The contribution of vision, proprioception, and efference copy in storing a neural representation for guiding trail leg trajectory over an obstacle

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Submitted 17 August 2011; accepted in final form 27 January 2012

Lajoie K, Bloomfield LW, Nelson FJ, Suh JJ, Marigold DS. The contribution of vision, proprioception, and efference copy in storing a neural representation for guiding trail leg trajectory over an obstacle. J Neurophysiol 107: 2283–2293, 2012. First published February 1, 2012; doi:10.1152/jn.00756.2011.—Stepping over obstacles requires vision to guide the leading leg, but direct visual information is not available to guide the trailing leg. The neural mechanisms for establishing a stored obstacle representation and thus facilitating the trail leg trajectory in humans are unknown. Twenty-four subjects participated in one of three experiments, which were designed to investigate the contribution of visual, proprioceptive, and efference copy signals. Subjects stepped over an obstacle with their lead leg, stopped, and straddled the obstacle for a delay period before stepping over it with their trail leg while toe elevation was recorded. Subsequently, we calculated maximum toe elevation and toe clearance. First, we found that subjects could accurately scale trail leg toe elevation and clearance, despite straddling an obstacle for up to 2 min, similar to quadrupeds. Second, we found that when the lead leg was passively moved over an obstacle (eliminating an efference copy signal and altering proprioception) without vision, trail leg toe elevation and clearance were reduced, and variability increased compared with when subjects actively moved their lead leg. Trail leg toe measures returned to normal when vision was provided during the passive manipulation. Finally, we found that altering lead leg proprioceptive feedback by adding mass to the ankle had no effect on trail leg toe measures. Taken together, our results suggest that humans can store a neural representation of obstacle properties for extended periods of time and that vision appears to be sufficient in this process to guide trail leg trajectory.

obstacle avoidance; locomotion; memory; corollary discharge; sensory feedback

NEGOTIATING OBSTACLES IS AN ESSENTIAL feature of locomotion. Vision plays an important role in providing the necessary information to successfully plan the required gait modification. For example, individuals fixate on an obstacle as they approach it (Patla and Vickers 1997), and this provides information about its characteristics and location with respect to the body to guide foot placement and subsequent clearance (Mohagheghi et al. 2004; Patla et al. 1996a).

Whereas direct visual information of obstacle properties, such as height, facilitates stepping over an obstacle with the first, or lead, leg (Patla 1998; Patla and Rietdyk 1993; Rhea and Rietdyk 2007), this continual visual guidance is not available for the second, or trailing, leg. Despite this predicament, quadrupeds are capable of straddling an obstacle for several minutes before accurately scaling their hindlimbs over an obstacle (McVea and Pearson 2006, 2007a; McVea et al. 2009). Specifically, McVea and Pearson (2006) trained cats to step over an obstacle with their forelimbs and stop before the passage of the hindlimbs. After a variable delay period (during which the obstacle was lowered without the animal’s knowledge), cats were encouraged to walk forward again, and the hindlimbs stepped over the now-absent obstacle as if it were still present. In these experiments, the obstacle memory was very persistent (up to 10 min) and represented the physical characteristics of the obstacle, as well as its location with respect to the body (McVea and Pearson 2006).

There is evidence to suggest that humans can store visual information for relatively short periods of time. For instance, Zettel et al. (2007) have argued that young and older adults rely on stored visual information to guide recovery responses following a perturbation to standing balance. Specifically, most subjects accurately used a stepping strategy in response to an unexpected platform translation and avoided obstacles without directly looking at their feet, the landing area, or the obstacle following the onset of the perturbation. It is possible though that peripheral vision from the lower visual field was being used to monitor limb trajectory in relation to the obstacle, similar to that demonstrated for avoiding obstacles while walking on a treadmill (Marigold et al. 2007). In addition, humans can navigate toward a distant target for up to 8 s without vision (Thomson 1983); however, there were no gait modifications required during this task. More recently, Patla (1998) and colleagues (Mohagheghi et al. 2004) have shown that human subjects are able to negotiate obstacles with relatively few accidental contacts when vision is removed for several steps during the approach phase after an initial viewing period, although toe elevation and toe clearance are elevated without vision.

Our first objective in this study was to determine whether human subjects could retain obstacle characteristics in memory for extended periods of time, beyond that previously investigated, to successfully perform an obstacle-avoidance task similar to cats (McVea and Pearson 2006) and horses (Whishaw et al. 2009). In an experiment using three different delay periods, while subjects straddled one of three different height obstacles after stepping over it with the lead leg, we hypothesized that trail leg toe elevation and clearance would scale to obstacle height, independent of the delay duration.

An important question arises as to what neural mechanisms are used to form a neural representation of the obstacle to appropriately scale the trail leg toe elevation when vision is no longer available, regardless of how long the representation is maintained in memory. There are at least three possible sources

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of input that may contribute either independently or in an integrative fashion to this representation. First, visual information of the obstacle’s properties obtained during the approach phase could be used. Second, proprioceptive feedback (e.g., muscle and/or joint receptors) from the lead leg stepping over the obstacle could be integrated within the nervous system to contribute to the obstacle representation or to reinforce the information estimated from vision. Third, a copy of the original motor command (i.e., efference copy) to the lead leg may contribute in a similar manner as proprioceptive feedback. Collectively, we refer to visual input, proprioceptive feedback, and an efference copy as sensorimotor signals.

Previous research on obstacle avoidance in humans has argued that the lead and trail legs are independently controlled on the basis of visual input regarding obstacle characteristics, implying that lead leg nonvisual sensorimotor signals play a relatively minor role in guiding trail leg trajectory. Specifically, Patla et al. (1996b) found a lack of correlation between lead and trail leg toe measures. Furthermore, obstacle contact with the lead leg results in changes in toe elevation and clearance in that leg but not the trailing leg in subsequent trials (Rhea and Rietdyk 2011). Finally, Mohagheghi et al. (2004) provided evidence that the scaling of the trail leg trajectory over an obstacle may be under the control of stored visual input, since removal of vision during the last portion of the approach phase and during obstacle crossing had no effect on trail leg toe measures. However, these studies did not investigate any nonvisual source. On the other hand, McVea and colleagues (McVea and Pearson 2007b; McVea et al. 2009) have argued that proprioceptive feedback and particularly an efference copy signal regarding the forelimbs are essential for establishing an obstacle memory and for scaling the hindlimbs in cats. For example, cats were stopped before crossing an obstacle with the forelimbs and were subsequently distracted with food as the obstacle was lowered. In this scenario, hindlimb toe elevations were generally lower or abolished compared with when the cats were stopped straddling the obstacle after stepping over it with the forelimbs.

There is evidence in humans that proprioceptive feedback and an efference copy signal are involved in the control of movement. Proprioceptive feedback is known to contribute to the regulation of the step cycle during locomotion (for a review, see Donelan and Pearson 2004; see also Ivunenko et al. 2000; Lajoie et al. 1996; Sorensen et al. 2002) and to mediate intersegmental interaction torques during reaching (Sainburg et al. 1995). Recently, in a patient with severe proprioceptive deficits from sensory peripheral neuropathy, it was shown that there was a significant correlation between the initial movement segment and the turn angle, even without vision of the hand for reaching movements to a target that jumped to a new location after movement initiation (Coslett et al. 2008; Medina et al. 2010). This suggests that this patient was able to obtain a relatively accurate estimate of the state of the limb through efference copy signals, at least for the initial phase of the movement (Medina et al. 2010).

Therefore, the second objective of this study was to determine the relative contribution of visual, proprioceptive, and efference copy signals in the formation of an obstacle representation that could subsequently be used to control the trail leg during obstacle avoidance in human subjects. We conducted two additional experiments that were designed to determine the roles of each of these sensorimotor sources by adapting the obstacle-avoidance paradigm used by McVea and Pearson (2006). In one experiment, we used passive manipulation of the lead leg over an obstacle (to eliminate an efference copy signal), with or without vision. This manipulation also alters muscle spindle (due to changes in $\gamma$ coactivation) and golgi tendon organ (GTO) output for this limb. In the other experiment, we altered an efference copy signal and GTO feedback related to the lead leg, while it stepped over an obstacle, by adding mass at the ankle. We hypothesized that a combination of sensorimotor signals contributes to the formation of a neural representation of an obstacle, and as such, scaling of trail leg toe elevation and clearance would be affected when proprioceptive feedback and efference copy signals related to the lead limb were altered. We further hypothesized that the trail leg toe measures would be altered to a greater extent when vision was not available. To our knowledge, these experiments provide the first detailed account in humans of which sensorimotor signals contribute to obstacle representations used to guide the trail leg.

METHODS

Subjects. A total of 24 subjects, naïve to the study, from Simon Fraser University, participated in one of three experiments. Subjects had no known visual, neurological, or musculoskeletal disorders that could affect their performance on the task. The Office of Research Ethics at Simon Fraser University approved the study, and all subjects gave informed consent prior to being tested.

General protocol. In each experiment, subjects were required to step over one of three different wooden obstacles (see Fig. 1A). Each obstacle was 81 cm wide with a depth of 9 cm and ranged in height—low (19 cm), medium (28 cm), high (36 cm). After stepping over the obstacle with their right leg (i.e., lead leg), subjects paused, straddling the obstacle for a certain delay period. Subjects were instructed to refrain from looking down at the obstacle during this period. The delay period and experimental manipulation that occurred during this interval depended on the experiment and are described in greater detail below. During the delay period, an experimenter turned the obstacle over, without the subjects’ knowledge, so that it was not present when the subjects stepped over the obstacle with their trail leg. In this position, the obstacle was only 2.5 cm high (due to the thickness of the wood) and didn’t interfere with the task. This technique was similar to the cat experiments (McVea and Pearson 2006, 2007b), where the experimenters lowered the obstacle. This process serves to ensure that subjects do not contact the obstacle if they incorrectly recall its height from memory. In certain studies, when subjects hit an obstacle, they show large overcompensations in later trials (Alexander et al. 2011; Rhea and Rietdyk 2011), and this would confound the results of the study. The subjects were informed that one of the experimenters would be taking measurements while they straddled the obstacle. This was done to explain why one of the experimenters was crouching down near them during the delay. Throughout the delay period, subjects watched a movie playing on a 21-inch monitor placed at eye level in front of them (at a distance of 1 m) so that they didn’t look down at the obstacle and/or see when one of the experimenters turned over the obstacle. An experimenter watched to ensure that the subject didn’t look down. Note that it was not possible to see the obstacle while straddling it unless subjects made large, obvious head movements toward the ground. Subjects were told to remain still during the delay period but were otherwise provided no additional instructions. After the delay period, subjects stepped over the obstacle with their left leg (i.e., trail leg). Subjective reports from subjects confirmed that they were unaware of the obstacle manipulation, which
was also supported by the fact that the trail leg was elevated to accommodate the obstacle as if it were present.

**Delay experiment protocol.** Eight subjects (four males and four females; age = 24.8 ± 2.3 yrs; height = 177.4 ± 8.1 cm; mass = 74.3 ± 18.2 kg) participated in this experiment. For each trial, subjects were instructed to start from the same fixed position in front of an obstacle and upon hearing a “Go” signal, they were to take one step with the left foot and step over the obstacle with their right foot (i.e., lead leg; see Fig. 1B). Subsequently, they were instructed to remain in place while straddling the obstacle for one of three delay periods (20 s, 1 min, or 2 min). Pausing of the movie signaled the end of the delay period and was the cue to the subjects to step over the obstacle with their right foot (i.e., trail leg). The duration of the delay period and the height of the obstacle were assigned randomly for each trial. There were 25 trials for each delay period (10 at the high-obstacle height, 10 at the low-obstacle height, and 5 at the medium-obstacle height) for a total of 75 trials. We reduced the number of medium obstacle-height trials to decrease the amount of time required for data collection, as the protocol required at least 3 h to perform.

**Passive experiment protocol.** Eight subjects (five males and three females; age = 22.1 ± 3.3 yrs; height = 174.1 ± 6.9 cm; mass = 66.1 ± 5.7 kg), not associated with the delay experiment, participated in this experiment. There were three conditions, presented in blocks of 30 trials, with obstacle height randomized within each condition. The first condition [no-vision passive (NV passive)] was designed to eliminate both visual and lead leg efference copy signals. The nature of the passive manipulation would also alter muscle spindle (due to changes in ery coactivation) and GTO output, although joint receptor output would remain intact. Specifically, subjects were blindfolded, and their right leg was placed in a rig (two straps, one above the knee

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Fig. 1. Experimental set-up. A: 3 obstacles of different heights (low = 19 cm; medium = 28 cm; high = 36 cm) used in all 3 experiments. B: overhead view of the sequence of foot placements taken by subjects to step over the obstacle (denoted by solid black rectangle). Depending on the experiment, the delay between foot placement 2 (lead leg step over the obstacle) and foot placement 3 (trail leg step over the obstacle) varied between 20 s and 2 min. Subjects watched movies on a monitor in front (see text for details). C: set-up for the passive limb manipulations in the passive experiment. Two experimenters used ropes and pulleys attached to the lead leg of the subject (at ankle and knee level) to passively move it over the obstacle. During the passive movement, subjects held onto a handrail positioned on the opposite side of the body (not shown) to facilitate relaxing their lead leg muscles. Subjects actively moved their trail leg over the obstacle following a 30-s delay period. D: example trials from a single subject illustrating the vertical lead leg toe trajectory during an active (control) condition (solid black line) and a passive condition (dashed gray line) for stepping over a high obstacle. Data are aligned to toe-off (time zero).
and one around the ankle) so that the leg could be moved passively with a system of ropes and pulleys (see Fig. 1C). At the beginning of each trial, subjects stood in a staggered foot position, with their left leg placed closer to the obstacle, and they were instructed to relax the muscles of their lead leg as much as possible; this was facilitated by transferring a portion of their weight onto their opposite leg. Subsequently, two well-practiced experimenters passively moved the lead leg over the obstacle, controlling the vertical and horizontal components of the movement. An obstacle was present to help the experimenters ensure that the lead leg was scaled, based on the obstacle height for a particular trial. There was a handrail next to subjects, which they held for support and to facilitate relaxing the lead leg muscles. The vertical toe trajectories were similar between the active (control) condition and the passive conditions (see Fig. 1D), although the experimenter manipulation in the passive condition resulted in a delayed time to maximum toe elevation. Subjects straddled the obstacle for a delay period of 30 s. A verbal instruction was used to cue subjects to actively move their trail leg over the obstacle. This condition was always presented first, and subjects were not shown the obstacles prior to being blindfolded. This was done to prevent subjects from becoming familiar with the obstacle heights, thus eliminating any visual memory of the obstacles from previous conditions.

The order of presentation of the second and third conditions was counterbalanced across subjects. The second condition (passive) consisted of the same passive leg movement using the rope and pulley system, except that vision was provided. In this condition, vision was available, but lead leg efference copy was absent, and proprioceptive output (i.e., muscle spindles and GTOs) was altered. In the third condition (control), subjects actively moved their lead leg over the obstacles and had all three sources of input available (i.e., vision, lead leg proprioception, and lead leg efference copy).

**Added mass experiment protocol.** In this experiment, we added mass to the ankle of the lead leg to alter nonvisual sensorimotor signals. Specifically, an efference copy signal and GTO output related to the lead leg would be modified with the added mass. However, joint receptor and muscle spindle feedback would be unaltered, provided similar limb trajectories were adopted. As a result of this manipulation, inertial properties of the lead leg and metabolic cost associated with stepping over the obstacle were also modified (Browning et al. 2007; Noble and Prentice 2006). Eight new subjects (two males and six females; age = 22.3 ± 3.5 yr; height = 169.0 ± 12.2 cm; mass = 62.2 ± 12.4 kg) participated in this experiment, which comprised 60 trials with a delay period of 30 s. Subjects were given the same instructions as for the delay experiment, except that for one-half of the trials, a mass (ankle weights, 4 kg) was strapped to their lead leg, but not to their trail leg. The added mass and control trials were alternated in sets of three, with obstacle height randomized.

**Data collection and analysis.** For all experiments, data regarding limb trajectories over obstacles were collected using an Optotrak Certus motion analysis system (Northern Digital, Waterloo, Ontario, Canada). Infrared-emitting diodes (IREDs) were placed bilaterally on the middle of the subjects’ shoes over the toes, on the left lateral malleolus, and on the right medial malleolus. All IREDs were oriented in the sagittal plane facing leftward and their locations recorded by a camera positioned perpendicularly to the subjects’ plane of progression. Position data were sampled at 100 Hz and stored on a computer. Videos of each trial for every subject were recorded with a Panasonic high-definition camcorder (model #HDC-SD60) and later transferred to a computer. All data were processed using custom-written LabView (National Instruments, Austin, TX) programs and then prepared for statistical analysis.

We determined maximum toe elevation and toe clearance over the obstacle for the lead and trail legs, as well as the toe elevation and clearance variability. Maximum toe elevation was defined as the maximum vertical position of each leg’s toe marker during the stepping trajectory over the obstacle. Toe clearance was defined as the vertical distance between the toe marker and the height of the obstacle when the toe marker of each foot crossed the leading edge of the obstacle. For the trail leg toe clearance measure, this value is theoretical, as the obstacle was turned over and thus was not actually in a position to need clearing.

In the passive and added mass experiments, an MA300 electromyogram (EMG) system (Motion Lab Systems, Baton Rouge, LA) was used to record leg muscle activity at 2,000 Hz from surface electrodes placed on the skin. In the passive experiment, muscles were recorded from the lead leg only and bilaterally for the added mass experiment. The muscles recorded included the tibialis anterior (TA) and biceps femoris (BF). These muscles (responsible for flexing at the ankle and knee joint, respectively) were used because they are known to be important muscles for stepping over an obstacle (Carrière and Beuter 1990; Patla et al. 1991; Patla and Rietdyk 1993). EMG data were collected and synchronized via the Optotrak data acquisition unit (ODAU II) and system software.

EMG data were full-wave rectified and low-pass filtered (zero lag, Butterworth algorithm) at 50 Hz. For both experiments, we calculated the area under the muscle activity profiles (integration using the trapezoidal method) from 200 ms before toe-off until maximum toe elevation for each muscle. This interval was determined, via visual inspection of individual subjects, to be the most appropriate period to capture muscle activity causing leg flexion.

For the added mass experiment, the muscle activity was used to determine the effect of the added mass. For the passive experiment, muscle activity was used as an indication of whether our passive limb manipulation successfully eliminated active muscle contraction (and hence, an efference copy signal). On a trial-by-trial basis for each subject, the experimenters (and a person not part of the study) visually inspected the BF and TA muscle activity profiles to ensure no activity. Figure 2 shows BF and TA muscle activity of a typical high-obstacle trial for the two passive conditions and the active (control) condition for a representative subject. If muscle activity were not obviously absent from visual inspection, the integrated EMG activity of the passive condition trial was compared with the mean ± 1 SD of the integrated EMG activity of the control condition for the appropriate muscle and obstacle-height condition. If the integrated EMG activity of the passive condition trial exceeded this threshold, then the trial was removed from the kinematic analysis.

Results of the EMG data demonstrated that the passive conditions successfully eliminated active muscle activity. Only 9% of trials was removed because of excessive BF/TA activity, which was spread across the two passive conditions and different obstacle heights. Six of the eight subjects had two or fewer trials removed (accounting for 1% of trials).

**Statistical analysis.** For each experiment, we performed repeated two-way ANOVAs to compare mean trail leg maximum toe elevation and mean trail leg toe clearance between obstacle heights and conditions. The fixed factors were obstacle height and condition. The random factors in the model were subject, subject by condition, and subject by obstacle height. Log linear models were used to compare the variances (intrasubject variability) between the conditions and obstacle heights. If the fixed effect factors were significant, post hoc tests using Tukey’s method were used to compare mean response values between the factor levels. In addition, we performed Pearson correlations between lead and trail leg toe measures. For the added mass experiment, we also performed similar ANOVAs for the lead and trail leg EMG data after it was log transformed to ensure normality. All statistical analyses were carried out using JMP 8.2 with an α level of 0.05.

**RESULTS**

**Delay experiment.** For this experiment, we wanted to determine whether human subjects could retain the physical characteristics of an obstacle in working memory, for a variable
delay period, and use this information to accurately scale their trail leg trajectory over that obstacle. This scaling for obstacle height is illustrated in Fig. 3. In Fig. 3A, toe elevation and clearance of the trail leg are plotted against the lead leg for a representative subject. Trail leg toe elevation depended on the height of the obstacle. Furthermore, trail leg toe elevation was comparable across the three delay periods for each obstacle height. For example, note the similarity in trail leg toe elevation among the 20-s delay, 1-min delay, and 2-min delay for the low-obstacle condition. A discernable pattern for the trail leg trajectory over that obstacle. This scaling for obstacle height is important in that it allows us to perform our manipulations in the subsequent experiments without the confound of a decay in obstacle memory.

**Passive experiment.** This experiment was designed to study the relative influence of sensorimotor signals in forming an obstacle representation for guiding trail leg trajectory over an obstacle. To test the roles of these sources, we had subjects step over obstacles of different heights. In the control condition, subjects actively stepped over the obstacle with the lead leg. In the other two conditions, the subjects’ lead leg was passively brought over the obstacle, to eliminate an efference copy signal from being generated, either with vision (passive) or without vision (NV passive) available. This passive manipulation would also have an effect on proprioceptive feedback, as described above. The passive condition was highly effective in reducing or completely removing muscle activity in the relevant muscles of the lead leg, as demonstrated in Fig. 2.

Figure 4A illustrates data from a representative subject. The most striking observation from this figure is the toe elevation and clearance data in the NV passive condition. In this condition, the subject was unable to scale the trail leg toe elevation or clearance to lead limb values or obstacle height, and the subject’s toe elevation/clearance was more variable than in the other conditions. The lack of scaling resulted in unsuccessful clearing of the obstacle, as reflected by the negative trail leg toe clearance values. However, when vision was available during the passive manipulation of the lead leg (passive condition), trail leg toe elevation appeared to scale according to obstacle height, similar to the control condition.

Mean and variability of trail leg toe elevation and clearance averaged across all subjects and based on obstacle height for the three conditions (control, NV passive, and passive) are shown in Fig. 4, B and C, respectively. As evident from Fig. 4C, toe elevation variability was increased in the NV passive condition compared with the other conditions (main effect of condition: F2,56 = 12.64, P < 0.0009). In addition, our analysis revealed an interaction between obstacle height and condition (F4,227 = 4.66, P = 0.006) for mean trail leg toe elevation. Post hoc tests demonstrated that trail leg toe elevation was signifi-
cantly lower in the NV passive condition compared with the control condition for the low-obstacle height (see Fig. 4B). Furthermore, we found a main effect of obstacle height, such that trail leg toe elevation significantly increased with increasing obstacle height in a similar manner as found in the delay experiment ($F_{2,14} = 39.89, P < 0.0001$).

As evident from Fig. 4C, variability of trail leg toe clearance also demonstrated a main effect ($F_{2,56} = 14.45, P = 0.0005$), such that the variability was highest with the NV passive condition. There was also an interaction between obstacle height and condition ($F_{2,56} = 7.90, P = 0.0003$) for trail leg toe clearance; post hoc tests indicated that the toe clearance was significantly lower in the NV passive condition compared with the control and passive conditions for the medium-obstacle height only.

Since the NV passive condition was always performed first (to eliminate visual memory of the obstacle from previous conditions), it is possible that the lack of differences between the passive and control conditions was due to the fact that subjects had learned from the novel (passive) task. As such, we performed a repeated two-way ANOVA to compare trials at the beginning vs. the end of the NV passive condition for trail leg toe elevation and clearance. Subject was a random factor, and fixed factors were obstacle height (low = diamonds; medium = triangles; low = squares) and delay period (20 s = gray; 1 min = black; 2 min = white). $B$: group mean trail leg toe elevation and clearance across the 3 obstacle heights and delay periods (20 s = gray bars; 1 min = black bars; 2 min = white bars). Error bars represent SD. Asterisks indicate significant main effect of obstacle height ($P < 0.05$). There was no effect of delay period on trail leg toe measures.

Taken together, the results of the mean and variability of trail leg toe elevation and clearance measures support our observations (and subjective reports from subjects) that the NV passive condition was the most challenging.

**Added mass experiment.** To further probe the contribution of proprioceptive and efference copy signals, we added mass at the level of the ankle to the lead leg in this experiment. The average EMG activity in a representative subject for the added mass and control conditions for TA and BF (responsible for ankle and knee flexion, respectively) of the lead and trail legs is shown in Fig. 5. As expected, muscle activity of the lead leg was increased in both muscles for the added mass condition in the single-subject example (Fig. 5, A and B) and supported by the group means shown in Fig. 5, E and F (main effect of condition: TA, $F_{1,7} = 214.30, P < 0.0001$; BF, $F_{1,7} = 42.50, P = 0.003$). In addition, muscle activity of lead leg increased with increasing obstacle height in both muscles (main effect of obstacle height: TA, $F_{2,14} = 11.40, P = 0.001$; BF, $F_{2,14} = 43.75, P = 0.0001$). There was no condition by obstacle-height interaction (TA, $F_{2,425} = 0.06, P = 0.945$; BF, $F_{2,425} = 0.96, P = 0.385$).

For the trail leg muscle activity, there were no significant differences between the added mass and control conditions for either muscle in the single subject (Fig. 5, C and D), which was also supported by the group means shown in Fig. 5, E and F (no main effect of condition: TA, $F_{1,7} = 0.18, P = 0.685$; BF, $F_{1,7} = 0.10, P = 0.757$). However, there was a main effect of obstacle height (TA: $F_{2,14} = 8.87, P = 0.003$; BF: $F_{2,14} = 13.58, P = 0.0005$), such that activity was larger for the high obstacle compared with the low obstacle for the TA and was larger for the high obstacle compared with both the medium and low obstacle for the BF.
Figure 6 illustrates the toe elevation and clearance measures of a representative subject and the group means. The individual subject successfully scaled toe elevation, according to obstacle height, as seen in previous experiments. However, there was no obvious effect of an added mass to the lead leg on trail leg toe elevation.

Group means showing trail leg toe elevation and clearance based on obstacle height for the two conditions (control and added mass) are illustrated in Fig. 6B. Trail leg toe elevation measures showed a main effect of obstacle height ($F_{2,14} = 25.99, P = 0.0001$), with post hoc tests showing differences between each obstacle height. More importantly, our analysis showed no main effect of condition ($F_{1,7} = 2.16, P = 0.182$) on trail leg toe elevation, despite a main effect of condition for the lead leg toe elevation ($F_{1,7} = 15.94, P = 0.005$), such that elevation was higher with added mass. These results indicate that adding mass to the lead leg didn’t influence trail leg toe elevation over the obstacles.

Trail leg toe clearance measures followed a similar trend (main effect of obstacle height: $F_{2,14} = 50.15, P < 0.0001$; no main effect of condition: $F_{1,7} = 0.06, P = 0.814$). There was also no main effect of condition on the lead leg toe clearance ($F_{1,7} = 1.33, P = 0.286$). In addition, we found no interaction between obstacle height and condition ($F_{2,13} = 1.17, P = 0.357$), and the variability of trail leg toe elevation and clearance measures was not significantly different between conditions ($P > 0.05$).

**DISCUSSION**

In these series of experiments, we first sought to determine whether human subjects could retain the properties of an obstacle (e.g., height) for extended periods of time while straddling it to step over it with the trailing leg. Subsequently, we examined the contribution of sensorimotor signals, including stored visual input of the obstacle, proprioceptive feedback from the lead leg, and an efference copy signal from the lead leg in forming an obstacle representation that could be subsequently used to guide the trajectory of the trail leg over obstacles of varying heights. Our results suggest that humans are capable of retaining a neural representation of obstacle properties for at least 2 min. In addition, a stored visual representation of the obstacle is sufficient in facilitating the trail leg in stepping over the obstacle. Manipulation of propri-
oceptive feedback and efference copy signals did not influence trail leg trajectory. Maintaining a neural representation of obstacle properties to scale trail leg trajectory. The ability to retain environmental details in memory is an essential feature of locomotion. For instance, visual information from the ground is not readily available when walking in the dark in a familiar room or when holding an object in front while walking. Previous research has shown that humans and cats can step over or around an obstacle or onto targets with only intermittent visual sampling of the environment (Hollands and Marple-Horvat 1996; Patla et al. 1996a; Wilkinson and Sherk 2005), suggesting that pertinent visual information can be stored for short durations. In humans, the trailing leg step is normally initiated almost immediately after the lead leg has crossed over an obstacle. This implies that the information regarding obstacle properties in memory needs only to be maintained for a very short period of time after vision of the obstacle is no longer available to guide the trail leg. Here, we demonstrated that this neural representation could be formed and retained while straddling an obstacle, even after a delay of up to 120 s before the trail leg stepped over it. The fact that trail leg toe elevation was scaled by 10.220.32.247 on October 25, 2016 http://jn.physiology.org/ Downloaded from

Fig. 5. Muscle activity associated with stepping over obstacles with added mass on the lead leg in the added mass experiment. Ensemble averaged lead (A) and trail (C) leg BF and lead (B) and trail (D) leg TA muscle activity from a representative subject for control (solid, black line) and added mass (dashed, gray line) conditions. Only the high-obstacle condition is shown. Time zero represents toe-off for stepping over the obstacle. Note the larger muscle activity in the added mass condition for the lead leg muscles. E and F: group mean ± SD integrated BF and TA muscle activity for the added mass (white bars) and control (black bars) conditions across the 3 obstacle heights. The muscle activity was integrated from 200 ms before toe-off until maximum toe elevation for each muscle. EMG, electromyogram. Asterisks indicate significantly greater activity during the added mass condition compared with the control condition in the lead leg only (P < 0.05). Activity also increased with increased obstacle height (P < 0.05; significance not shown).
to the different obstacle heights, despite the delays imposed in these experiments, indicates that the stable neural representation was not simply a default strategy to step high. Rather, it contained relevant information about the obstacle height and location with respect to the individual. Although we did not perform a zero-delay condition in our experiment, previous research has shown that trail leg toe elevation is scaled to obstacle height when subjects are not paused and forced to straddle the obstacle (Mohagheghi et al. 2004; Patla et al. 1996b). Taken together with our results, it is likely that a zero-delay condition for our experiment would show a similar trail leg toe elevation scaling.

Animals performing similar tasks also show memory for an obstacle height for 2 min or longer. In fact, obstacle representation could be retained for up to at least 10 min in both cats and horses (McVea and Pearson 2006; Whishaw et al. 2009). Regardless, the delays used in the present study are of significantly longer duration than typically used in other memory-related tasks, including grasping objects (Hu et al. 1999) and visual psychophysical tests (Pasternak and Greenlee 2005). As suggested by McVea and Pearson (2006) for cats, this obstacle-avoidance paradigm may prove useful for research on memory in humans.

Sensorimotor signals contributing to an obstacle representation for guiding trail leg trajectory. The passive manipulation in our experiment served to eliminate an efference copy signal related to the lead leg and alter both muscle spindle (due to changes in αγ coactivation) and GTO feedback compared with an active step over an obstacle. Given that the limb trajectories were similar between the passive and control conditions (see Fig. 1), joint receptor feedback was relatively preserved. Our results showed that individual subjects in the NV passive condition were unable to scale trail leg toe elevation with respect to obstacle height, which would have resulted in contact with the obstacles had they been left in their original position. There was also increased variability in trail leg toe elevation and clearance measures in this condition. When vision was available during the passive manipulation (passive condition), trail leg toe elevation and clearances were similar to the control condition. Taken together, the results of the two passive conditions imply that visual information obtained prior to and during lead leg crossing is sufficient to form a neural representation of the obstacle and to allow subjects to properly scale trail leg trajectory. Furthermore, we found no effect on trail leg toe elevation and clearance despite modified GTO feedback with added mass attached to the lead leg ankle and the known changes in joint kinetics associated with this scenario (Noble and Prentice 2006). One limitation of using a fixed mass around the ankle is that it would require different effort for each subject, given inevitable differences in body mass and muscle strength. This could increase intersubject variability and potentially mask results. However, the within-subject nature of our statistical analysis should have addressed this concern.

The fact that manipulations of lead leg feedback had no effect on trail leg toe measures agrees with our finding of weak and variable correlations between these limbs and previous research on obstacle avoidance in humans (Mohagheghi et al. 2004; Patla et al. 1996b; Rhea and Rietdyk 2011). This is not unexpected, given the different biomechanical configuration associated with lead vs. trail leg obstacle-crossing phases. Although it is still possible that nonvisual sensorimotor signals related to the lead leg may reinforce an estimated visual height of the obstacle, our results do not appear to support this idea.

In contrast, McVea and Pearson (2007b) have argued that in cats, the obstacle memory is formed based on feedback and/or an efference copy signal from the passage of the forelimbs over the obstacle and that visual information regarding the obstacle details is not necessary. Preventing cats from stepping over an initially visible obstacle with the forelimbs before stepping...
with the hindlimbs demonstrated substantially lower hindlimb step heights compared with when the cats were stopped straddling the obstacle after stepping over with the forelimbs. Furthermore, when the forelimbs of cats were tripped with a rod that was not visible, they were still able to scale the hindlimbs appropriately to step over it. It is possible that an efference copy signal could provide adequate information in the absence of vision in humans as well. However, we did not perform a NV active condition in the passive experiment to show whether it would be similar to the control or passive conditions. Without vision of the obstacle though, it would not be possible to perform the task unless obstacle height was signaled in a different manner, such as through auditory cues (van Hedel et al. 2002). This would require considerable training and the assumption that subjects properly perceive the height, based on the cue, but would still not necessarily tease out an efference copy. The discrepancies between research in cats and humans may stem from their quadrupedal vs. bipedal posture, respectively, when walking and stepping over obstacles.

Extrapolating the present results to walking must be done with caution, since straddling an obstacle for a period of time is not the same as when one steps over an obstacle while walking continuously. For example, there is no approach phase to derive obstacle characteristics from optic flow during our stepping paradigm, and speed is likely slower. Given that the limb trajectories are similar between stepping over an obstacle after straddling it for a period of time and when walking and stepping over an obstacle [and neural discharge in cats is identical in both cases (Lajoie et al. 2010), as described below], it is likely that our results would also apply to the more natural form of obstacle negotiation during walking.

Possible brain regions responsible for storing obstacle characteristics. Humans can easily scale trail limb trajectory over obstacles in their path, even though direct vision of the object is not available. There are several different brain regions that may be involved in storing the neural representation of the obstacle in working memory and relating this information to the state of the body. These regions include the posterior parahippocampal and retrosplenial cortices, due to their known roles in human spatial memory and navigation (Epstein 2008; Kravitz et al. 2011), and the posterior parietal cortex (PPC), due to its role in visual processing and sensorimotor integration (Marigold et al. 2011). Insight into the role of the PPC in storing this information stems from five findings reported in studies on obstacle negotiation in cats. First, McVea et al. (2009) demonstrated that lesions to area 5 of the PPC impaired the ability of cats to maintain the height of an obstacle in working memory. Indeed, the maximum step height for the hindlimbs was greatly reduced over longer delay periods (10–40 s), during which the animal straddled an obstacle between the fore- and hindlimbs. Second, single-cell recordings in area 5 demonstrated populations of neurons that increased their discharge and maintained it for as long as an obstacle was straddled under the body when the cat was in a static position (Lajoie et al. 2010). Third, this increased and prolonged discharge was also present when the cat stepped over moving obstacles while walking (Lajoie et al. 2010). However, this discharge does not appear to be simply related to the visual properties of the obstacle (e.g., velocity, size). The discharge was prolonged when the cats took an extra step with their hindlimb before stepping over the moving obstacle (a double-step strategy) (Lajoie and Drew 2007), suggesting that the representation of the obstacle was integrated with an estimate of the position of the cat’s limbs/body. Fourth, lesions to area 5 of the PPC induced deficits in the ability to correctly position the paws in front of moving obstacles, which resulted in obstacle contact with the fore- or hindlimbs (Lajoie and Drew 2007). Fifth, Marigold and Drew (2011) recently reported that cats are able to step over an obstacle following brief interruptions in visual input. More importantly, they found that a large proportion of neurons in area 5, which discharge in advance of stepping over a moving obstacle, remained active during the visual interruption.

Conclusions. Our results suggest that visual input plays a major role in forming an obstacle representation, which can be retained for extended periods of time and used to scale the trail leg based on obstacle height. Future work should address: 1) whether the obstacle representation is formed subconsciously (which can be assessed using a dual-task paradigm), 2) whether manipulating muscle spindle input through muscle/tendon vibration influences the results, 3) whether multiple obstacles can be retained in memory for extended periods of time, 4) isolating the role of an efference copy signal, and 5) which brain regions are responsible for storing the obstacle representation in humans. Additionally, the use of this delay obstacle-avoidance paradigm for research on spatial working memory should be explored.

ACKNOWLEDGMENTS

The authors thank Brent Flodin, Erin Jang, Casey Ruff, and Jordan Sernaglia for their help with data collection, Ian Bercovitz for consulting on the statistical analysis, and Dr. Trevor Drew for comments on an earlier version of the manuscript.

GRANTS

This study was supported by a grant from the Natural Science and Engineering Research Council of Canada (D. S. Marigold).

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS


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