Connecting the Dots Between Animal and Human Studies of Locomotion.
Focus on “Infants Adapt Their Stepping to Repeated Trip-Inducing Stimuli”

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Submitted 30 June 2003; accepted in final form 2 July 2003

INTRODUCTION

During an infant’s first well-baby examination, the clinician may lift the neonate from under her arms, place her feet in contact with a firm surface, and lean her upper body forward to evoke the infant stepping reflex. In recent years, researchers have taken interest in infant stepping as a transitional model to connect the dots between basic animal studies and human locomotor function. In this issue, Pang et al. (“Infants adapt their stepping to trip-inducing stimuli”, pp. 2731–2740) contribute new findings that advance our understanding of locomotor development in humans and extend the list of similarities between human and animal locomotion.

From mollusks to vertebrates, evidence indicates that networks of neurons, called central pattern generators (CPGs), produce the repetitive stereotypic features of locomotion (Orlovsky et al. 1999) although evidence in man is limited (Dietz 2003). In lower vertebrates, surgically reduced preparations demonstrate that locomotor CPGs are located in the spinal cord. For example, hindlimb stepping is observed in cats placed on a treadmill after thoracic spinal transection (Forssberg et al. 1980). Observations in human fetuses and young infants suggest that CPGs also control stepping movements for locomotion in humans. Ultrasound recordings have captured in utero images of human fetuses at 13–14 gestational weeks (“creeping and climbing” (Ianniruberto and Tanji 1981) and producing alternating steps during somersaults (de Vries et al. 1982). Further, infant stepping can be evoked in premature infants <30 gestational weeks (Allen and Capute 1986), suggesting a continuum between fetal and neonatal stepping. Kinematic similarities between infant stepping and cat locomotion suggest that the human locomotor CPG is similar to that in cat. For example, neonates lack a heel strike at stance onset (Forssberg 1985); infant stepping patterns during treadmill locomotion vary with belt speed (Yang 1998a); and corrective stumbling adjustments are made when foot progression is interrupted (Yang 1998b). Onset of stepping in the fetus precedes development of most descending brain pathways, strongly suggesting the locomotor CPG is located in the human spinal cord (Forssberg and Dietz 1997). Collectively, studies across the first postnatal year indicate that a locomotor continuum extends from neonatal stepping to the onset of independent walking further suggesting human locomotion is controlled by a CPG (Forssberg and Dietz 1997).

Infant stepping can be readily evoked during the first postnatal weeks but infrequently thereafter. Thus it was thought the maturing brain inhibits the reflex as an essential step in the acquisition of adaptive locomotion (McGraw 1945). This view gave way when Zelazo et al. (1972) demonstrated that infant stepping can be retained by active stepping exercises and suggested that it is amenable to learning. The role of learning was unclear, however, because an impressive collection of studies by Thelen and colleagues revealed the important role of mechanics and environmental variables (Thelen and Ulrich 1991). They found, for example, that infants practice stepping motions beyond the neonatal period when kicking while lying on their back, a position that reduces gravitational forces acting at the hip (Schneider et al. 1990; Thelen and Fisher 1982). Further, stepping could be evoked upright if their chubby legs were supported by buoyancy in a fish tank of water (Thelen 1983). More recently, Yang et al. (1998a) demonstrated that daily treadmill training increases the incidence of infant stepping and improves the alternating activation of antagonist leg muscles. In the current study, Pang et al. extend evidence that infant stepping is amenable to learning. Borrowing from methods applied in animal studies, they demonstrate that during infant locomotor development, brief training stimuli can induce modifications in locomotor commands that are sustained after a training stimulus is removed.

Infants 6–12 mo old and not yet having achieved independent walking were manually supported on a treadmill bearing approximately a third of their body weight. The left leg was instrumented for electromyographic (EMG) and kinematic recording of stepping movements, and the treadmill was equipped with force plates to measure vertical ground reaction forces. Manual perturbations during the swing phase of one to six consecutive step cycles were randomly introduced by contacting the dorsum of the foot with a baton instrumented to register contact force. All infants exhibited corrective stumbling during perturbed steps characterized by increases in vertical toe clearance, knee flexion angle, and swing phase duration. In approximately half of all infants, principally those >9 mo of age, repeated application of the perturbation over two or more consecutive steps resulted in greater vertical toe clearance and decreased vertical toe clearance.

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clearance and swing phase duration during the first one to two post-perturbation steps (after effects). In a particularly nice touch to their design, the thigh was stimulated during separate experiments, demonstrating that the aftereffects were selective to toe perturbations and not increased arousal associated with repeated stimulation.

A key question arising from the study is why aftereffects occurred at 9 mo and seldom before? This form of learning can be induced in lower decerebrate vertebrates (reviewed by Pang et al.) and may indicate subcortical maturation also underlies the emergence of after effects in infants. However, recent anatomic and electrophysiological evidence in infants indicate even monosynaptic corticospinal connections are already present at birth and may contribute to refining spinal circuits long before behavioral milestones are established (Eyre et al. 2000, 2001). Nonetheless, findings of Pang et al. encourage us to consider that even immature neuromotor systems in humans exhibit adaptive plasticity. Identifying the underlying mechanisms will be important in connecting the dots between animal and human control of locomotion.

REFERENCES
