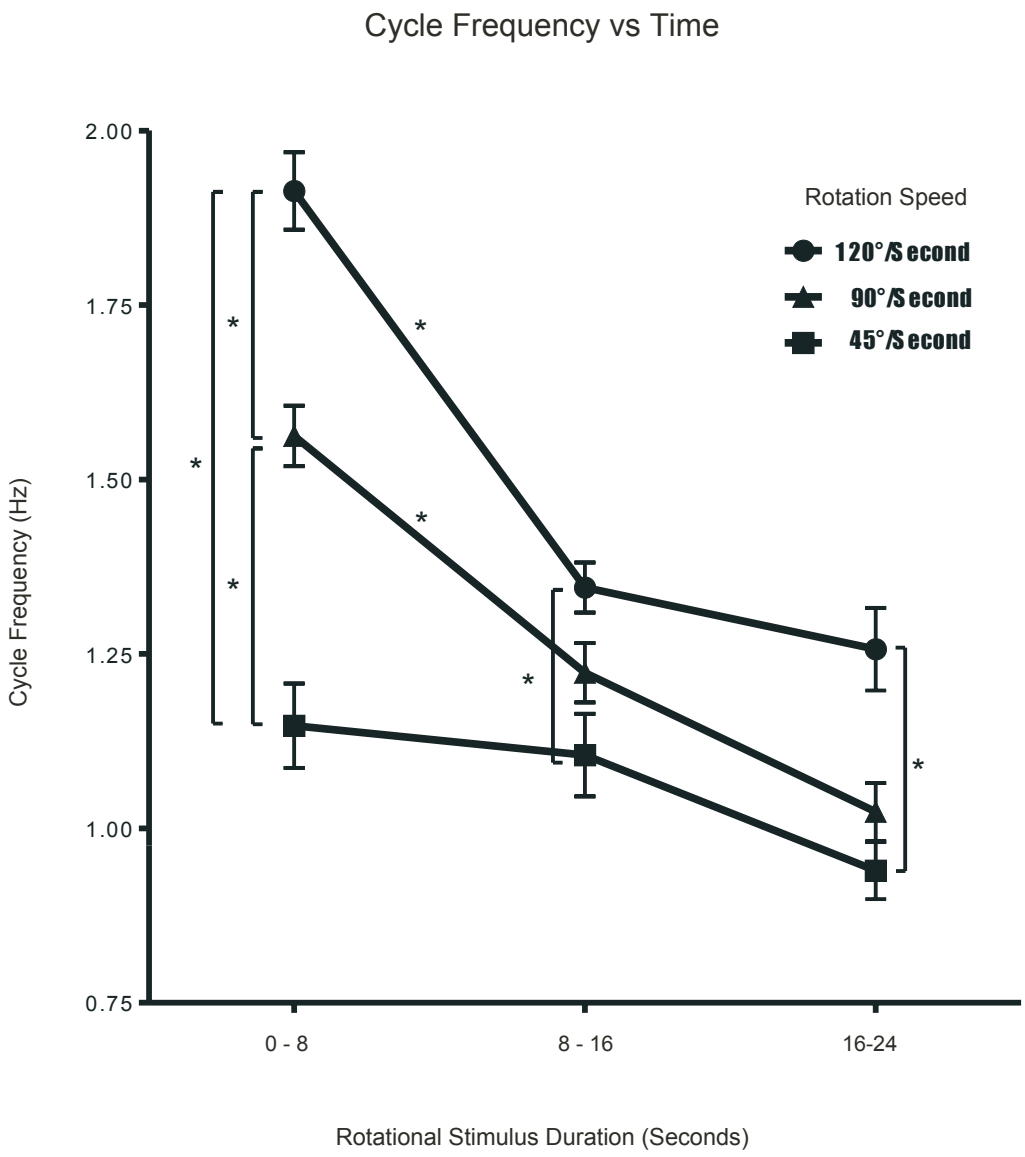


Figure 2-4. The cycle frequency of turn swimming limb movements increased as a function of the imposed rotational velocity ($p<0.01$), but decreased over time following stimulus-onset ($p>0.042$; repeated measures ANOVA). Data was collected for three counter-clockwise rotational velocities, 45, 90, 120 degrees per second, with each episode lasting 24 seconds (n=4 turtles). Cycle frequency was measured for forward swim (FS) hip protraction onsets on the outer side of turns, pooled and averaged over three consecutive 8-sec time bins for each rotational velocity. The error bars are standard errors. We used t-tests to isolate the differences between groups in our ANOVA analysis. Post hoc pair-wise comparisons (with Bonferoni corrections) were made to assess the differences between mean cycle frequency values for different rotation velocities within the same time-bin and for different time-bins at the same rotational velocity. Asterisks indicate pairs that are significantly different from each other. The effect of rotational velocity on cycle frequency was most pronounced during the first 8 seconds of rotation. The most significant run-down of cycle frequency over time occurred between the 1rst and 2nd time-bins during rotation at 120°/sec and 90°/sec.

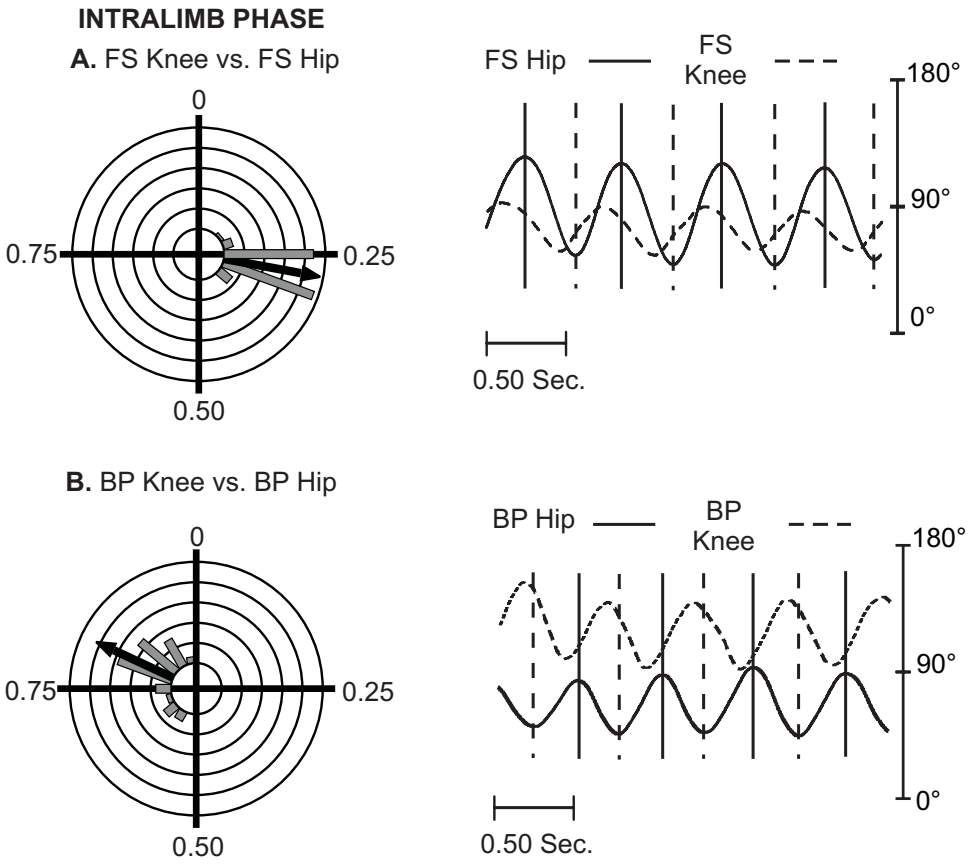


Figure 2-5. The intralimb (knee-hip) phase relationships for the forward swimming (FS) hindlimb on the outer side of the turn and the back-paddling (BP) hindlimb on the inner side of the turn during right turn-swimming episodes evoked by counter-clockwise rotation. Circular histograms (left of figure) indicate phase values for the onset of knee extension (KE) movements within the hip protraction cycle (HP onset – onset); data was pooled from 5 turtles. Each concentric circle represents 12 cycles for each range of phase values. The direction of the vectors (arrows) indicates that mean phase, and vector length indicates the strength coupling (r) on a scale of 0.0 (innermost circle) to 1.0 (outermost circle). Representative kinematic sequences (right side of figure) were selected from turtle D19. Knee (target) angle is shown as dashed lines; hip (referent) angle is shown as solid lines. A. Phase relationships between the "outer" (left side) forward swimming (FS) knee and hip (127 cycles pooled in histogram). Mean intralimb phase = 0.28, r=0.97, P <0.0001 (Rayleigh test). B. Phase relationship between the "inner" (right side) back-paddling (BP) knee and hip (110 cycles pooled in histogram). Mean intralimb phase = 0.82, r = 0.84, p < 0.0001. A statistical comparison of knee extension onsets within the hip cycle between FS and BP was made with the Watson U2 test. The phase values for FS and BP were found to be statistically different, p < 0.001.

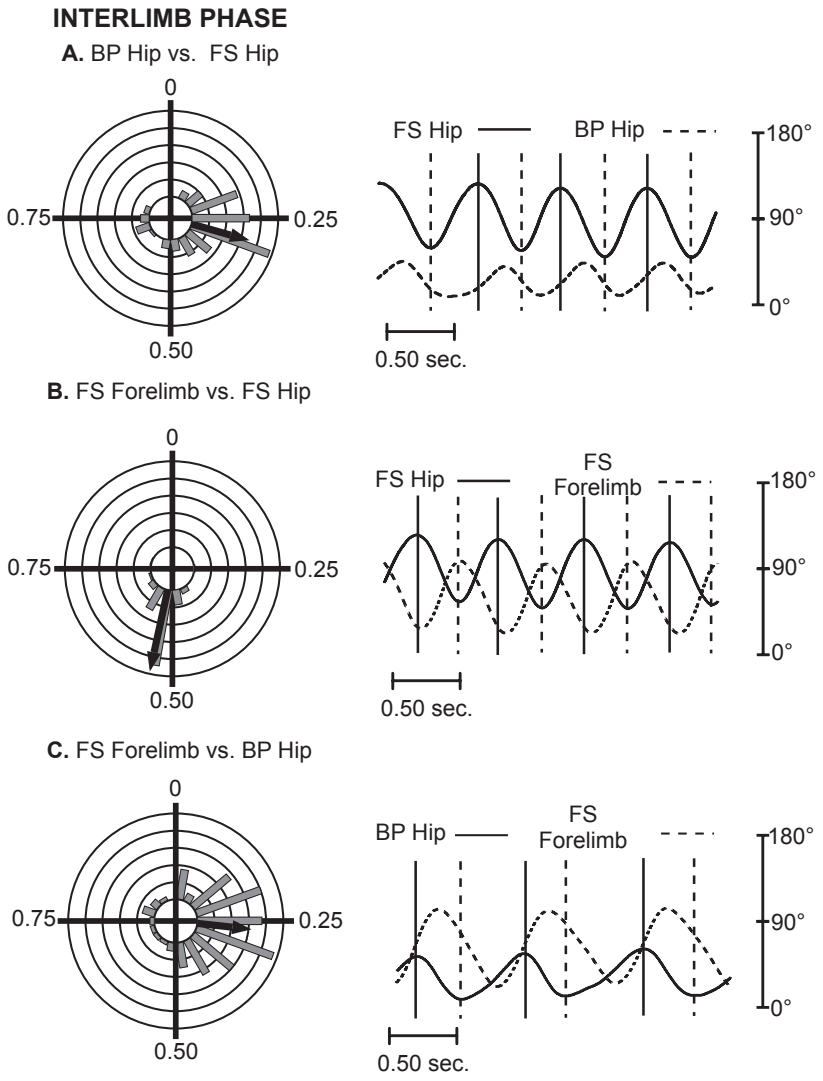


Figure 2-6. Interlimb phase relationships during right turn-swimming episodes evoked by counter-clockwise rotation. Circular histograms (left side of figure) indicate phase values pooled from 5 turtles. Representative kinematic sequences (right side of figure) were selected from turtle D19. A. Phase relationship of "inner" (right side) back-paddling (BP) hip protraction onsets within the "outer" (left side) forward swim (FS) hip protraction cycle (110 cycles pooled in histogram). Each concentric circle represents 6 cycles for each range of phase values. The direction of the vectors (arrows) indicates the mean phase, and vector length indicates the strength of interlimb coupling (r) on a scale of 0.0 (innermost circle) to 1.0 (outermost circle). Mean interlimb phase = 0.29, r = 0.67, p < 0.0001 (Rayleigh test). B. Phase relationship of "outer" (left side) FS forelimb protraction onsets within the ipsilateral (left side) FS hip protraction cycle (123 cycles). Each concentric circle represents 16 cycles for each range of phase values. Mean interlimb phase = 0.54, r = 0.94, p < 0.0001. C. Phase relationship of "outer" (left side) FS forelimb protraction onsets within the contralateral (right side) BP hip protraction cycle (109 cycles). Each concentric circle represents 4 cycles for each range of phase values. Mean interlimb phase = 0.27, r = 0.60, p < 0.0001.

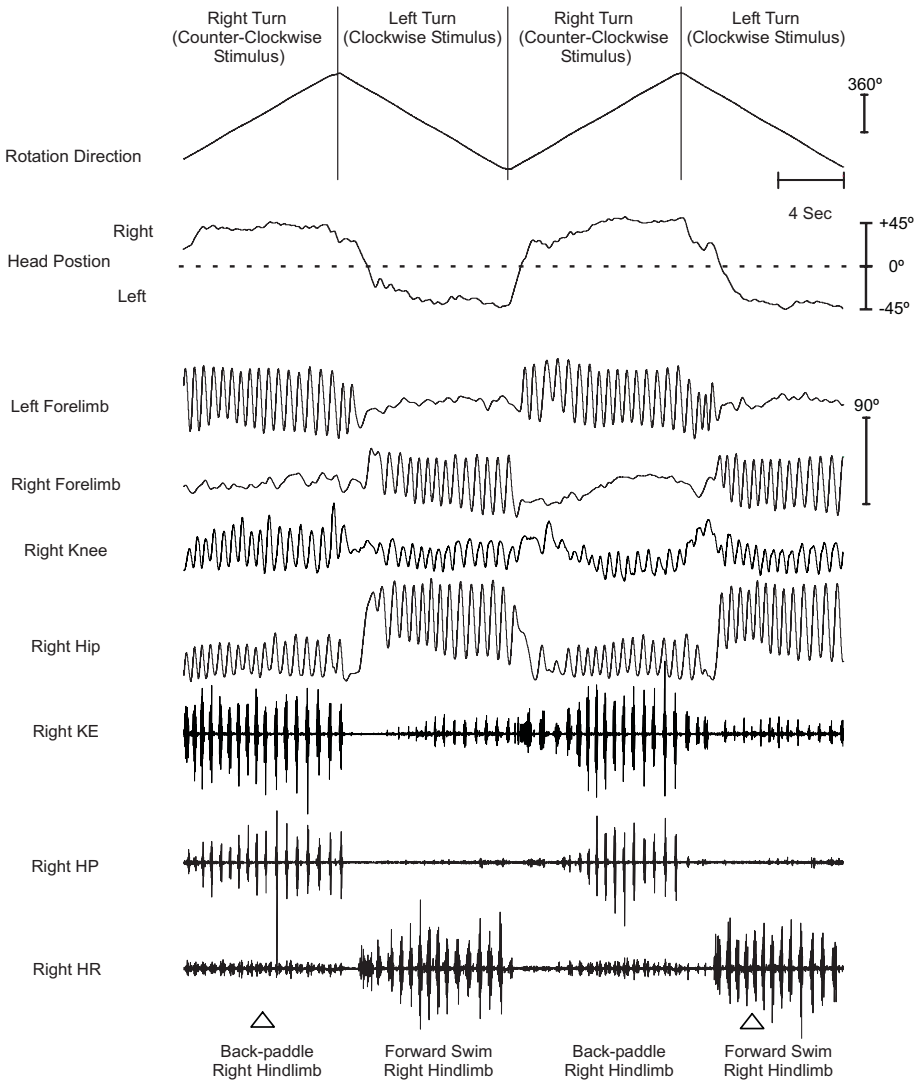


Figure 2-7 Synchronized kinematic and EMG recordings of right and left turn-swimming in response to abrupt switches in the direction of rotation (90°/sec) from turtle D21. Top trace: output of rotational position sensor (see Methods: Rotation of carapace-restrained turtles). Second from top trace: head position, with 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 knee extensor (KE), hip protractor (HP), and hip retractor-knee flexor (HR) muscles (see Methods: Electromyography for muscle identities). Counter-clockwise rotation of the turtle via the motorized band-clamp evoked right turn-swimming (head turned to the right, forward swimming in left forelimb (shown) and hindlimb (not shown), motionless right forelimb, back-paddling in right hindlimb. Clockwise rotation evoked left turn-swimming: head turned to the left, motionless left forelimb, back-paddling left hindlimb (not shown), forward swimming in right forelimb and hindlimb. Triangles below bottom trace indicate the onset of 2-sec back-paddle and forward swim recordings shown with expanded time-bases in Figure 2-8.

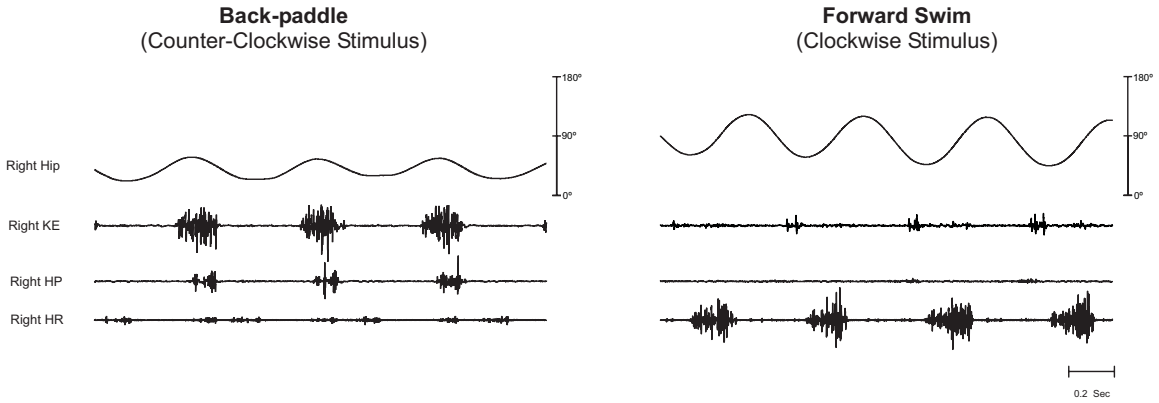


Figure 2-8. Hip angle (upper trace) and EMG recordings (lower 3 traces) from the right hindlimb of turtle D21 during 2-sec back-paddle and forward swim sequences, taken from the turning episode shown in Figure 2-7 and shown with expanded time-bases. The onsets of these sequences are indicated by triangles in Figure 2-7. Note that the back-paddle motor pattern was dominated by large-amplitute 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). Corresponding EMGs during backpaddle and forward swim are shown with the same amplification.

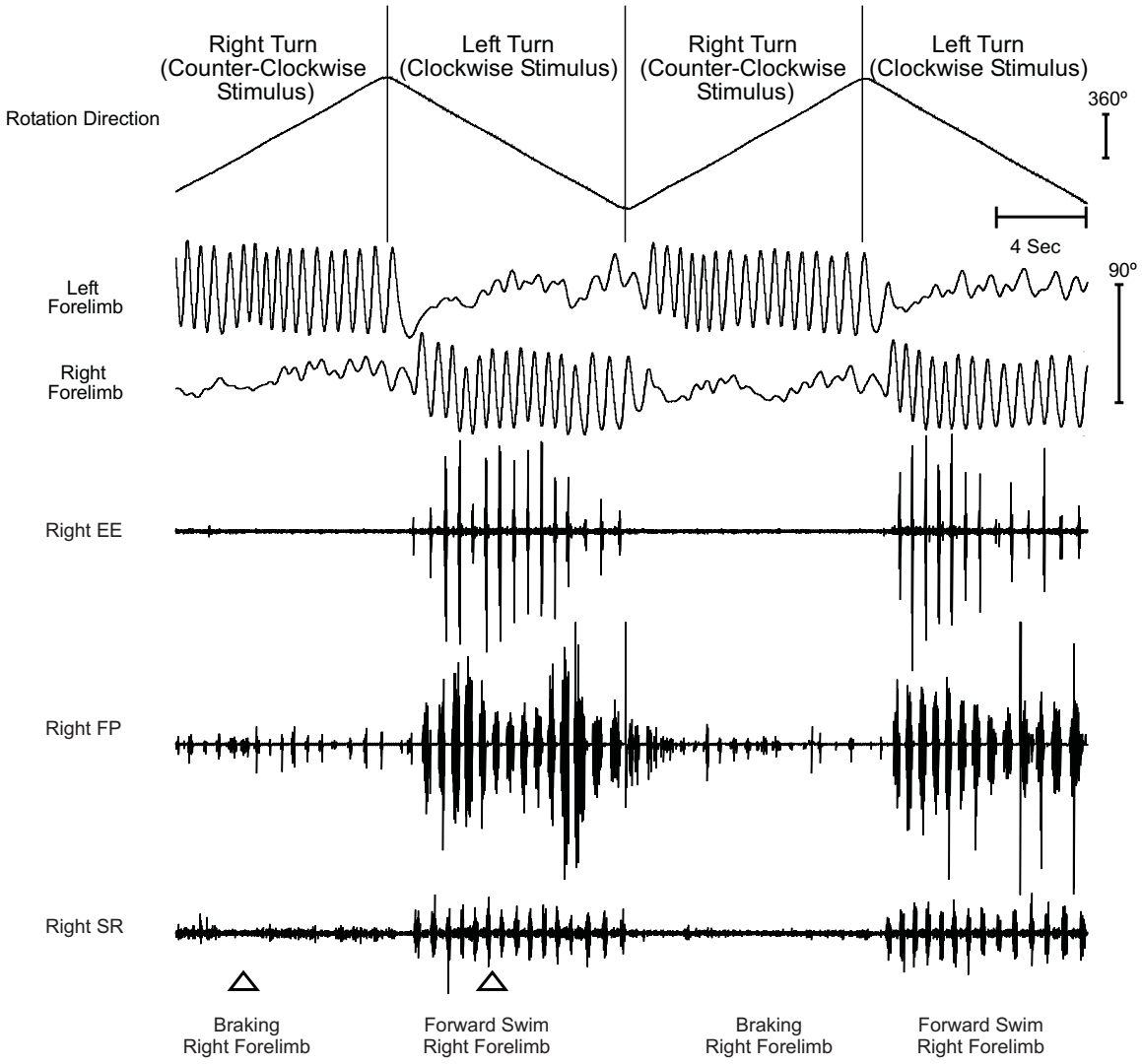


Figure 2-9. Synchronized kinematic and EMG recordings of right and left turn-swimming in response to switches in the direction of rotation (90°/sec) from turtle D20, focusing on forelimb activity. Top trace: output of rotational position sensor. Second and third traces from top: kinematic recordings of left and right forelimb angles. Bottom 3 traces: EMG recordings from right elbow extensor (EE), forelimb protractor (FP), and shoulder retractor (SR) muscles (see Methods: Electromyography for muscle identities). Counter-clockwise rotation of the turtle evoked right turn-swimming: forward swimming left forelimb, braking right forelimb (hindlimb movements not shown). Clockwise rotation evoked left turn-swimming: braking left forelimb, forward swimming right forelimb. Triangles below bottom trace indicate the onset of 2-sec braking and forward swim recordings shown with expanded time-bases in Figure 2-10.

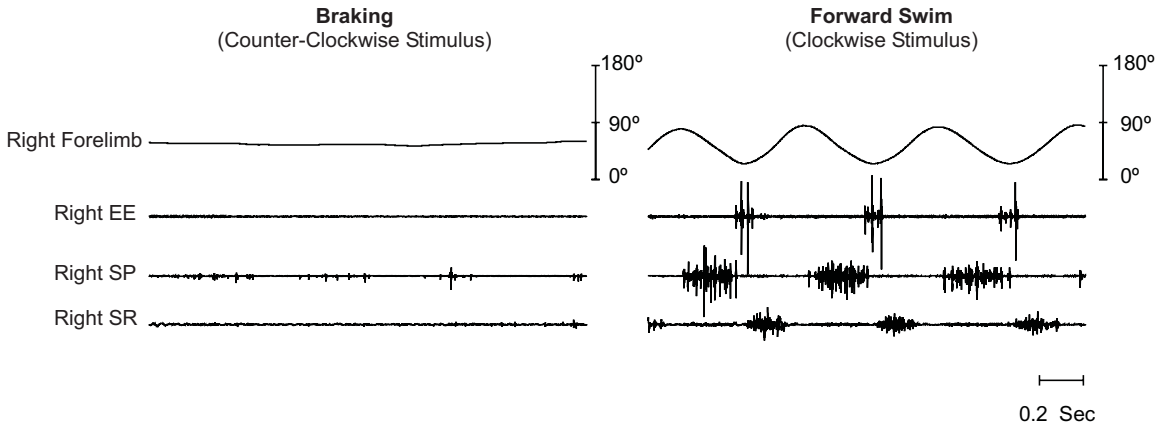


Figure 2-10. Forelimb angle (upper trace) and EMG recordings (lower 3 traces) from the right forelimb of turtle D20 during 2-sec braking and forward swim sequences, taken from the turning episode shown in Figure 2-9 and shown with expanded time-bases. The onsets of these sequences are indicated by triangles in Figure 2-9. Note that during braking, the largely stationary forelimb exhibited only weak rhythmic discharge in the FP muscle, while EE and SR were silent. In contrast, forward swimming was characterized by large-amplitude bursting EMG discharge in EE, FP 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 movements evoked by spinal cord stimulation (Stein, 1978). Corresponding EMGs during braking and forward swim are shown with the same amplification.

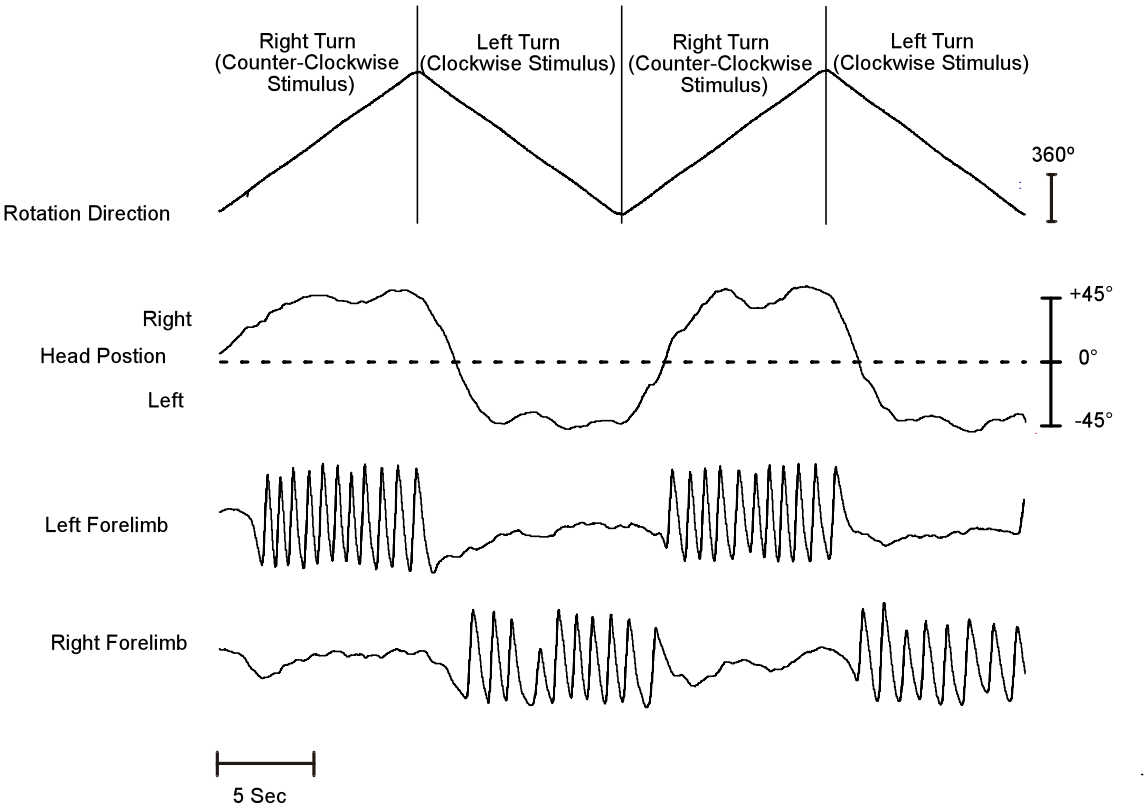


Figure 2-11. Rotation (90°/sec) still elicited robust turn-swimming responses to the right and left when the animal (D20) was suspended in the air (to abolish proprioceptive sensations caused by water currents) and blind-folded (to prevent movement related visual stimuli), suggesting that the turning response may be driven primarily by vestibular inputs (n=2 turtles). Hindlimb movements are not shown.

CHAPTER 3

COGNITION OF VISUAL-MOTOR CONTROL SYSTEMS

COGNITION

The previous chapters examined sensory motor integration and control function during the production of locomotor behavior. However, many vertebrates are also capable of cognitively driven fine motor movements. Fine motor movements can work separately, synergistically or in parallel with locomotor production. Chapter 4 will focus on the sophisticated manner with which humans use their hands to manipulate objects as a result of a complex blend of sensory-motor control mechanisms. Previously learned patterns of responses can improve our performance in certain tasks; while some sensory-motor control mechanisms are innate.

In the early Neuroethology literature, the antithesis of learned behaviors were named "fixed action patterns" (Lorenz, 1957). Essentially, fixed action patterns are innate specific behaviors that are complete and distinct, even from the first time they are ever executed. For example, suddenly appearing visual stimuli will often cause an eye movement (a saccade) toward that location, even if we intend to look at something else (Theeuwes et al., 1998). Some types of automatic behavior can be maladaptive during special circumstances. Such as becoming distracted by an irrelevant visual stimulus while driving a car. As such, it is important that our nervous system is capable of inhibiting certain kinds of innate behaviors.

Inhibition

Our survival can depend on our ability to modulate or interrupt ongoing actions especially when those actions are suddenly rendered inappropriate by altered conditions or events.

There are obvious situations of this, such as when we have to inhibit ourselves from stepping onto the street after noticing life threatening vehicles approaching. To accomplish this, nervous systems must produce continuous fine motor adjustments (turtle: Welch and Currie, 2011, and hummingbird: Welch and Altshuler, 2007), or completely inhibit an ongoing behavior (Human: Welch and Koshino, 1998). Inhibition of an ongoing motor response is considered to be of crucial importance for accurate performance in a variety of cognitive tasks (Burle, Posamai, Vidal, Bonnet, & Hasbroucq, 2002; Ridderinkhof, 2002).

The term "Inhibition" is a broad concept that has frequently been used in the context of neuroscience as well as cognitive studies. Neuroscientists often define inhibition in terms of decrements in neural activity in either sensory or motor pathways. For example, we know that during a ballistic process such as when contraction of a muscle is initiated, there is a simultaneous inhibition of the motoneurons for the antagonist muscle produced within the spinal cord itself (Sherrington, 1906).

Cognitive researchers usually describe inhibition in operational terms as an increased latency in reaction time after presentation of stimuli that elicit competing responses or an invalid selection cue (Kok, 1999). Inhibition has also been a central issue not only in theories of motor control but also in theories of executive processes (de Jong, Coles, & Logan, 1995; Logan & Cowan, 1984; Meyer & Kieras, 1997; Osman, Kornblum, & Meyer, 1986).

Simon Task

The Simon task is a useful procedure used to study inhibitory motor control processes in human subjects. The Simon task is based on a spatial compatibility conflict (Simon & Wolf, 1963). During a Simon task, subjects have a shorter reaction time to visual targets that are are presented in a spatial location that corresponds to the location of the correct response, than the inverse condition (Simon & Wolf, 1963).

For example, Simon and Small (1969) had subjects make left or right responses to low or high-pitched tones with key presses. The tones were presented either to the left or right ear. Responses to the "right" command (e.g., high-pitched tone) were 62 msec faster when it was heard in the right ear rather than the left ear. The responses to the "left" command (e.g. low-pitched tone) were 60 msec faster when it was heard in the left ear rather than the right ear. The location of the auditory stimulus, although irrelevant to the task, directly influences response-selection. Simon and Small, (1969) argued that this is due to an automatic (innate) tendency to respond towards the source of the stimulation. The delay in reaction time (RT) that occurs when stimulus position and response position do not correspond is currently known as the Simon effect (Simon and Berbaum, 1990). This enhancement for corresponding stimulus-response mappings is broadly called a spatial compatibility effect (Proctor & Vu, 2006). The compatibility effect is commonly viewed in terms of a dual-process model in which voluntary, goal oriented response activation competes with an automatic (innate) environmental response that corresponds to features of the task stimulus (Osman et al., 1986).

However, the idea that the Simon effect is due to a stimulus-response compatibility has been questioned (Hasbroucq and Guiard, 1991). Hasbroucq and Guiard (1991) argue that previous accounts of the Simon effect have overlooked stimulus congruity. This is the correspondence relation due to the two simultaneous features of the stimulus, a factor inevitably confounded in the Simon paradigm with irrelevant spatial stimulus-response correspondence. Hasbroucq and Guiard (1991) also state that the Simon effect is simply a spatial variant of the Stroop effect and is irrelevant to the stimulus-response compatabilty issue.

Neural substrates of the Simon effect

While the Simon task does not evaluate our entire range of Sensory-Motor functions, it is a well-established behavioral assay that can be used to specifically assess the functional relationship between cognitive visual processing and motor responses. However, the cognitive models are limited by the fact that it is difficult to verify the underlying physiological processes involved. However, newer neuroimaging techniques, transcranial stimulation, electroencephalograms, and electromyograms may lead to new developments that can provide additional lines of evidence that can be used as a basis for comparision. The premotor cortex, motor cortex, and several other brain regions have generated significant interest in this area.

Premotor cortex

The PMd is thought to be involved with processing visuospatial information. The reduction of the Simon effect with training, may involve the PMd.

The role of the PMd in resolving the conflicting demands during interference tasks has been studied by disrupting PMd function with repetitive transcranial magnetic stimulation (TMS). This technique makes it is possible to produce increased interference effects (Praamstra, et al., 1999). Praamstra, et al. (1999), found that the effect of TMS on the Simon task was confined to trials immediately following an incongruent trial. For these trials, interference with PMd function by TMS resulted in a larger Simon effect. However, the Simon effect was nearly unchanged for the subset of trials following compatible trials. The reduction of the Simon effect might be due to an increase in the repressive effects produced in part, by the PMd.

Motor cortex

The role of the primary motor cortex (M1) also seems to be important for inhibitory function (Stinear et al., 2009). M1 receives and integrates inputs from a vast array of cortical and subcortical sites. M1 is also the final cortical processing site for voluntary motor commands, prior to descending through the spinal cord. The pyramidal tract provides the fastest route in the spinal cord from the cortex to the motor neuron pools (Brunia and Böcker, 1995). The pyramidal tract both excites the cells in the ventral horn that project to the inter-neurons and to the motor neurons, and also excites the cells in the posterior horn that might be responsible for pre-synaptic inhibition (Brunia and Böcker, 1995). As such, inhibitory networks within M1 may be an important mechanism for the prevention or suppression of cortically controlled motor responses (Brunia and Böcker, 1995).

The lateralized readiness potential (LRP) is an event-related electroencephalogram component that has been used to investigate the underlying mechanisms of the Simon effect. The LRP is thought to measure the increase in activity in the motor cortex contralateral to the intended movement (Wascher et al., 2001). These waveforms can be time-locked to a motor response rather than time locked to a stimulus, making it possible to observe EEG components that lead up to a motor response. When a participant is instructed to make self-paced responses, a substantial voltage is recorded from the electrodes placed over the motor cortex. This signal builds up gradually over a period of several hundred milliseconds, and has been referred to as the Bereitschaftspotential (BP) or readiness potential (RP) (Brunia and Böcker, 1995). A portion of the LRP is larger in magnitude over the hemisphere contralateral to the response than over the ipsilateral side. The difference in voltage between the two hemispheres is used to isolate what is thought to be motor specific activity. This difference has been labeled LRP (Smulders et al., 1995). Using this technique, Wascher et al., (2001) has argued that spatial properties of the visual stimuli might activate motor functions directly via a visuomotor pathway. Other types of measurements have been used as well.

A functional imaging study using positron emission tomography (PET) during a spatial stimulus-response compatibility task has been conducted and relative cerebral blood flow (rCBF) changes were measured (Iacoboni et al., 1996). The subjects were instructed to respond with their left hand to a left visual field visual stimulus and with the right hand to a right visual field light stimulus (compatible condition).

They were also asked to respond with the right hand to a left visual field light stimulus and with the left hand to a right visual field light stimulus (incompatible condition). Six rCBF measurements per condition were performed. They found a bilateral relative increase in rCBF in the superior parietal lobule of both hemispheres during the incongruent verses congruent condition. This finding suggests that both rCBF regions in the left and right superior parietal lobules might influence the mapping of the visual stimulus spatial attributes onto the motor response attributes. As such, the rCBF increases in the incompatible response condition may represent the more complex computational remapping required when stimuli and responses are incongruent. In addition, reaction times decreased with practice according to a linear trend, and practice-related linear rCBF increases were observed in the dorsolateral, prefrontal, premotor, and primary motor cortex of the left hemisphere while no significant decreases were observed. This finding is consistent with evidence for the dorsal premotor cortex being involved with working memory for visuospatial information (Funahashi & Kubota, 1994).

Additional brain regions

In a more recent study, Peterson et al., (2002), examined event-related functional magnetic resonance imaging (fMRI) measurements during a Simon task. These are referred to as Blood-oxygen-level dependence (BOLD) measurements, and are the fMRI contrast of blood deoxyhemoglobin. They examined the change in signal during each run of the Simon task as a function of change in the behavioral interference effects.

This indicated the regions of the brain that were involved in learning (and here learning is taken simply to mean improved performance, or progressively reduced interference effects) during successive presentations of the incongruent stimuli. For each run in each subject, the mean difference in reaction time between the incongruent and congruent stimuli was calculated. Positive correlations, indicating that signal change lessened as subjects learned (i.e., as interference effects lessened) across runs, were detected in premotor and inferior parietal cortices and in the right hippocampus. Negative correlations, indicating that signal changes increased as subjects learned the task, were observed in anterior cingulate, dorsal visual association, and superior parietal cortices. In essence the premotor areas seem to be involved when the Simon effect is reduced with training. This also suggests that the Simon effect might occur at some kind of response selection stage, prior to the initiation of a motor response. The Simon effects do not depend on which hand operates the left or right key. When subjects are asked to cross their hands during a Simon task, the reaction time is still shorter when the stimulus and response locations correspond than when they do not (Rubichi and Nicoletti 2006; Wallace 1971). This indirect convergent line of evidence supports the argument that the Simon effects are based mainly on correspondence of spatial stimulus and response codes (Riggio et al.,1986). There is also some preliminary physiological evidence for visual object perception and object information being processed separately.

Goodale et al., (1991) tested a patient with lesions in the ventral stream of projections from the striate cortex to the inferotemporal cortex.

Despite a pronounced disorder in the perception of object features, such as form, orientation, and size, this patient showed accurate guidance of hand and finger movements toward objects. This suggests, that different neural substrates underlie visual object perception on the one hand and the use of object information for the control of manual movement on the other. During certain tasks or conditions (e.g. Simon task), a conflict between these various sources of information can be produced.

Taken together, many different regions of the nervous system are involved in producing the Simon effect. However, our incomplete knowledge of how the various nervous system regions interact makes it challenging to form a complete physiological model. Fortunately, behavioral studies can often help us to understand how these regions interact at a systems level. The following chapter describes a behavioral study that attempts to shed light on how the nervous system is able to adapt to training, during a Simon task.

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CHAPTER 4

PROCESSING IRRELEVANT LOCATION INFORMATION: PRACTICE AND TRANSFER EFFECTS IN A SIMON TASK

ABSTRACT

How humans produce cognitively driven fine motor movements is a question of fundamental importance in how we interact with the world around us. To examine this process, we are using a well-known behavioral assay called the Simon task (Simon et al., 1973). In the present study, the subjects trained for four days with a visual stimulus presented with central and bilateral locations. They responded with one hand moving a joystick in either the left or right direction. They were instructed to ignore the irrelevant location information and respond based on color (e.g. red to the right and green to the left). On the fifth day, an additional testing session was conducted where the task changed and the subjects had to respond by shape (e.g. triangle to the right and rectangle to the left). They were instructed to ignore the color and location, and respond based solely on the task relevant shape. We found four primary effects from this study. (1) the magnitude of the Simon effect decreases with training, (2) the visual Simon effect is abolished with an infrequent break schedule, (3) the Simon effect is reduced with training, however within each session it is found and that the rate of dissipation increases with training, (4) task-defined associations between response direction and color did not significantly effect the Simon effect based on shape. Therefore, our results support the conclusion that the reduction of the Simon effect might be due to route suppression/gating of the irrelevant location information.

INTRODUCTION

How humans produce cognitively driven fine motor movements is a question of fundamental importance in how we interact with the world around us. The sophisticated manner with which humans use their hands to manipulate objects is a result of a complex blend of sensory-motor control mechanisms. To examine this process, we are using a well-known behavioral assay used to examine sensory-motor integration and control, and it is called the Simon task (Simon et al., 1973).

Simon task

During the development of the Simon task, Simon and Small (1969) had subjects make left or right responses to low or high-pitched tones with key presses. The tones were presented either to the left or right ear. Responses to the "right" command (e.g., high-pitched tone) were 62 msec faster when it was presented in the right ear rather than the left ear; and the responses to the "left" command (e.g. low-pitched tone) were 60 msec faster when it was heard in the left ear rather than the right ear. The location of the auditory stimulus, although irrelevant to the task, directly influences response-selection. Simon and Small, (1969) argued that this is due to an automatic tendency to respond towards the source of the stimulation. The delay in reaction time that occurs when stimulus position and response position do not correspond is currently known as the Simon effect (Simon and Berbaum, 1990). This effect has been found to exist during various conditions.

The Simon effect for visual stimuli has since been conducted and replicated several times using color (e.g., Hedge & Marsh, 1975; Simon & Craft, 1972; Simon, Small, Ziglar, & Craft, 1970; Umilta & Nicoletti, 1985). It also has been obtained with a variety of other relevant stimulus dimensions (Nicoletti & Umilta, 1989) and geometric forms (Umilta & Liotti, 1987). Taken together, the Simon effect seems to be a robust phenomenon that can be observed with a variety of stimuli.

Even though the Simon effect is robust, it seems to be effected by practice. For example, Simon et al., (1973) instructed subjects to press a left or a right key in response to a high or low pitched tone presented in the left or the right ear. The subjects performed 192 test trials a day for 5 days. They found that the magnitude of the Simon effect would decrease from an average of 60 msec in the first session to 35 msec in the 5th session, but the effect was not eliminated. In a related study, Proctor and Lu, (1999) found that the reduction in magnitude of the Simon effect that occurs as a function of practice apparently requires that location vary in an irrelevant manner. The Simon effect is also affected by the sequence of congruent and incongruent trial presentations (e.g. sequential effects). The Simon effect is present after congruent trials, and is reduced or reversed after incongruent trials (Hommel et al., 2004).

Two competing dual-route models

There are two leading dual-route models that provide a possible explanation of how the Simon effect is reduced, due to training. The first model states that the reduction in the Simon effect from training might be due to intentional processes that are strengthened (Notebaert et al., 2001).

The second model states, that the reduction of the Simon effect is due to automatic responses that are be suppressed or gated (Valle-Inclán et al., 2002) (Fig. 4-1).

Evidence for the first model was produced by (Notebaert et al., 2001), that attributes the reduction in the Simon effect due to the automatic consequences of the sequence of specific stimulus-response features. When the stimuli were presented at the same location in close temporal succession, no significant difference in the reaction times between congruent and incongruent trials was found. This suggests that attentional shifts are a necessary and sufficient condition for the Simon effect to occur. The direction of the shift towards the stimulus, rather than the relation of the stimulus to a referent, causes the Simon effect. The automatic response-priming route is primarily caused by the interaction between response color and location repetitions. This would be consistent with the attention-shift hypothesis, that argues for a spatial stimulus code that originates in the movement of an attentional spotlight (Stoffer, 1991).

The second model proposed by (Valle-Inclán et al., 2002), attributes the disappearance of the Simon effect following incongruent trials. This suggests that the automatic response may be influenced by voluntary control. Stürmer et al., (2002) has hypothesized that control over both routes of information processing in the Simon task is possible. To resolve this controversy, the use of a transfer design experiment will be used.

Experimental design, hypothesis and predictions

For investigations that examined perceptual learning, transfer designs are heavily used (e.g. Seitz et al., 2009).

Transfer designs can be used to evaluate the nature of the changes in information processing that occurs as a function of training (Proctor et al., 1995). The specificity of learning can be evaluated by comparing the conditions for which transfer has occurred with those for which it did not (Pashler and Baylis, 1991). Studies using practice transfer designs (Proctor and Lu, 1999) have shown that learning can modulate the Simon effect. Different kinds of tasks when performed before the Simon task, eliminate or reverse the Simon effect (Tagliabue et al., 2002; Tagliabue et al., 2000). For the present study, we evaluated the transfer effects from fours days of training based on responding for color, to a subsequent testing session based on responding for shape. As a control condition, we will have stimuli presented in the center of the screen for 1/3 of trials. This control condition will allow us to evaluate the effects of associative learning without having the stimuli confounded with a location.

The main hypothesis is that intentional processes are strengthened and/or the automatic responses may be suppressed or gated with training. We predict that we will be able to replicate previous results, where we find a reduction of the Simon effect with repeated trials. If the first model is correct, then we should also observe an effect of the color and the location during testing trials when the subjects are asked to respond for shape. For example, if an association between red and right was made, then a reduced reaction time should be observed when the shapes have a consistent color and location (e.g. red and right). These effects should be most noticeable during trials where the stimuli are located in a central position where the confound of location is not present.

These effects should also be observable during lateralized trials, as an additive effect. However, if the second model is correct, then we should observe an overall reduction of the Simon effect during the shape tests, but with no influence on the reaction time for color location associations. Support of the route suppression/gating model would predict that training would carry over to a testing session where the associative learning conditions of color are no longer part of the implicit task. We should also see no significant difference during the testing session with centrally located trials when the shape and color are consistent verses inconsistent with the training.

METHODS

Subjects

Thirty-six students enrolled in introductory psychology classes at University of California, Riverside, participated to fulfill a course requirement. They were required to have normal or corrected-to-normal vision in order to participate. Informed consent was obtained in writing from all the subjects and the experiments were conducted in accordance with the IRB approved by the Committee on Human Research at the University of California Riverside. The subjects were naive as to the purpose of the experiment.

Apparatus

A Macintosh G4 (Apple) personal computer was used to generate the stimuli and record the responses. A custom program was written in Matlab (The MathWorks, Natick, MA) using the Psychophysics Toolbox (Brainard, 1997).

The stimuli were displayed on a Mitsubishi Diamond Pro 2070^{SB} monitor with a resolution of 1024x768 pixels using a refresh rate of 100 Hz. The experiments were conducted with binocular viewing during all conditions. Subjects sat on a height adjustable chair, and a chin rest was used to reduce head movements during the task. The subjects responded with an Attack 3 Joystick (Logitech).

Procedure

In the laboratory, each subject was familiarized with the testing equipment, procedure, and seated in a dimly lit, sound-attenuated testing room. The subjects were instructed to maintain their visual focus on a central fixation point displayed on the computer screen. The main experiment consisted of 5 days. At the end of each block, they are given feedback based on the percentage of trials that were correct, and the amount of money that they earned so far. They were paid up to five dollars a day based on the percentage of trials that they got correct for all five days, for a total up to 25 dollars.

Practice

On the first day, a practice session (24 trials) was used to acquaint subjects with the Simon Task. A practice session was administered for both the Training (Simon task by color) and for the Testing (Simon task by shape). The subjects received feedback from a computer generated percentage score at the end of each block (12 trials). During the practice session, the experimenter remained in the testing room and carefully monitored the subjects to ensure that they were doing the procedure correctly.

Simon task by color (Training)

During the first four days, the subjects trained with a Simon task by color with 960 trials per day. The subjects were presented with circles that appeared in the center, left and right hand side of the display screen. The subjects were instructed to move a joystick to the right or to the left when they saw a circle appear on the screen (e.g. red to the right and green to the left). The subjects were told to ignore the location of the stimulus and base the responses on the task-relevant color. The subjects were asked to respond as quickly and as accurately as they could. The subjects were prompted to return the joystick to the exact center position at the end of each trial. During each daily session, the subjects were given a break for up to 1 minute after every 48 trials. The purpose of the task was to determine if the visual Simon effect could be reduced from performing task to the point of near extinction, and build up an association with response side and color.

On the fifth day, they were given a mini test in order to verify the reduction of the Simon effect due to the 4 days of training (48 trials). The mini test was a Simon task based on color, except with a break and feedback every 12 trials. At the end of each block, the subjects were given computer generated feedback based on the percentage of trials that were correct, but were not paid money for those trials. This was administered prior to the Simon Task based on shape (testing session).

Simon task by shape (Testing)

The subjects were asked that they move a joystick to the right or to the left when they saw a shape appear on the screen (e.g. a triangle to the right and a square to the left). They were told to ignore the location and color of the stimulus and base the responses on the task-relevant shape. In this task we wanted to determine if improved performance (reduced Simon effect) could be transferred after practice to one or more conditions that share important features of the practice conditions. A separate pool of subjects (n=14) was given the shape test without the four days of training by color as a control.

Analysis

In the Simon task literature, the relative latency in reaction times is what is routinely compared (Simon and Berbaum, 1990; Simon & Rudell, 1967; Hommel et al., 2004; and Hommel, 1993). The Simon effect was calculated by subtracting the congruent mean reaction times from the incongruent mean reaction times for each condition and day respectively. Planned comparisons between sessions were performed by means of two tailed t-tests (with bonferoni corrections). Results were averaged over all subjects and error bars in the figures are standard errors. For the analysis of the Simon effect, we only used trials where the subjects responded correctly. The mean accuracy rate was 98% after training, so very few trials were eliminated from each session and respective condition.

RESULTS

Training

During the first day of training, a robust Simon effect was present (50.5 ms ± 4.1 SEM). There was a clear effect of training on the Simon effect over the 4 days of training [$F(1,21) = 58.313$, $p < 0.001$, one-way repeated-measures ANOVA]. The Simon effect was reduced from performing task to the point of near extinction by the second day of training and remained suppressed for days 3-4 (see Fig. 4-2). The mean reaction times for Congruent vs Incongurent conditions persisted only during the first day of training [$t(21) = -12.355$, $p < .001$, Post hoc paired t-tests (bonferoni corrections].

Assessment of continued suppression

On the fifth day we administered a mini color based Simon task consisting of only 48 trials, with a break every 12 trials (Fig. 4-3). We wanted to determine if the Simon effect was still suppressed on the fifth day, prior to testing. An unexpected return of the Simon effect (31.9 ms ± 5.3 SEM) was found with the trained group using a break schedule that occurred after every 12 trials [$t(21) = -6.074$, $p < .001$,paired t-test]. As a control, we ran additional subjects that did not receive any training (n=14). The Simon effect (45 ms ± 6.8 SEM) was slightly larger for the untrained control, but, a paired t-test revealed that the two groups were not statistically different from one another.

Since the Simon effect was observed with the 12 trials per block in the mini color task (see Fig. 4-3), we wanted to determine if the Simon effect was also present during the first 12 trials after each break during the four primary training sessions (Fig. 4-2).

To do this, we analyzed the first 12 trials after each break for the four days of training and plotted them. We found that the Simon effect was also present during the first 12 trials of the training sessions (Fig. 4-4). These preliminary results indicate that the suppression of the Simon effect is diminished for the first 12 trials after each break. As indicated by the line of best fit, the overall Simon effect for those first 12 trials after each break decreased over the four days of training (Fig. 4-4).

Testing

On the fifth day, an additional testing session (960 trials) was conducted where the task changed, and the subjects had to respond by shape (e.g. triangle to the right and rectangle to the left). They were instructed to ignore the color and location, and respond based solely on the task relevant shape (Fig. 4-5). We compared the Simon effect found with the trained (-2.5 ms ± 2.9 SEM) verses an additional untrained group (9.5 ms ± 4.5 SEM). We compared the effects of the training verses a control group that did not receive training (Fig. 4-5). Results were averaged over all subjects and error bars represent standard error. We found that the training based on color carried over to the Simon shape task [$f(1)= 4.678$, $p <.05$, one-way ANOVA]. ,

Task-defined associations

Task-defined associations between response direction and color did not significantly affect the Simon effect based on shape for lateralized stimuli (Fig. 4-6).

A one way repeated measures ANOVA revealed that the Consistent (352.5 ms ± 14.7 SEM) verses Inconsistent (353.5 ms± 16.1 SEM) groups were not statistically different from one another. For the central stimuli (Fig. 4-7), a one way repeated measures ANOVA revealed that the Consistent (335 ms± 13.9 SEM) verses Inconsistent (332 ms± 10.5 SEM) groups were not statistically different from one another. Together, the task defined association tests failed to support the conclusion that the reduction of the Simon effect is not due to an association with stimulus features and responses.

DISCUSSION

Main findings

The five major points illustrated by the present study, is that (1) the magnitude of the Simon effect decreases with training, (2) the Simon effect is abolished with an infrequent break schedule, (3) task-defined associations between response direction and color did not significantly effect the Simon effect based on shape, (4) the reduction of the Simon effect from the training (based on color) did have a significant effect on reducing the overall Simon effect based on shape, relative to subjects that did not receive training and, (5) no significant associative learning from the specific stimulus-response features was found for the centrally located stimuli.

We did not find any evidence (see Fig. 4-6) from the testing sessions that the reduction of the Simon effect was due to an association with stimulus features and responses. In fact, the current study provides further evidence for rejecting this model (see Fig. 4-1a).

The central (neutral) stimulus condition is another line of evidence that allows us to observe the absence of any reaction time differences without confounding stimulus location (see Figs. 4-6 and 4-7).

We did find evidence that the training with color did improve the performance relative to subjects that did not receive training (see Fig. 4-5). This carry over from one task to another is consistent with the findings by Valle-Inclán et al., (2002), that attributes the disappearance of the Simon effect following incongruent trials. Our results support this finding by demonstrating that the carry over effects can last longer than the length of one trial.

On the other hand, Hommel et al. (2004) has argued that gating/suppression of the automatic response-selection route is not the only possible explanation for the sequential variation in the Simon effect. Hommel et al. (2004) used two stimulus response pairs that were presented during each trial, the first was a prime and the second a probe. In one condition, the participants did not perform the response. The overall finding was that the Simon effects were eliminated when the preceding responses did not depend on the preceding stimulus, or when the preceding trial did not require an actual response. Since an actual response for the previous stimulus was not necessary, the conclusion was that even if gating/suppression is responsible for the sequential effects, it is not under voluntary control.

We also found an unexpected effect from the different break schedules that were used.

This suggests that the learned suppression of the Simon effect will degrade over time. This is an intriguing characteristic of the system, and should be investigated more systematically in a future study.

Processing stages

Several investigators have tried to determine the processing stage in which the Simon effect occurs. This can provide a rich context for our current model. The Simon effect is considered by some investigators to be a response-selection phenomenon (Lu and Proctor, 1995). In essence, the latency is thought to occur at a response-selection stage of information processing. Evidence to support this view is that, the Simon effect has also been obtained when the stimulus location is made to be a relevant attribute for determining the response (Proctor and Dutta, 1993).

Other investigators attribute the Simon effect to a type of response competition (Umiltà and Nicoletti, 1990). The basic argument is that some kind of response code is generated for the stimulus features. These response codes are then used for generating a response. According to Umiltà and Nicoletti (1990), a response code is formed relative to the egocentric axes, and another is formed relative to an external reference location. For example, during trials where the irrelevant response code corresponds with the response code signaled by the relevant stimulus dimension, there is no competition. Contrariwise, for trials where the irrelevant response code does not correspond with the relevant response code, it produces competition.

This competition of response codes must be resolved before the correct response can be made. It is this response competition that is assumed to be the primary cause of the slower reaction times for the noncorresponding trials relative to the corresponding trials.

Additional, alternatives to the response-selection phenomenon have been proposed. Hasbroucq and Guiard, (1991), argue that the effect is due to a stimulus-identification process. The Simon effect is a function of stimulus-stimulus congruity, the correspondence between the two dimensions of the stimulus. The assignment of the stimulus property signifies that position. The stimulus event amounts to the presentation of two simultaneous left-right messages. This makes the stimuli either intrinsically congruent or incongruent (Hasbroucq and Guiard, 1991). Therefore, the stimulus identification process is longer when the identification is prolonged when the irrelevant location of a stimulus (position) is incongruent with the relevant feature dimension.

The explanation by Hasbroucq and Guiard, (1991), seems to be in conflict with prior evidence collected with the Hedge and Marsh task (Hedge and Marsh, 1975). In brief, the subjects were asked to respond with either the key of the same color as the stimulus or the key of the alternative color. With this task, it is argued that the instructions for this specific task do not directly link stimulus color with response location (O'Leary and Barber, 1994). However, Guiard et al., (1994) responded by saying that neither version of the Simon task (O'Leary and Barber, 1994), allows one to disentangle irrelevant spatial Stimulus response correspondence and Stimulus congruity, and that in both versions of the experiment, the two effects are perfectly confounded.

In the present study, we believe that the training and testing sessions used disentangled the irrelevant spatial stimulus correspondence and stimulus congruity that was not fully addressed in previous studies (Guiard et al., 1994; O'Leary and Barber, 1994). The training sessions had subjects inhibit irrelevant location information with color that carried over to another task based on shape. We believe that the transfer design experiments used in the current study can be used as a useful tool for disentangling the many different competing models even further.

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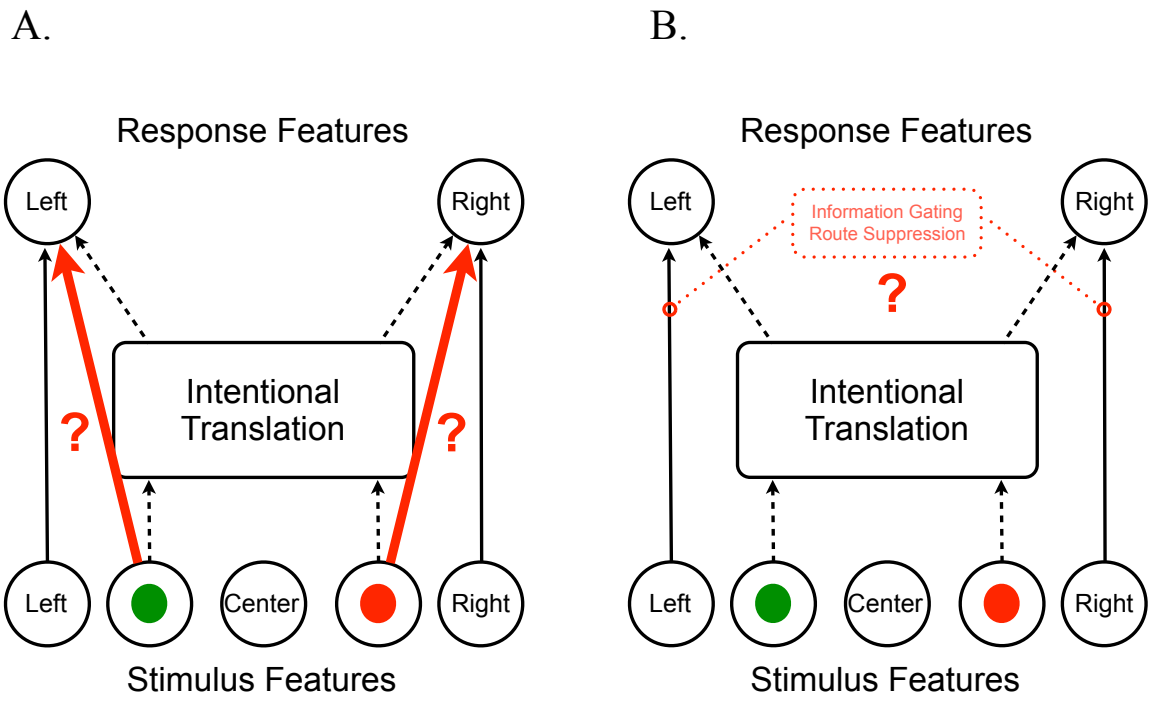


Figure 4-1. Two competing dual-route models for our Simon task. The broken lines represent intentional processes, and straight lines for automatic processes. The red lines are the proposed mechanisms for the reduction of the Simon Effects. A. Notebaert et al., (2001), attributes the reduction in the Simon effect to associative learning from the specific stimulus-response features. B. Valle-Inclán et al., (2002) believes that the reduction of the Simon effect is due to Information Gating/Route Suppression of the automatic processes. Modified from Hommel et al. (2004).

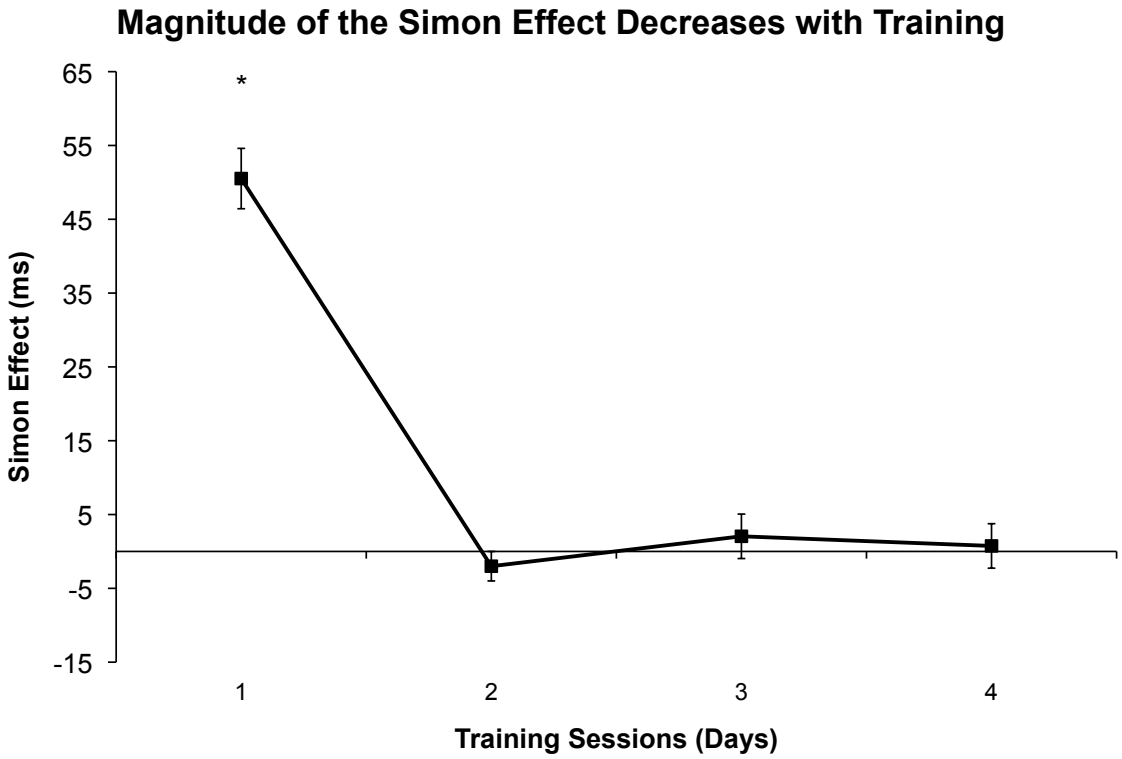


Figure 4-2. We administered a choice reaction time task to undergraduate students (n=22) that moved a joystick either to the right or left in response to red or green circles (Intentional translation: signifying right or left) displayed on a computer monitor. The circles appeared on the left or right (Automatic processes: that elicits an initial tendency to react toward the stimulus source), or center (Control condition: neutral) of the display. Each subject performed 960 test trials a day, for 4 days. The Simon effect was calculated by subtracting the mean reaction times from the congruent and incongruent conditions for each day. The error bars are Simon effect standard errors. A one way repeated measures ANOVA was used to compare the magnitude of the Simon effect for each day of testing. We found that a strong Simon effect persisted only throughout the 1rst day of training ($p < .05$).

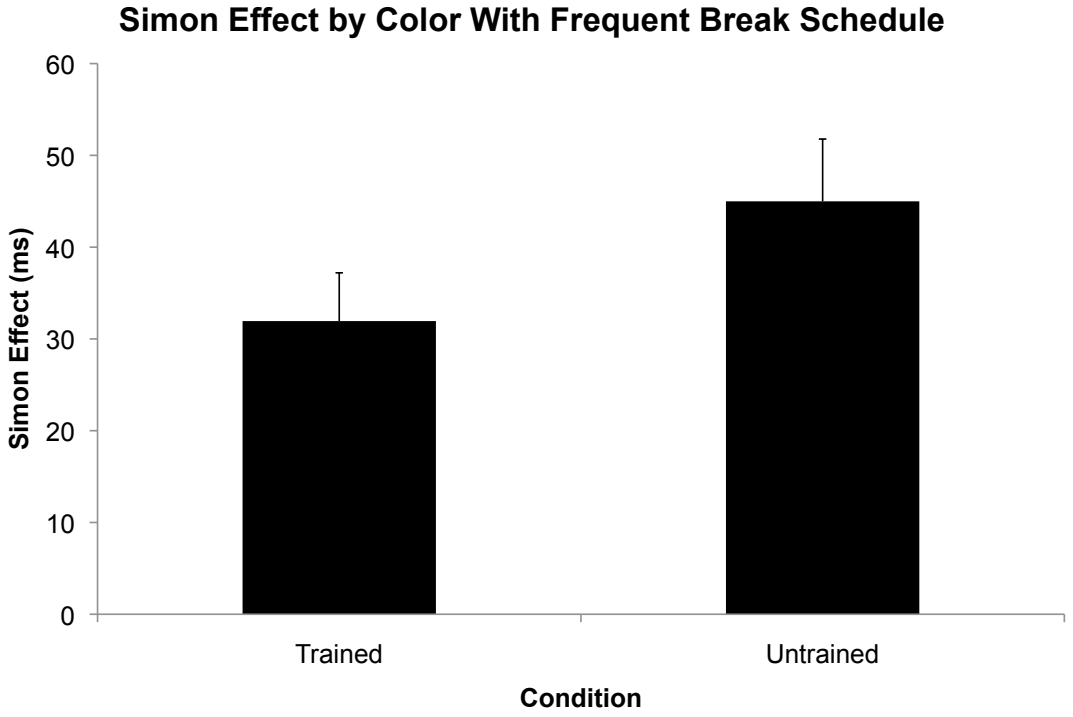


Figure 4-3. An unexpected return of the Simon effect occurred with a short break schedule. As a control, we ran additional subjects that were untrained (n=14). Results were averaged across subjects and the error bars are Simon effect standard errors. A paired t-test revealed that the two groups were not statistically different from one another.

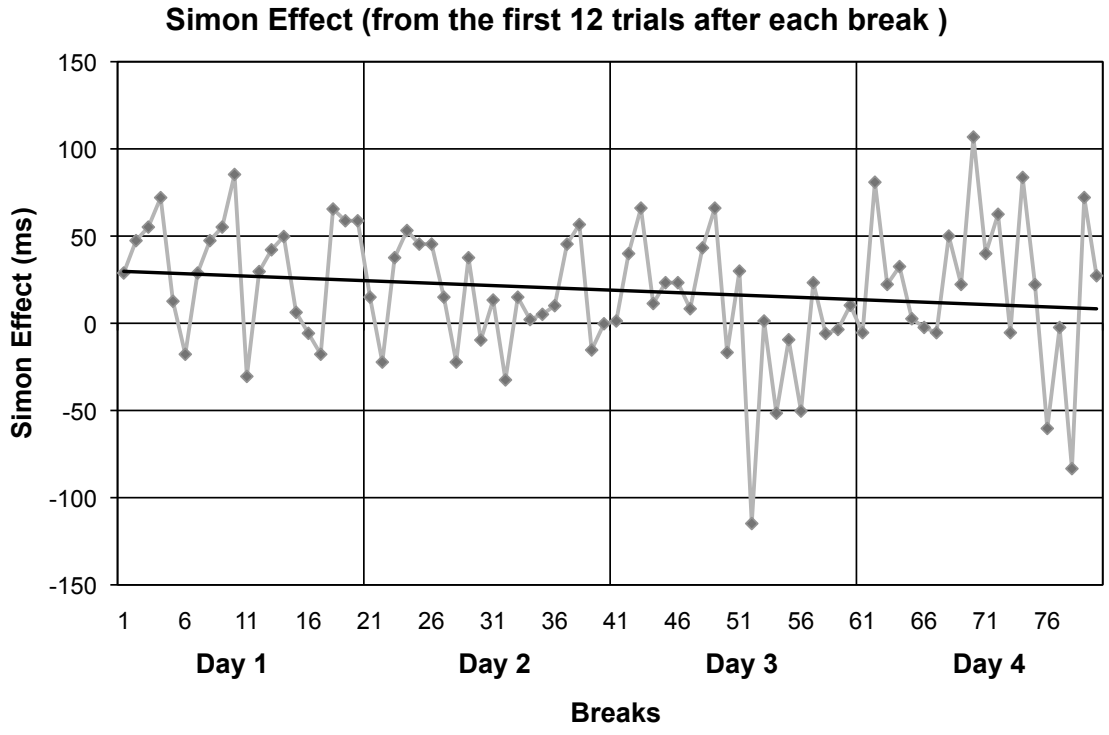


Figure 4-4. The Simon effect was calculated using the first 12 trials after each break. All four days of testing were plotted together for comparison. These preliminary results indicate that the suppression of the Simon effect is diminished for the first 12 trials after each break. As indicated by the line of best fit, the overall Simon effect still decreased over the four days of training.

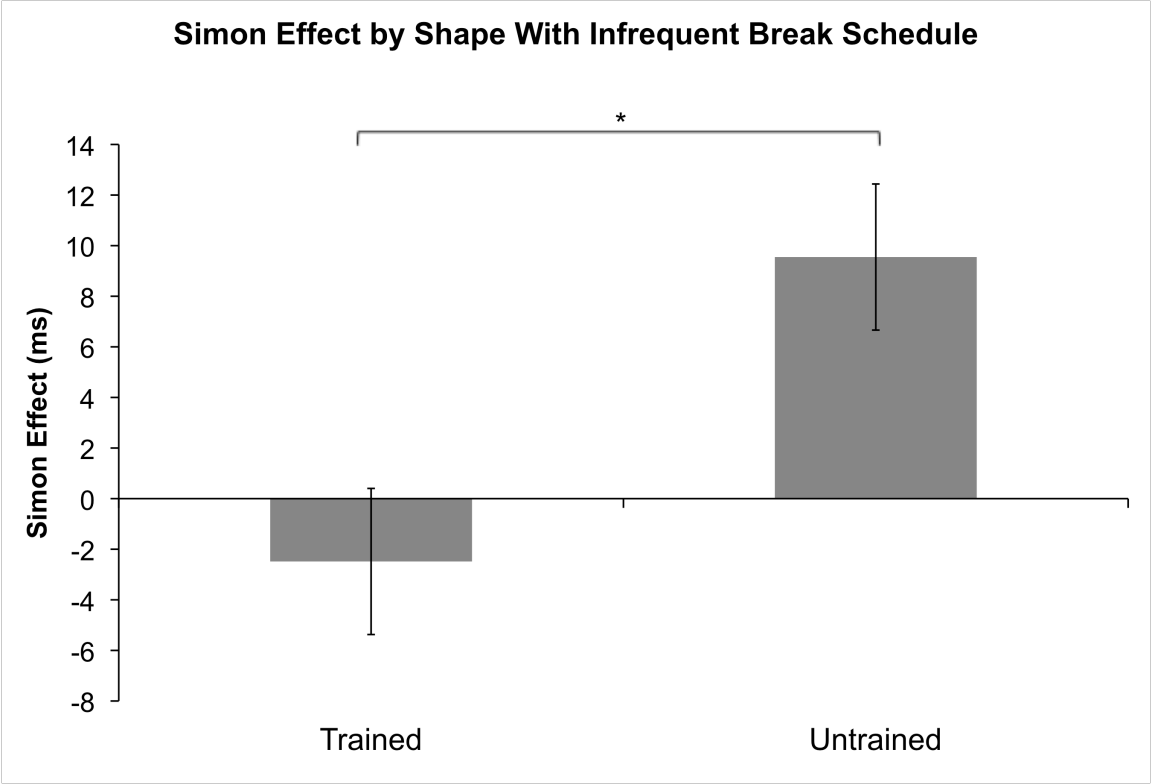


Figure 4-5. Simon task based on shape. We found that the four days of training based on color carried over to the other task when compared to a separate group without training (P < .05).

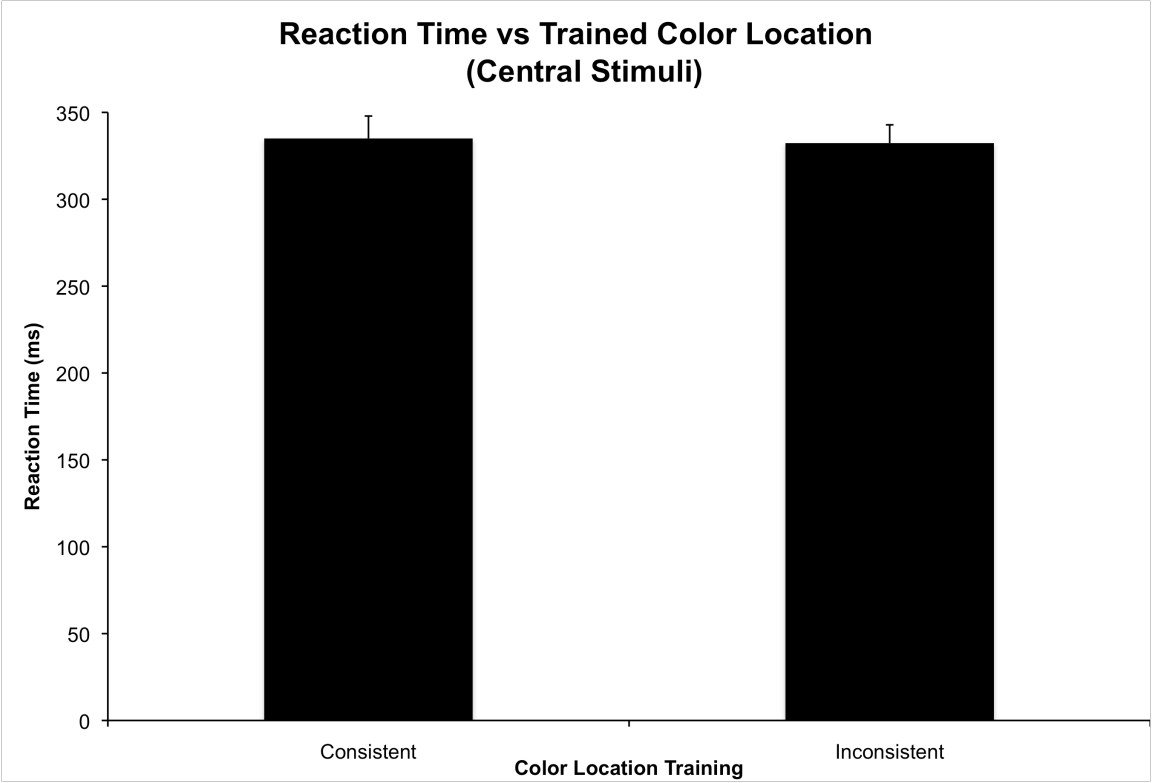


Figure 4-6. No significant associative learning from the specific stimulus-response features was found, for the lateralized stimuli. A one way repeated measures ANOVA revealed that the Consistent (352.5 ms) verses Inconsistent (353.5 ms) groups were not statistically different from one another. Results were averaged over all subjects and error bars represent standard error.

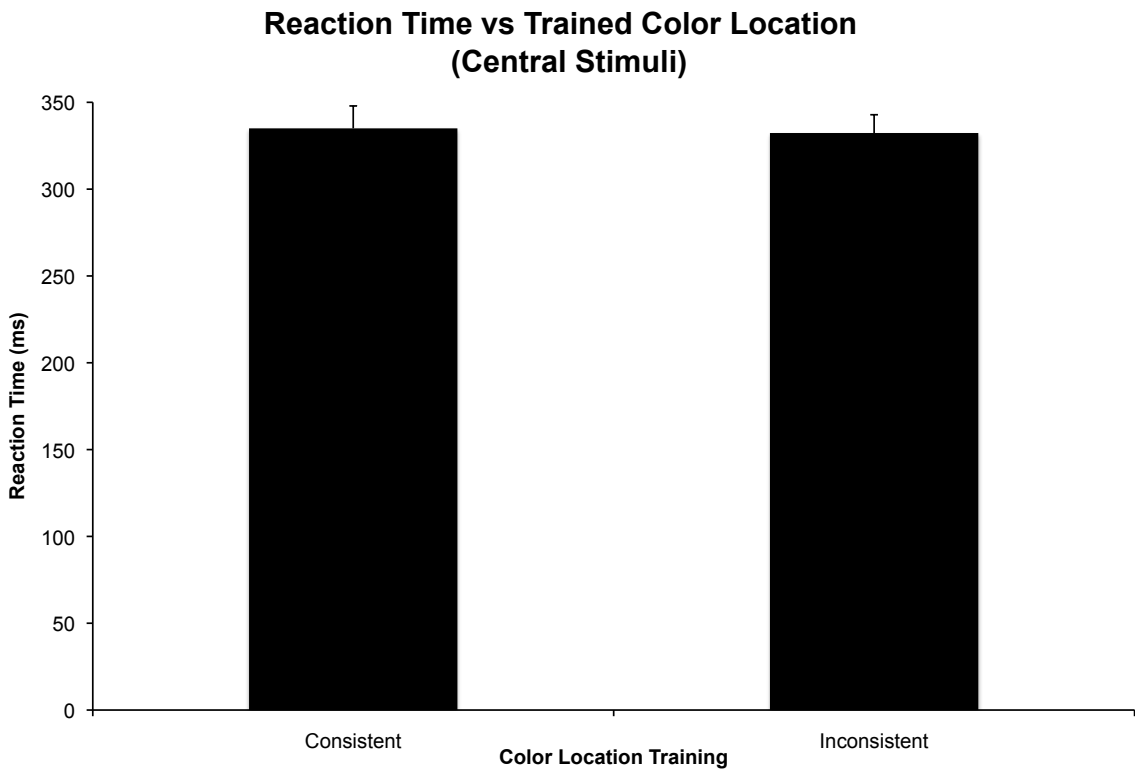


Figure 4-7. No significant associative learning from the specific stimulus-response features was found, for the centralized stimuli. A one way repeated measures ANOVA revealed that the Consistent (335 ms) verses Inconsistent (332 ms) groups were not statistically different from one another. Results were averaged over all subjects and error bars represent standard error.

CHAPTER 5

GENERAL CONCLUSIONS

CONCLUSION

The experiments presented in this dissertation sought to examine some of the primary functions of the nervous system used to regulate behavior. Two leading vertebrate animal models were used in studying sensory motor integration and control. [1] Red eared turtles-Trachemys scripta elegans, (Locomotion) and [2] Humans- Homo sapiens (Cognition).

Sensory motor integration and control during locomotion

In the locomotor study, we elicited a turn swimming response by rotating turtles with a motor. The rotation is a multimodal stimulus that provided the animal with visual, vestibular, and proprioceptive cues. We manipulated the rotation speed and noticed that the cycle frequency of the turn swimming increased with the rate of the imposed rotation. We also notice that a run-down of the swimming behavior was exhibited over the 24-second duration of the stimulus. Afterwards, we wanted to characterize the kinematics and motor patterns of this behavior. This characterization provides us with insights on the underlying neurophysiology producing these behaviors.

First, we found that rotation-evoked turning caused the turtles to exhibit a stereotyped pattern of forward swimming in the hindlimb and forelimb on the outer side of the turn. Second, we observed backpaddling in the hindlimb on the inner side of the turn. Third, we observed a stationary and extended forelimb on the inner side of the turn. Finally, we observed neck bending in the direction of the turn. Reversing the direction of rotation caused the animal to rapidly switch the direction of its turn, and the pattern of right and left limb activities.

We measured the movement amplitude of each limb, since the range of movement exhibited from each limb angle was used separately as a form discriminator. In addition, we also measured interlimb and intralimb phase values based on these forms. The intralimb phase values for both forward swim and backpaddle were tightly coupled. The tight coupling between these was expected, since highly coordinated muscle contractions between antagonistic muscles of the same limb is necessary for productive movements. We also found tight coupling with the ipsolateral forelimb and hindlimb when they were both engaged in forward swimming movements. The kinematic patterns were similar to those found when both sides of the animal are producing forward swim movements. However, when interlimb coordination is measured between the backpaddle hindlimb and the forward swim patterns of the contralateral forelimb and hindlimb, we observed loose coupling between them. This suggests that different redundant coordinating systems can dominate during different combinations of limb movements.

Previous work has shown that there are two spinal cord pathways that can function together or separately to maintain out-of-phase right-left hindlimb coordination during voluntary rectilinear swimming (Samara and Currie, 2007). There are descending propriospinal (forelimb-hindlimb) tracts communicating between the ipsilateral forelimb and hindlimb locomotor CPGs. There are also crossed-commissural (hindlimb-hindlimb) tracts within the spinal hindlimb enlargement that communicate between the right and left hindlimb CPGs (Samara and Currie, 2007).

Samara and Currie (2007) also found that turtles will continue to exhibit robust right-left hindlimb alternation during voluntary rectilinear swimming, even after all the

commissural fibers in the hindlimb enlargement were surgically lesioned mid-sagittally, separating the right and left halves of the posterior cord. Samara and Currie (2007) argue that the maintained hindlimb alternation in split-cord animals resulted from descending propriospinal drive originating in the alternating right and left forelimb CPGs. In a future study, it is possible to test this hypothesis by surgically splitting the hindlimb enlargement longitudinally, and then monitor the right-left hindlimb coordination (kinematics and EMGs) both during voluntary rectilinear swimming, and rotation evoked turning behaviors. If descending drive from the right and left forelimb enlargement is required to sustain alternating coordination between the hindlimbs in split-cord turtles, then right-left hindlimb coordination should continue only during voluntary rectilinear swimming, but should be lost during rotation evoked turning. This would provide additional evidence for "redundant coordinating systems" hypothesis, and suggest that propriospinal or commissural pathway signals could dominate during different combinations of limb movements.

In the current study, we blindfolded the turtles in order to remove the visual cues. We found that the 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. Although this was an experimental manipulation, this can happen on a regular basis in nature, such as when the animal finds itself in an unfamiliar environment, where familiar visual cues are no longer available, or when the water becomes murky or turbulent.

As such, rotation-evoked turning may provide a useful experimental platform in which to examine the underlying sensory pathways, as well as the brainstem commands, redundant coordinating systems, and spinal neural networks that underlie switching between different locomotor forms.

Cognitive visual processes and motor responses

Our survival can depend on our ability to modulate or interrupt motor responses especially when those actions are suddenly rendered inappropriate by altered conditions or events. The location of a salient stimulus, even when it is irrelevant to a task, directly influences response-selection due to an automatic tendency to respond towards the source of the stimulation. The Simon task is a well-characterized behavioral assay used to assess some aspects of this process. The Simon effect might be due to a conflict between an intentional response, and an automatic preparatory process. The major question of the human subject study is to determine if the reduction in the SE with training is due to a strengthening of the association with stimulus features and responses, or due to information gating/route suppression. An answer to these questions helps us build a framework for the very minimal physiological evidence that is currently available.

To do this, we asked the question if previous training with colors would impact performance on a shape based Simon task. So we developed a task that would measure if a change in performance could be transferred after practice to one or more conditions that share important features of the practice conditions. First, we found that the magnitude of the Simon decreases with training. An assessment on the fifth day was conducted prior to the test based on shape.

The visual Simon effect is resilient and will return with a frequent break schedule. We found that the training with task-defined associations between response direction and color did not significantly effect the Simon based on shape. Therefore, the reduction of the Simon effect with practice might not be due to an association with stimulus features and responses.

Integration

Cognitively controlled fine motor movements can work separately, synergistically or in parallel with locomotor production. The reductionist approach to studying control systems is very useful. By examining locomotor and cognitively controlled fine motor movements separately, we are able to uncover the general principles of how the nervous system produces effective behavior. Future studies can expand on our current knowledge by learning how these various sub-systems function together as a complete integrated sensory-motor ensemble.

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