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COORDINATION BETWEEN THE FORE- AND HINDLIMBS IS BIDIRECTIONAL, ASYMMETRICALLY ORGANIZED, AND FLEXIBLE DURING QUADRUPEDAL LOCOMOTION IN THE INTACT ADULT CAT

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Abstract—Despite the obvious importance of inter-girdle coordination for quadrupedal locomotion in terrestrial mammals, its organization remains poorly understood. Here, we evaluated cycle and phase durations, as well as footfall patterns of four intact adult cats trained to walk on a transverse split-belt treadmill that could independently control fore- and hindlimb speed. When the hindlimbs walked at faster speeds than the forelimbs, an equal rhythm was always maintained between the fore- and hindlimbs, even at the highest fore–hindlimb speed ratio of 1:3 (0.4:1.2 m/s). The locomotor pattern adjusted through changes in both hindlimb stance and swing phase durations, whereas only the forelimb stance phase was affected. In such conditions, when fore- and hindlimb values were compared to those obtained at matched speeds during tied-belt walking (i.e. predicted values based on treadmill speed), hindlimb cycle, stance and swing durations were consistently longer than predicted. On the other hand, forelimb cycle and stance durations were shorter than predicted but only at the highest split-belt speed ratios. Forelimb swing durations were as predicted based on front-belt speed. The sequence of footfall pattern when hindlimb speed was faster was identical to tied-belt walking. In stark contrast, when the forelimbs walked at slightly faster speeds than the hindlimbs, the rhythm between the fore- and hindlimbs broke down. In such conditions, the locomotor pattern was adjusted through changes in stance and swing phase durations in both the fore- and hindlimbs. When the rhythm between the fore- and hindlimbs broke down, hindlimb cycle and phase durations were similar to predicted values, whereas forelimb values were shorter than predicted. Moreover, several additional sequences of footfall patterns were observed. Therefore, the results clearly demonstrate the existence of a bidirectional, asymmetric, and flexible control of inter-girdle coordination during quadrupedal locomotion in the intact adult cat.

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Abbreviations: ANOVA, analysis of variance; CPGs, central pattern generators; DS, diagonal sequence; LFC, left forelimb contact; LHC, left hindlimb contact; LS, lateral sequence; RFC, right forelimb contact; RHC, right hindlimb contact.

Key words: quadrupedal locomotion, inter-girdle coordination, transverse split-belt treadmill.

INTRODUCTION

Proper coordination of the fore- and hindlimbs (i.e. inter-girdle coordination) in terrestrial mammals is essential to maintain stability during the forward progression of quadrupedal locomotion. Human infants also use quadrupedal forms of locomotion (Yang et al., 2004) and despite its bipedal nature, human adults are thought to have conserved a quadrupedal form of coordination during walking (Dietz et al., 1994; Zehr and Duysens, 2004; Zehr et al., 2009; Dietz, 2011). However, the general framework of inter-girdle coordination during quadrupedal locomotion in terrestrial mammals remains poorly understood and the results often seem to conflict [recently discussed in Thibaudier and Hurteau (2012)]. For instance, some have suggested that forelimb activity exerts greater influence on the hindlimbs (Miller et al., 1977; Akay et al., 2006), while other studies have proposed the opposite (Juvin et al., 2005, 2012).

Although there is disagreement regarding the influence of ascending and descending inhibitory or excitatory pathways on inter-girdle coordination, most studies agree that spinal locomotor networks controlling the fore- and hindlimbs are asymmetrically coupled. Flexible patterns of inter-girdle coordination are undoubtedly required to orchestrate different rhythmic tasks, such as walking, running, and swimming. This, in turn, would require functional changes in the organization of pathways coupling the cervical and lumbosacral locomotor networks. As such, the task being performed must be considered when evaluating the organization of inter-girdle coordination. Specific patterns of inter-girdle coordination might also appear only under certain experimental conditions, such as following decerebration (Akay et al., 2006) or in isolated spinal cord preparations (Juvin et al., 2005, 2012). To evaluate the organization of fore- and hindlimb coordination during quadrupedal locomotion it is important to study it during that very same task. Surprisingly, few data are available with such a model.

Here, we evaluated some features of the locomotor pattern in intact adult cats trained to walk on a transverse split-belt treadmill that independently controlled the speed of the fore- and hindlimbs. Such an approach was used before to study fore- and hindlimb

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coordination in intact juvenile cats (Cruse and Warnecke, 1992) and in decerebrate adult cats (Akay et al., 2006). Cruse and Warnecke (1992) used only two slow treadmill speeds (0.3 and 0.46 m/s) and concluded that ascending and descending influences were largely symmetric. Akay et al. (2006) used a wider range of speeds (i.e. 0.3–0.6 m/s) and concluded that forelimb activity had greater influence on hindlimb activity in decerebrate cats. However, they only detailed the effect of increasing the speed of the front treadmill while keeping hindlimb speed constant.

In the present study, we used a wide range of speeds (0.4–1.2 m/s) for the fore- and hindlimbs in freely behaving intact adult cats to probe the coordination between locomotor networks located at cervical and lumbar girdles. By changing the speed of the fore- or hindlimbs, while maintaining the speed of the limbs located at the other girdle constant, we provide the first evidence that inter-girdle coordination in quadrupedal intact adult mammals is bi-directional and asymmetrically organized.

We also evaluated patterns of footfall during transverse split-belt walking. In general, the vast majority of tetrapods, including cats, employ what is term a lateral sequence (LS) during terrestrial locomotion, whereby contact of a hindlimb is directly followed by contact of the ipsilateral forelimb (e.g. Muybridge, 1957; Hildebrand, 1967; Wetzel et al., 1976; Lemelin et al., 2003; Stevens, 2006). In contrast, a diagonal sequence (DS) during terrestrial locomotion is characterized by contact of a hindlimb followed directly by contact of the contralateral forelimb, a pattern mostly found in non-human primates (e.g. Muybridge, 1957; Prost, 1965; Hildebrand, 1967; Vilensky and Larson, 1989; Larson et al., 2000; Lemelin et al., 2003; Schmitt, 2003; Stevens, 2006, 2008; Young et al., 2007). In the present study, we show that cats can adopt DS gait patterns when forelimb speed exceeds hindlimb speed.

Therefore, we present transverse split-treadmill in freely behaving cats as a novel technique to probe the functional organization and flexibility of inter-girdle coordination in an intact adult mammalian system.

EXPERIMENTAL PROCEDURES

Animals and ethical considerations

All procedures were approved by the Animal Care Committee of the Université de Sherbrooke and were in accordance with policies and directives of the Canadian Council on Animal Care. Before the experiments, animals were housed and fed within designated areas. Four adult cats weighing between 4.0 and 9.0 kg were selected based on their ability to walk for prolonged periods (10–15 min) on an animal treadmill with a single running surface (Fit-Fur-Life Ltd., Surrey, UK). Cats were then trained to walk on a transverse split-belt treadmill composed of four independently controlled running surfaces 120 cm long and 30 cm wide (Bertec Corporation, Columbus, OH, USA). In the present study, only the front and back surfaces on the left side of the treadmill were used. A Plexiglas box (120 cm long, 50 cm high) constrained the animals to walk with the fore and hindlimbs separately on the two belts. The box was open at the top and at the front. Food and affection were given as reward and the cats did not contact the Plexiglas box following training. Recording sessions started once the animals could walk comfortably with the fore- and hindlimbs on the front and rear belts, respectively, which required approximately four additional weeks of training on the transverse split-belt treadmill.

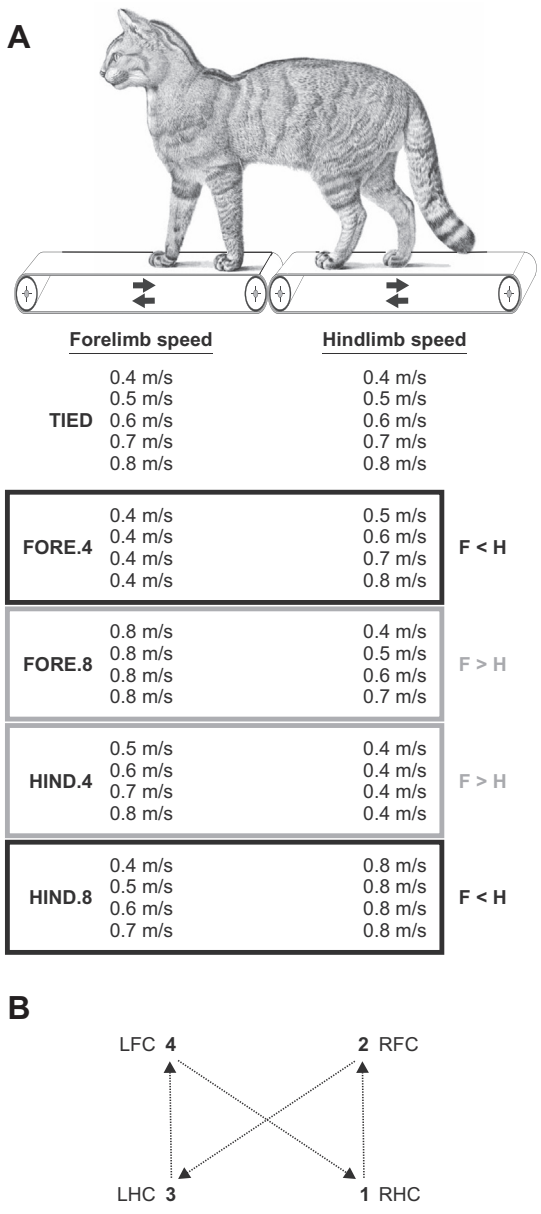

Fig. 1. Experimental set-up and conditions. (A) Transverse split-belt treadmill was used to evaluate inter-girdle coordination using five conditions: (1) fore- and hindlimbs walking at equal speeds (TIED) from 0.4 to 0.8 m/s; (2, 3) forelimbs walking at a constant speed of 0.4 m/s (FORE.4) or 0.8 m/s (FORE.8) with hindlimb speed increasing from 0.4 to 0.8 m/s, and (4, 5) hindlimbs walking at a constant speed of 0.4 m/s (HIND.4) or 0.8 m/s (HIND.8) with forelimb speed increasing from 0.4 to 0.8 m/s. Black boxes represent conditions when the hindlimbs walked faster than the forelimbs, whereas gray boxes represent conditions when the forelimbs walked faster than the hindlimbs. B shows an example of a footfall pattern that followed a sequence of right hindlimb contact (RHC) → right forelimb contact (RFC) → left hindlimb contact (LHC) → left forelimb contact (LFC). In the footfall patterns shown in Figs. 4, 8 and 12, RHC, RFC, LHC, and LFC are located in the same positions. F = forelimbs; H = hindlimbs.