ARTICLE
A Laboratory Exercise Demonstrating the Limited Circumstances in which the Cerebral Cortex is Engaged in Over Ground Locomotion

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For neuroscience, memorable demonstrations of principles in action are crucial. Neural control of walking is particularly difficult to understand because the interaction of the cerebral cortex with a central pattern generator (CPG) makes the mode of control context-dependent. Beginning students tend to consider corticospinal control the basis of all movement, so they may not distinguish the limited circumstances in which the cerebral cortex bypasses the CPG to control leg movements directly for walking. The demonstration described here is designed to show that cortical involvement in normal walking is minimal unless visual control of foot placement is required. Cortical involvement in motor control is assessed by probing for spare attention while a student volunteer performs three different tasks: sitting, walking down a hallway, and walking through an obstacle course. Simple math quizzes with 20 oral questions are the probes. The class observes the demonstration and discusses the results. To evaluate learning, a multiple-choice question was administered two months after the demonstration, as well as 14 months later to cohorts from the previous year's class. The demonstration succeeded: quiz scores were similar for sitting and level walking, but lower for the obstacle course. Two months later, 86% of students correctly answered the multiple choice question; 42% of the previous year's cohorts answered correctly after 14 months. The demonstration shows that the cortex is engaged by walking through an obstacle course, not walking on a flat indoor surface. Initially, most students learned this distinction well, but after a year, many reverted to the idea that the corticospinal tract controls details of leg movements during walking. Thus this result emphasizes the need for review of advanced concepts. Overall, the experience was fun and could easily fit into basic or clinical neuroscience courses.

Key words: cerebral cortex; corticospinal tract; voluntary movement; motor control; central pattern generation; locomotion; dual task

One difficult aspect of neuroscience is the volume of complicated material that must be learned and the extent to which it must be integrated before understanding can emerge. For example, to understand motor control, learning the descending tracts is basic knowledge. The student must also understand how commands from these tracts interact with spinal segments and peripheral input. The neural control of locomotion may be one of the most difficult interactive motor control problems for students to understand. This article describes a simple demonstration that helps students understand which situations require extensive involvement of the corticospinal system for the control of walking and which modes of walking may be governed with only minor involvement at the level of the cortex. An evaluation of the efficacy of the lesson for teaching the students these concepts is also presented.

For background, students are taught that the control of locomotion depends on a tripartite system (Smith et al., 1993) consisting of descending commands for activation and regulation of the locomotor pattern, peripheral input for monitoring the movement and adapting to the environment, and a central pattern generator (Dietz, 2003; Harkema et al., 2000; MacKay-Lyons, 2002; Nymark et al., 1998). A central pattern generator (CPG) is a system within the central nervous system that responds to a general command for activation with a specific pattern of sensorimotor control sufficient to produce the rudiments of a complex behavior (Grillner, 1981). From the basic animal literature, there is consensus that locomotion, respiration, mastication, and suckling are all examples of behaviors that are produced by a CPG (Arshavsky et al., 1997; Sigvardt and Miller, 1998). Evidence from patients with spinal cord injuries demonstrates that a CPG probably underlies locomotor control in humans, as well (Nymark et al., 1998; Harkema et al., 2000; Dietz, 2003; Dietz and Harkema, 2004).

For motor systems neuroscience, however, control of walking is only one concept. The corticospinal system and its role in voluntary motor control, especially fine control of the hand, are critical (Kuypers, 1981; Scheiber, 2001). As students struggle to understand models of voluntary motor control that have the cerebral cortex at the top of the hierarchy, they tend to overgeneralize and assume that corticospinal control dominates all movements. Evidence from the animal literature clearly demonstrates, however, that the cerebral cortex controls the details of locomotion only in situations like avoiding and responding to obstacles (Armstrong and Drew, 1984; Drew, 1993; Drew et al., 1996; Drew et al., 2002). In these circumstances, the cortex appears to intervene and superimpose specific commands on the general pattern produced by the CPG. The basic lower extremity motor pattern for walking over level ground, however, does not seem to engage the cortex except in a general way that follows the basic locomotor rhythm created at subcortical levels (Armstrong and Drew, 1984;Capaday et al., 1999;Drew et al., 2004).

In the human subject, measurement of cortical involvement in various motor tasks can be assessed by imaging of regional changes in cerebral blood flow (Rowe and Frackowiak, 1999). Unfortunately, these powerful methods are impracticable for locomotion. Further, functional imaging methods are expensive and would be difficult to incorporate into a classroom demonstration. A simpler method for assessing the cortical load imposed by a motor activity can be found in the motor learning literature (Schmidt and Lee, 1999; Shumway-Cook and Woollacott, 2001). For a motor task where normal subjects will rarely demonstrate overt errors, a secondary task can be used as a probe for spare attention. This paradigm is referred to by different authors as the "probe," "dual-task," or "divided attention" method (Brown, 1962; Chen et al., 1996; Schmidt and Lee, 1999; Shumway-Cook and Woollacott, 2001). The assumption behind this method is that the person has a fixed capacity for attention, such that when attention is divided between two tasks, performance will be worse than when each task is performed alone. This method works best when the behavior required to perform the probe task is separate from that required to perform the primary task and success at the primary task is more important than success at the secondary task. It is also best suited to assessment of attention during performance of a continuous task, where the timing of the probe need not be temporally linked to performance of discrete movement phases of the task (Schmidt and Lee, 1999). Locomotion provides an excellent scaffold for this design because the cost of falling is high; if failure at the secondary task presents no danger, locomotion will naturally receive first priority. The secondary task chosen for the present study was a simple oral math quiz. This secondary task did not require vision, no special mathematical aptitude was needed, the only response required was speech, the results were objective, and performance was measurable without equipment.

MATERIALS AND METHODS

The curriculum module on neural control of locomotion received one contact hour within a 72 contact-hour course focused on sensory and motor systems neuroscience for physical therapy students. There were 40 minutes of basic lecture content on CPGs, their role in the control of locomotion, and the role of cortical and brainstem systems for initiation and regulation of walking. After lecture, the 20-minute laboratory experience described here was provided. The analysis and reporting of human subjects data contained herein was approved by the Institutional Review Board of The Ohio State University.

The math quiz used as the probe consisted of 20 questions requiring three numbers to be added or subtracted, such as 19 + 17 - 14 = ? The quiz questions were randomly constructed so that the answers could range from -50 to +50, and the three addends in each equation could range from -30 to +30. To deliver the quiz, the instructor read a question aloud to the student, the student replied with an answer, and then the next question was asked. The student was not told whether the answers were correct as the quiz proceeded, but the instructor recorded responses as right or wrong on a tally sheet. The student was given two minutes to answer as many questions as possible. If the student finished all 20 questions within two minutes, the instructor used the time remaining to go back and re-ask questions that were initially missed. The score was the number of correct replies. In four years, students typically had a chance to retry only a few questions within the two-minute time frame; no one has reached 100% (20 correct) within two minutes.

To compare the demands of normal locomotion and navigating an obstacle course, three versions of the quiz were constructed. As illustrated in Fig. 1, a student volunteer took the first quiz while sitting, with her or his classmates watching. Next, the same volunteer took the second quiz while walking up and down the hallway, again with her or his classmates watching. Finally, the student took a third version of the quiz while walking back and forth through an obstacle course set up in the hallway, also with their classmates watching. The actual quizzes are presented in Appendix 1.

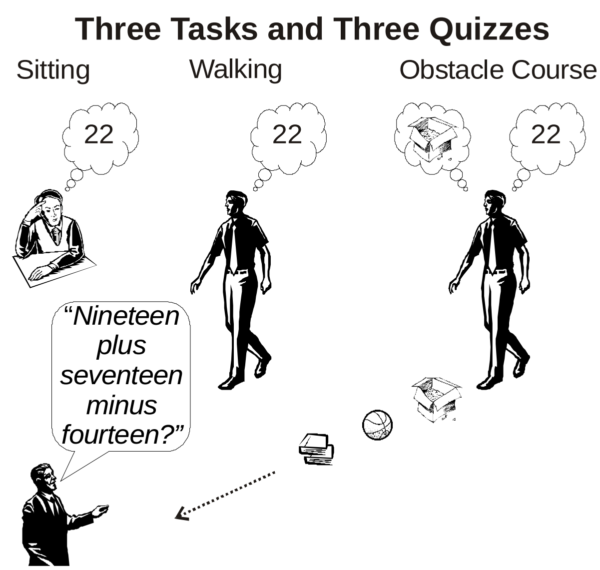

Figure 1. General setup for the demonstration. In each case, the instructor reads a question aloud and the student answers verbally. In the case of the obstacle course, the student's attention was divided between the math problem and the need to avoid tripping over the obstacles. As provided in the appendix, a separate quiz was given for each task, so no question was used for more than one task.

The obstacle course was about 10 meters long and included an assortment of items such as boxes, balls, books, chairs, foam and step-stools that the student had to step upon or over (Fig. 1). Any assortment of items will suffice, as long as they present a challenging obstacle course that a reasonably coordinated individual can walk though without having to use their hands. In requesting a volunteer, the instructor should ask for a student with no balance impairments or lower limb orthopedic problems.

For administration of the quiz in sitting, the student sat in a chair and the instructor stood at the front of the classroom. For walking up and down the hall and for the obstacle course, the instructor stood about midway down the course. In each case, the instructor used a loud, clear voice to ask the questions. An effort was made to ask the questions at about the same pace in all three conditions. Students were encouraged not to pause to answer questions, but to keep walking at a steady pace.

As described in results, the demonstration worked: quiz scores were similar for sitting and walking in the hall, but lower for walking through the obstacle course. After the demonstration, students worked in groups of two to four to develop written responses to the following question: “Explain the differences in results based on the degree of cortical involvement in each activity.” After providing a few minutes for the students to develop their answers, the instructor asked for volunteers to recite their explanations to the class. In the ensuing discussion, concepts about neural control of walking were reinforced, and applications of these concepts to rehabilitation were introduced.

To determine whether this demonstration was effective, a one-question post-test was administered two months after the demonstration and to cohorts from the previous class, for whom 14 months had passed. Both groups of students answered the question on the same day and could not discuss it with each other. The question was as follows.

During walking, which of the following circumstances would most likely require involvement of the cerebral cortex for the control of specific aspects of the leg movements?

a. *Walking indoors down a quiet hallway*
b. *Walking outdoors on a smooth asphalt pathway*
c. *Walking outdoors on a badly broken sidewalk*
d. *All of the above – the cerebral cortex controls all voluntary movement*
e. *None of the above – a central pattern generator controls walking*

The correct answer is c. Walking on a badly broken sidewalk, which is analogous to walking through an obstacle course, demands cortical control over specific aspects of the leg movements. In the context of cortical control of locomotion, there is nothing special about walking indoors or outdoors when the surface is level and unobstructed. Thus, answers a and b established a contrast, emphasizing the “badly broken sidewalk” in answer c. Although it is true that the cerebral cortex is involved in the control of all voluntary movement, the key phrase in the stem, “control of specific aspects of the leg movements,” makes answer d wrong in the context of locomotor control. Answer e is also wrong in this context because the CPG is not sufficient to fully govern locomotion for the situation described in answer c. Thus, answers d and e were designed to find students who had overgeneralized and forgotten the contingencies for interaction between the cerebral cortex and the CPG for control of walking.

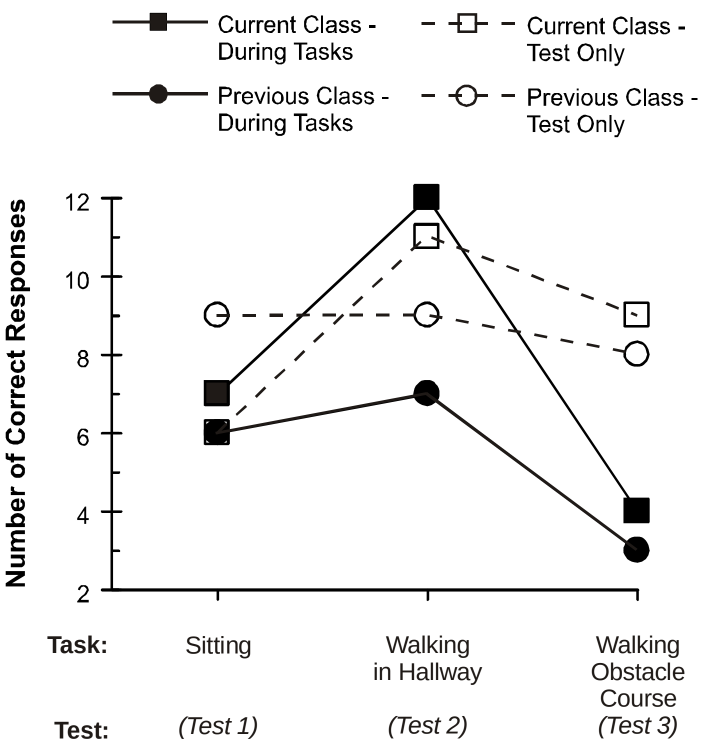

Figure 2. Scores on the math quizzes for different students and conditions. The key indicates which class and condition is represented by each symbol and line style. The solid lines and filled symbols show scores associated with in-class performance of the three tasks, sitting, walking in the hallway, and walking through the obstacle course. The open symbols and dashed lines show scores on the same three tests taken alone with the instructor at a later date, with the student sitting for each test.

RESULTS

For all four years this demonstration was used, the results were similar; data were recorded from years two to three, as presented in Fig. 2. The math scores were similar for the test taken while sitting and while walking in the hallway with no obstacles. Indeed, math scores appeared slightly higher for walking in the hallway, probably due to practice effects because that test was administered second. The math scores obtained while negotiating the obstacle course, however, have always been markedly lower than for the other two tasks. Despite the instruction not to pause, students typically pause or stop at least once in the two-minute quiz to attend to a question. To determine whether the three versions of the quiz were indeed of similar difficulty, the same two students took the tests again during a subsequent quarter, this time with the students sitting for each test. As illustrated in Fig. 2 (dashed lines, test only), the lowest scores were associated with the obstacle course. The student from the current class showed better performance on tests two and three, indicating that this individual may have demonstrated the expected warm-up effect (Fig. 2, open squares, dashed line). The student from the previous year scored fairly consistently on the three different tests in sitting (Fig. 2, open circles, dashed line). Thus, the lower scores obtained while walking the obstacle course appear to have been associated with the task, not order effects.

In the discussion that followed, students reached consensus that only walking the obstacle course required substantial engagement of the cerebral cortex, as indicated by the demand for attention. Follow-up discussion placed this information in the context of the role of the CPG in control of walking. The instructor suggested that gait rehabilitation should promote the ability to ambulate with minimal attention from the voluntary motor control system, except in situations such as navigating obstacles or walking on unusual surfaces, where cortical control is natural (Shumway-Cook and Woollacott, 2001).

This demonstration also provided the opportunity to teach students that conversation with persons in the midst of motor performance should be a variable controlled as a specific way to challenge attention when appropriate. Likewise, teaching people to stop talking and attend carefully to their environment in challenging situations, such as negotiating an outdoor curb, may promote safety in such circumstances (Chen et al., 1996). These applied examples were intended to help students organize the information in personally meaningful ways.

Table 1. Responses to the post test question.

	Answer Given (n)					*No.*	
Year	*a*	*b*	*c*	*d*	*e*	*Students*	*% correct*
Current	0	0	32	2	3	37	86%
Previous	0	0	14	15	4	33	42%

Responses to the multiple-choice question are presented in Table 1. After two months, the lesson was remembered well, with 86% of the class answering correctly. Fourteen months later, almost half the students from the previous year answered correctly. The most common error after 14 months was to indicate that the cerebral cortex controlled all voluntary movement, including specific aspects of leg movements during walking. No one selected unobstructed walking indoors or outdoors instead of walking on a broken sidewalk as the correct answer.

DISCUSSION

With a simple demonstration, students had an opportunity to learn an important concept about the neural control of locomotion. Specifically, only for obstacle avoidance and other adaptations to special situations is the cerebral cortex extensively involved in detailed control of leg movements (Drew et al., 2004). Retention was good two months after the demonstration and fair 14 months later. Part of the drop at 14 months may have been because this group had just completed a course where cerebral palsy and the importance of cortical control were emphasized. They were also entering a course on adult neurology, where CVA and cortical control would again be a focus. This indicates that when neuroscience is taught as a foundation early in the curriculum and applied later, review of critical content is warranted. Such a review is a part of our curriculum, and the present results indicate that this is worthwhile.

By framing the demonstration as an experiment, students were engaged in the scientific method and active, discovery-based learning. By incorporating the use of a secondary task as a probe into the design, students were exposed to a valuable method of investigation for studies of motor control and learning (Schmidt and Lee, 1999). The laboratory experience took only about 20 minutes and required no special equipment.

As a probe, the math quiz had certain advantages. First, it only required addition and subtraction, so it was more a test of attention than mathematical aptitude. Secondly, it was objective and there was no concern about misinterpretation or ambiguity in questions or answers. Finally, and most importantly, the test did not require vision or use of the hands. The subjects listened to the question and replied orally. This left them free to use their eyes, arms, trunk, and legs in pursuit of the locomotor tasks.

The lack of control over order effects (Portney and Watkins, 2000) is the one aspect of the demonstration that would be most questionable if this was an experiment rather than a demonstration. However, in the present case, placing the conditions in the order selected actually strengthened the demonstration. One would expect the typical individual to demonstrate a warm-up effect, with performance improving after the first quiz. The fact that performance was lowest on the last quiz, when the subject had the most practice with the math quizzes, only strengthens the conclusion that the decreased score was due to the attention demands of the obstacle course. While discussing the results with the students afterwards, this point was emphasized to help them appreciate the importance of order effects in research design.

In conclusion, a simple demonstration requiring no special equipment and a relatively small amount of class time was designed to help students learn an important principle about the neural control of locomotion. Two months after the demonstration, 86% of the students could correctly answer a test question specifically designed to discriminate concept retention; 42% responded correctly after 14 months. This indicates that the demonstration was effective at teaching the concept initially, but some time devoted to reinforcement and extension of the learning is warranted later in the curriculum. Structuring the demonstration as an experiment afforded the opportunity for students to learn about research design and about the probe technique as a specific method for motor control research. A future question would be whether, if enough of these experiences were threaded through a curriculum, they could be designed to provide an active learning experience for research design, in addition to helping students learn course-specific content.

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APPENDIX

The Math Quiz

The subject has exactly two minutes to complete each test. The score is the correct number of items obtained in two minutes. If the subject completes all the items in less than two minutes, they can try for a perfect score by repeating any they missed in the time remaining. The examiner reads the question and awaits a response. For example, the examiner would say “three minus nineteen plus five” for the first question of test one, and the subject would be expected to say “minus eleven” (or “negative eleven”), and so on. The subject is not told during the test whether a response is right or wrong

Test 1							
Question						Answer	Correct
3	-	19	+	5	=	-11	
23	-	21	+	21	=	23	
14	-	9	-	14	=	-9	
18	-	9	-	6	=	3	
1	-	24	+	13	=	-10	
22	-	8	+	5	=	19	
17	+	18	+	11	=	46	
13	+	15	-	17	=	11	
2	-	10	+	10	=	2	
3	-	9	+	16	=	10	
8	+	4	+	23	=	35	
12	+	21	+	2	=	35	
11	-	3	+	5	=	13	
11	+	3	-	12	=	2	
12	-	7	+	8	=	13	
21	+	18	-	24	=	15	
9	+	11	+	20	=	40	
16	+	16	+	16	=	48	
						Total Score	

Test 2							
Question						Answer	Correct
20	-	20	-	4	=	-4	
5	-	8	+	7	=	4	
19	+	17	-	14	=	22	
3	+	24	-	5	=	22	
15	+	5	+	15	=	35	
20	+	23	-	3	=	40	
21	-	11	+	24	=	34	
3	+	6	+	13	=	22	
22	-	9	-	15	=	-2	
16	-	1	+	9	=	24	
5	-	12	-	3	=	-10	
14	+	13	+	18	=	45	
10	-	12	+	13	=	11	
12	+	20	-	4	=	28	
26	+	5	-	8	=	23	
12	-	21	+	13	=	4	
18	-	18	+	22	=	22	
18	+	4	-	5	=	17	
						Total Score	

Test 3								
Question							Answer	Correct
4	+	11	+	13	=		28	
21	+	16	+	5	=		42	
3	+	25	-	13	=		15	
17	+	24	+	3	=		44	
8	-	18	+	9	=		-1	
16	-	24	+	11	=		3	
6	+	19	+	12	=		37	
26	+	16	+	2	=		44	
10	-	8	-	23	=		-21	
26	-	4	+	5	=		27	
5	+	21	-	23	=		3	
13	+	13	+	24	=		50	
11	+	21	+	16	=		48	
14	+	25	+	2	=		41	
7	+	25	+	4	=		36	
8	+	19	-	15	=		12	
15	+	4	-	6	=		13	
22	-	1	-	26	=		-5	
							Total Score	

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