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Two-stage muscle activity responses in decisions about leg movement adjustments during trip recovery

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Potocanac Z, Pijnappels M, Verschueren S, van Dieën J, Duysens J. Two-stage muscle activity responses in decisions about leg movement adjustments during trip recovery. *J Neurophysiol* 115: 143–156, 2016. First published November 11, 2015; doi:10.1152/jn.00263.2015.—Studies on neural decision making mostly investigated fast corrective adjustments of arm movements. However, fast leg movement corrections deserve attention as well, since they are often required to avoid falling after balance perturbations. The present study aimed at elucidating the mechanisms behind fast corrections of tripping responses by analyzing the concomitant leg muscle activity changes. This was investigated in seven young adults who were tripped in between normal walking trials and took a recovery step by elevating the tripped leg over the obstacle. In some trials, a forbidden landing zone (FZ) was presented behind the obstacle, at the subjects' preferred foot landing position, forcing a step correction. Muscle activity of the tripped leg gastrocnemius medialis (iGM), tibialis anterior (iTA), rectus femoris (iRF), and biceps femoris (iBF) muscles was compared between normal trips presented before any FZ appearance, trips with a FZ, and normal trips presented in between trips with a FZ ("catch" trials). When faced with a real or expected (catch trials) FZ, subjects shortened their recovery steps. The underlying changes in muscle activity consisted of two stages. The first stage involved reduced iGM activity, occurring at a latency shorter than voluntary reaction, followed by reduced iTA and increased iBF and iGM activities occurring at longer latencies. The fast response was not related to step shortening, but longer latency responses clearly were functional. We suggest that the initial response possibly acts as a "pause," allowing the nervous system to integrate the necessary information and prepare the subsequent, functional movement adjustment.

stumbling; balance perturbations; obstacle avoidance; muscle activity; online corrections

IN THE STUDY OF NEURAL DECISION making, one of the prevailing issues is how the brain manages the task of making very fast corrective movements. In this domain, mainly arm movements toward a target have been studied (Desmurget et al. 1999; Gosselin-Kessiby et al. 2009; Prablanc and Martin 1992; Shadmehr et al. 2010). Typically a perturbation was introduced, such as a target shift, requiring the subject to make a correction during an ongoing movement (Prablanc and Martin 1992; Oostwoud Wijdenes et al. 2011). These corrective responses

are very fast and occur below the latency for initiation of voluntary movements (Goodale et al. 1986; Pélisson et al. 1986; Soechting and Lacquaniti 1983). To explain these fast reactions, some authors proposed a fast pathway over the parietal cortex (Pisella et al. 2000; Whitwell et al. 2014), while others suggested a subcortical pathway (Day and Lyon 2000).

Online correction of leg movements has received less attention, possibly because of more complex control of these movements, which are controlled by a combination of spinal and cortical control (Duysens and Van de Crommert 1998; Hoogkamer et al. 2014; Van de Crommert et al. 1998). Additionally, compared with arm movements, increased gravitational and postural challenges make these experiments more difficult, although not impossible (Reynolds and Day 2005; Rietdyk and Patla 1998). These studies showed that providing balance support improved leg movement adjustments, although adjustments were possible even without any balance support. Only few studies have addressed the issue of leg movement corrections by investigating step initiation from quiet stance, when subjects had to step on a target that shifts, similar to the dual step experiments for the arm (Reynolds and Day 2005; Tseng et al. 2009, 2010). In line with the findings from arm movement research, some of these experiments indicated that movement corrections during step initiation could occur at very short latencies, thereby suggesting that subcortical mechanisms could be involved (Reynolds and Day 2005). In contrast, others reported movement corrections occurring at longer latencies (Tseng et al. 2009, 2010). During gait, making corrections to foot trajectory and landing position is even more relevant and an ecologically important issue. This is not only the case for patients, who often have to counteract their own internally generated perturbations (Bouffard et al. 2014) but also for healthy people, since one often needs to quickly correct an ongoing step to avoid dangerous foot landing areas (e.g., a hole in the pavement) to prevent falls. A number of studies addressed avoidance of suddenly appearing obstacles during gait (Chen et al. 1991, 1994; Hofstad et al. 2009; Marigold et al. 2007; Moraes et al. 2007; Patla et al. 1991; Potocanac et al. 2014b; Weerdesteyn et al. 2004, 2005a, 2005b) and, similar to step initiation, leg movement corrections occurring at short latencies were found in some (Hofstad et al. 2009; Marigold et al. 2007; Weerdesteyn et al. 2004, 2005a), but not all, experiments (Moraes et al. 2007). When present, the fast responses

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support the possibility of a subcortical pathway (Weerddesteyn et al. 2004). Behaviorally, step corrections to avoid obstacles are accomplished in several ways. Most often step lengthening (i.e., stepping over the obstacle) or step shortening (i.e., stepping in front of the obstacle) were reported (Chen et al. 1994; Weerddesteyn et al. 2005b). One could imagine that the avoidance reactions would be “ballistic” in the sense that they would be immutable once triggered. However, this is not the case, since obstacle avoidance strategies can be altered online. In particular, young adults could correct their step trajectory during the process of obstacle avoidance if a cue was presented to change the landing position (Moraes et al. 2007; Patla et al. 1991). This implies that people have the ability to correct these fast leg movements online.

When people are not able to detect the presence of an obstacle or fail in obstacle avoidance, a trip occurs as their swing leg is obstructed by the obstacle. This results in fast reactions to clear the obstacle and regain balance (Eng et al. 1994; Forner-Cordero et al. 2003; Grabiner et al. 1993; Pijnappels et al. 2004, 2005a, 2005b; Schillings et al. 1996, 1999, 2000, 2005). Humans use two types of recovery strategies: they either lower the obstructed foot immediately and step over the obstacle with the other leg (“lowering” strategy), or they elevate the obstructed foot over and place it behind the obstacle (“elevating” strategy) (Eng et al. 1994; Schillings et al. 2000). These behavioral responses are driven by muscle activities showing several activity peaks at various latencies. The origin of the earliest muscle activity related to tripping is unclear, but possible sources are stretch reflexes (Schillings et al. 1999) or startle-related activation (Nieuwenhuijzen et al. 2000). In contrast, the activity occurring at a longer latency is easier to understand in terms of decision making, i.e., the longer latency (>110 ms) muscle activity was related to the behavioral outcome. It determined whether the ongoing perturbed step would be shortened for executing a lowering strategy or lengthened to use the elevating strategy for trip recovery (Pijnappels et al. 2005b; Schillings et al. 2000).

These behavioral responses had the appearance of triggered responses and raise the question whether such responses are still modifiable, e.g., when facing additional environmental constraints. If tripping responses were completely defined from the onset of collision onward, then one would expect to see a fixed response pattern, not allowing additional changes. A hint that this was not the case and that modifications are indeed still possible was provided by incidental observations of foot trajectory modification during tripping recovery (Forner-Cordero et al. 2003, 2005; Schillings et al. 2000) and confirmed in our recent study investigating the ability to correct leg trajectory during trip recovery (Potocanac et al. 2014a). In the latter study, subjects were tripped in the swing phase, which induced an elevating balance recovery response. At trip onset, a forbidden landing zone (FZ) was projected at their preferred landing position, and, to avoid landing their foot on the FZ, subjects had to correct the trajectory of their balance recovery step. The results showed that all young adults tested were able to modify their responses and successfully land their foot outside the FZ. For this they used strategies of either shortening their recovery steps (84%) or stepping to the side of the FZ (16%) (Potocanac et al. 2014a).

These behavioral observations did not answer the question as to how the decision for leg movement correction was made.

To address this question, in the present study we analyzed activity of leg muscles involved in the correction. For this study, a subset of successful FZ avoidances was selected, during which the most common leg trajectory correction was made (step shortening). By analyzing muscle activity we aimed to address three specific questions. First, we wanted to describe changes in muscle activity driving the observed leg trajectory adjustments. To shorten the normal trip recovery step, we expected additional activation of hip extensors and ankle plantar flexors, leading to an earlier recovery step landing. Second, we wanted to evaluate whether these muscle activity changes consist of functionally different components with respect to the observed step shortening. Namely, in analogy with the simple tripping data (Schillings et al. 2000), we expected early responses seemingly unrelated to the behavioral outcome, along with later responses that are in line with the behavioral changes. If this is indeed the case, it might help to better understand the nature of fast decision making processes when adjusting leg trajectory to avoid inappropriate foot placement under time pressure. Finally, we wanted to address the influence of anticipation on the process of decision making for fast leg movement adjustments by analyzing muscle activity changes on “catch” trials, when no movement adjustment was required. Because our experiment included no penalty for movement adjustments in the absence of an FZ, subjects might anticipate by adapting their forward model (Shadmehr et al. 2010) to shorten trip recovery steps irrespective of FZ appearance. Based on our previous analysis of behavioral data (Potocanac et al. 2014a) we expected anticipation of the FZ to influence the adjustment behavior, and we wanted to investigate whether the underlying mechanisms were similar to those used when adjustments were required.

METHODS

Sixteen young adults (age 25.1 ± 3.2 yr, height 178.4 ± 8.8 cm, weight 73.2 ± 12.9 kg, 6 females) who had no walking problems, normal or corrected to normal vision, and were able to understand the instructions participated in this study. Eight subjects exhibited consistent behavior during the experiment and successfully avoided the FZ in all T-FZ trials by using step shortening, but electromyographic (EMG) data for one of these subjects were unavailable. The EMG data of the remaining seven subjects (age 24.6 ± 3.2 yr, height 180.4 ± 4.9 cm, weight 71.1 ± 10.5 kg, 1 female), who exhibited consistently successful step shortening behavior, were the main focus of our analyses. For comparison, we also analyzed the behavior of other subjects, who failed to avoid the FZ in at least one trial. In this second group, consisting of eight subjects, one of the subjects was excluded from the analysis for using the left leg for recovery, and EMG data were unavailable for two subjects. Hence, EMG data of five subjects (3 using side steps and 2 using step shortening on their successful FZ avoidance trials) were analyzed for comparison. Detailed behavioral data of all subjects were reported previously (Potocanac et al. 2014a). The study was approved by the local ethics committee (no. 2013-7), and all subjects gave their informed consent before participating.

Experimental setup. A detailed description of the methods has been provided in a previous publication (Potocanac et al. 2014a); therefore, only the main features are repeated here, along with the information concerning the EMG analysis. Subjects walked at comfortable self-selected speed over a walkway (2.5 m wide and 12 m long), equipped with a force plate and 14 obstacles (15 cm high) hidden over a length of 1 m (Fig. 1). Based on the subjects’ kinematic parameters during obstacle approach any of these obstacles could be released from the

floor, causing the subject to be tripped (Pijnappels et al. 2001). Different obstacles could cause the trip in different trials, but the trips always occurred at midswing of the right leg and elicited an elevating strategy, meaning that subjects made a recovery step by lifting the obstructed (right) foot over the obstacle (Eng et al. 1994).

Subjects were presented with 10 tripping trials in between a random number (3–15) of normal walking trials to ensure that they regained their normal walking pattern (Pijnappels et al. 2001; Potocanac et al. 2014a) and to prevent them from knowing whether or not they would be tripped in that specific trial. For each subject, we limited the experiment to 10 trips in total to prevent changes in the walking behavior observed following repeated tripping in previous experiments (Pater et al. 2015; Pijnappels et al. 2001, 2006; Rhea and Rietdyk 2011; Wang et al. 2012). The experimenter encouraged the subjects to maintain the walking velocity that was self-selected at the start of the experiment. Subjects wore a safety harness attached to a ceiling-mounted rail, protecting them from falling in case they were not able to regain balance after a trip. The safety ropes provided enough slack for unrestrained motion, and a spring, in series with the ropes, ensured smooth restraint in case of a fall (Pijnappels et al. 2004). None of the subjects fell.

The experiment consisted of two tripping conditions: “normal tripping” trials and tripping with a presentation of a FZ. The FZ was a 30-cm-wide and 50-cm-long rectangle projected on the floor by a generic projector, and its size covered the group variability of the recovery foot landing positions of 10 subjects from previous experiments (Pijnappels et al. 2004). Due to technical limitations the FZ appeared ~50–100 ms before obstacle release and was individually positioned at the subject’s average recovery foot landing position relative to the tripping obstacle during normal tripping. Therefore, the distance between the tripping obstacle and the FZ was kept constant throughout the experiment, irrespective of the obstacle causing the trip. For the seven subjects our analysis focused on (i.e., who successfully used step shortening to avoid the FZ in all trials), the FZ was positioned on average 0.80 m from the tripping obstacle (range

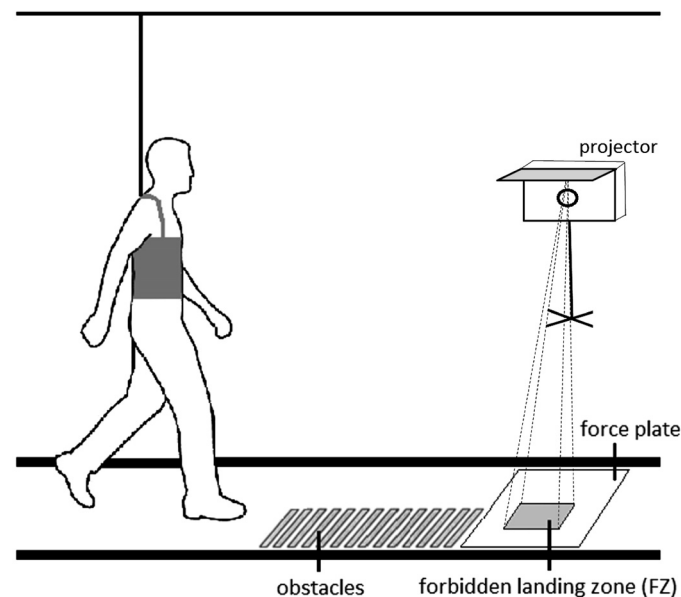


Fig. 1. Experimental setup. Subjects walked on a walkway equipped with a force plate and 14 hidden obstacles. The obstacles could be released and trip the subject at right midswing, causing an elevating recovery strategy. In 5 out of a total of 10 tripping trials, a forbidden landing zone (FZ) was projected on the floor at the subject’s preferred recovery step landing position, relative to the obstacle causing the trip. Subjects were instructed to regain their balance following a trip, but avoid landing their foot in the FZ, if presented. With permission, reprinted from Potocanac et al. (2014a).

0.97–0.70 m). Subjects were instructed to land their recovery foot outside the FZ, if it was presented.

At the start of the experiment, following familiarization with the setup, three normal tripping trials (T trials) were performed, with the subjects instructed to regain balance in any way that came naturally. Kinematic data of the foot were used to calculate the average recovery step landing position relative to the obstacle, and the FZ was centered at the average position of the foot cluster marker at landing for each subject individually. For the following trials, the subjects were instructed to regain balance in case of a trip but to avoid stepping in the FZ if presented. Seven more trips and five trials that included only the FZ without a trip (FZ trials) were performed in a pseudorandom manner, with normal walking trials in between. Five trips included the FZ (T-FZ trials) and two did not, serving as catch trials (TC trials).

Full body kinematic data were collected at a sample rate of 50 samples/s using an Optotrak system (Northern Digital, Waterloo, Ontario, Canada) consisting of a 4×3 camera array. Following anthropometric measurements, 12 clusters of 3 infrared light emitting diodes were attached to the body segments (lower arms, upper arms, lower legs, upper legs, feet, trunk, and pelvis), and a pointer was used to indicate 36 anatomical landmarks. Most importantly, the feet were defined by two anatomical points: tip of the second toe and the calcaneus. This allowed for offline reconstruction of the subject’s body using a three-dimensional full body kinematic model (Kingma et al. 1996). Kinetic data were collected using a custom-made strain gauge force plate of 1×1 m (sample rate of 200 samples/s), embedded in the walkway in the area where the recovery foot landed. EMG data of the ipsilateral (obstructed) leg muscles rectus femoris (iRF), tibialis anterior (iTA), gastrocnemius medialis (iGM), and biceps femoris (iBF) were recorded at a sample rate of 1,000 samples/s using a Porti 17 system (22 bits AD conversion after 20 times amplification, input impedance $>10^{12} \Omega$, CMRR >90 dB for the relevant range of frequencies; TMSi, Enschede, The Netherlands). The skin was prepared, and bipolar surface electrodes were placed in line with the SENIAM guidelines (Hermens et al. 1999).

Data analysis. We selected data from seven subjects who successfully avoided the FZ by step shortening in all T-FZ trials for our main data analyses. For comparison, we also analyzed successful short stepping trials of two subjects who were initially unsuccessful in avoiding the FZ and successful side stepping of another three subjects.

Analysis of kinetic and kinematic data are described in detail (Potocanac et al. 2014a), but, briefly, following the offline reconstruction of body segments, the foot was defined as the virtual line connecting the calcaneus and the tip of the second toe. If this line fell fully outside of the FZ at landing, the avoidance was considered successful. The step was classified as step shortening if the foot landed between the obstacle and the FZ (Chen et al. 1994). Obstacle contact time was determined as the local minimum of foot acceleration in the walking direction. The time of recovery foot landing was identified as the onset of a sudden increase in the vertical ground reaction force, since the force plate was unloaded before the recovery step landing. Toe velocity was calculated by differentiation of toe position. Foot position throughout the recovery step was described by the vertical distance between the toe and the heel and by ankle angle, which was calculated as the angle between the foot (line connecting the toe and the heel) and the shank (line connecting the ankle and the knee).

EMG data were whitened (5th order) (Clancy et al. 2002) to reduce the influence of tissue filtering and movement artefacts, Hilbert transformed, and low-pass filtered (3rd order Savitzky-Golay filter, frame size of 61). EMG data were then aligned to heel strike of the left leg, which served as obstacle and FZ trigger. Average normal walking EMG activity was calculated for each subject (based on 5 normal walking trials) and subtracted from EMG activity of the T, T-FZ, TC, and FZ trials. The residual FZ trials EMG was not included in the analysis but served to verify that the subjects’ EMG signals did not change in response to the visual stimuli alone. This was crucial because the FZ appeared slightly earlier than obstacle contact in T-FZ

trials. Finally, the T, T-FZ, and TC trials were aligned to obstacle contact and normalized by division with the maximal EMG activity during normal walking.

To describe muscle responses following tripping we visually identified the time windows in which first activity bursts occurred (0–90 ms for iRF and 0–200 ms for other muscles) and calculated the timing of peak muscle activity in these time windows for each trial. We used timing of activity peak rather than the onset latency to avoid subjectivity in onset detection.

Statistical differences between different types of trip trials were analyzed using wavelet-based functional ANOVA (wfANOVA) with trip type (T, T-FZ, and TC) and subject as factors. This method allows to show differences in the shape and magnitude of EMG signals with a high temporal resolution and statistical power by transforming the EMG signals into corresponding wavelet coefficients and running the statistical analysis in the wavelet domain (McKay et al. 2013). Following the analysis, significantly different wavelet coefficients were transformed back to the time domain, resulting in signals representing significant contrasts between different trip trials. Level of statistical difference was set to $\alpha = 0.05$. For interpretation, onsets of muscle activity were detected by visual inspection. Responses starting at a latency below 150 ms were considered early involuntary reac-

tions, whereas those starting at longer latencies were considered voluntary (Fig. 2).

All analyses were performed using MATLAB 2011b and 2014b (Mathworks, Natick, MA).

RESULTS

In the results section we present both descriptive data of individual subject performance, group performance data, and the results of wfANOVA statistical analysis. First, we start with a description of the predominant step-shortening behavior, which was the basis for a detailed analysis of muscle activity. Second, we describe the differences in muscle activity between the first trial responses and responses to subsequent trials by presenting trial-by-trial data of a typical subject (Figs. 2 and 3). Third, we report average group responses and illustrate group variability by presenting average responses of individual subjects (Fig. 4) and group average responses (Figs. 5A and 6A). Fourth, statistically significant differences in kinematics and muscle activity between T and T-FZ (Fig. 5B) and T and TC (Fig. 6B) trials are reported. Finally, to assist the

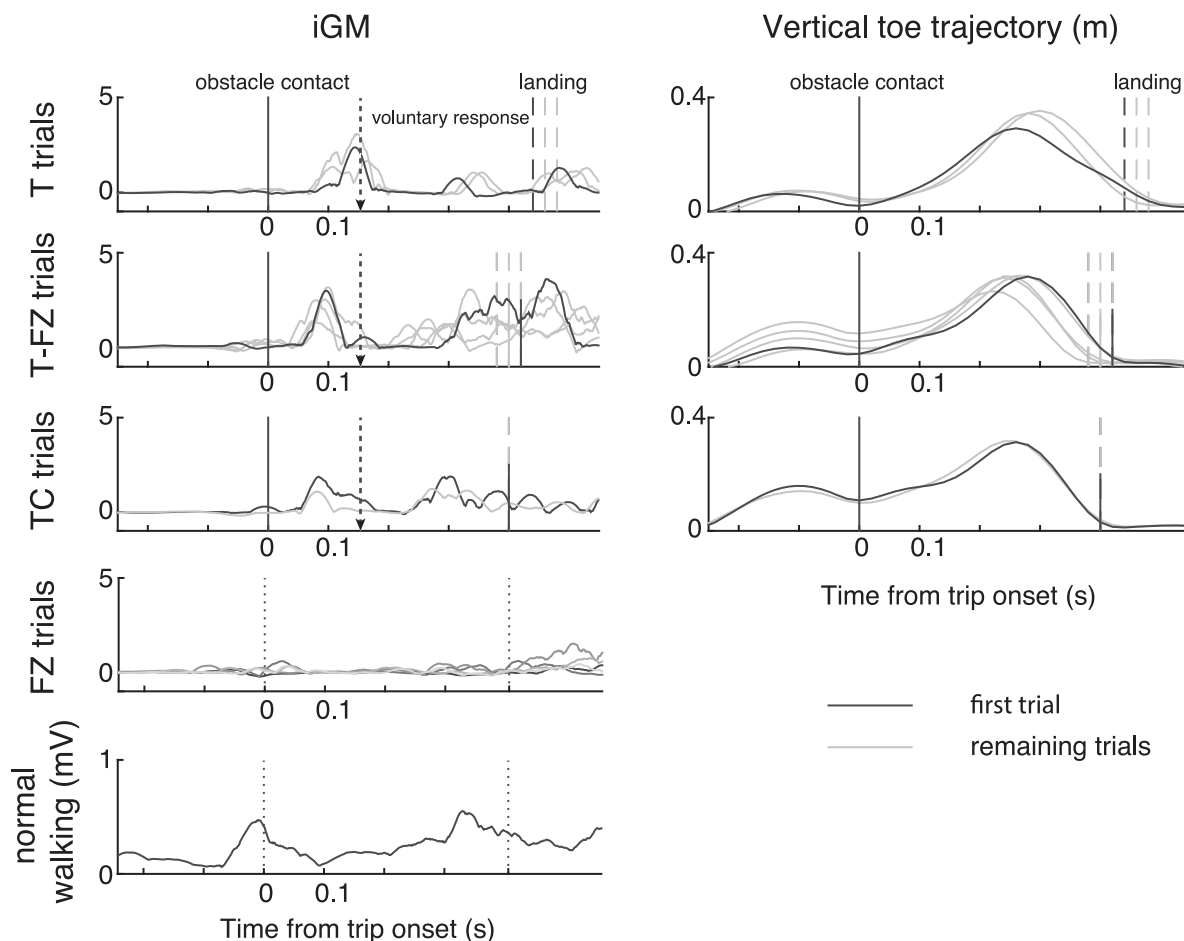


Fig. 2. Individual ipsilateral gastrocnemius medialis (iGM) activity and vertical toe trajectory of responses to tripping (T), trips including the FZ (T-FZ), and catch (TC) trials by a representative subject (*subject no. 11* in Fig. 3 of Potocanac et al. 2014a). Also shown are iGM muscle activity during FZ trials and average normal walking of the same subject. Data of the first trial are shown in black and of subsequent trials in gray. Black vertical line (at *time 0*) indicates obstacle contact, and broken lines indicate recovery step landing, color coded to match the trial order. Note that for some T-FZ and TC trials there is an overlap in the landing time, indicated by a vertical line that is one-half solid (in the color of the first trial landing at this time) and one-half broken (in the color of the second trial landing at this time). Vertical arrows presented in the T, T-FZ, and TC plots indicate latencies of 150 ms. Responses occurring earlier than this are considered early involuntary responses, whereas those occurring at longer latencies are considered voluntary. During the FZ trials and average normal walking no trip occurred, and the dotted vertical lines indicate expected obstacle contact and recovery step landing, based on this subject's average performance during tripping trials. Electromyographic (EMG) data of T, T-FZ, TC, and FZ trials are normalized to average normal walking and thus are unitless (a value of 1 indicates that the amplitude of the response was equal to the maximal EMG activity during normal walking in that muscle).

interpretation of statistically significant differences in muscle activity between T, T-FZ, and TC trials we show detailed foot kinematics data (Fig. 7) and individual muscle activity data of other nondominant stepping behaviors (i.e., subjects initially failing to avoid the FZ and/or using the alternative side stepping behavior; Fig. 8).

Step shortening behavior. On average, the recovery steps lasted 0.48 ± 0.03 s during the T trials and were shortened to 0.41 ± 0.03 s during the T-FZ trials. Subjects landed the center of their foot 0.09 ± 0.04 m from the position where the FZ would be centered during the T trials and 0.51 ± 0.06 m from the center of the FZ during the T-FZ trials. Interestingly, the TC trials, which served as catch trials and during which no FZ was shown, also resulted in altered duration of the recovery step (0.43 ± 0.04 s) and positioning of the foot (0.39 ± 0.12 m). In 9 out of 14 TC trials the FZ would have been avoided successfully, if it had been presented. This indicates that anticipation of a forbidden zone influenced the subjects' performance. Therefore, special attention was given to the first trial responses to ensure these are not fundamentally different from the rest (see below).

First trial responses. Overall, subjects' EMG responses were consistent across trials, as can be seen in Fig. 2 for iGM of a typical subject. However, while fundamentally consistent, with increasing experience (i.e., on later trials) responses started slightly earlier and often decreased in magnitude. This can be seen in Fig. 2 by comparing the first trial response with ensuing responses for T and T-FZ trials. A similar pattern was present in the kinematic data of the T-FZ trials, where one can

see that the response to the first trial was fundamentally consistent with responses to ensuing trials, although slightly delayed. Additionally, responses to T-FZ trips started earlier than responses to T trials. TC trials, during which no FZ was presented, were also different from T trials and exhibited earlier response onsets, similar to T-FZ trials. However, unlike the T-FZ trials, they showed less activation around the time of landing. Figure 2 also illustrates the average normal walking activity on trials without any perturbation and responses during the FZ trials, when no trip occurred, but the FZ was presented. These latter graphs show that there is almost no muscle activity associated with the presentation of the FZ during the time window of interest, i.e., between the average trip onset and recovery step landing of tripping trials.

In the descriptive data of the typical subject, shown in Fig. 2, it can be seen that the iGM responses to the first T-FZ trial did not basically differ from the responses seen in later T-FZ trials. This was further confirmed for the other muscles recorded as well. Figure 3 illustrates the first trial responses and average of remaining responses of all ipsilateral leg muscles in the same typical subject, for T, T-FZ, and TC trials. Comparing the first trial responses with the average responses, it can be seen that the response patterns were similar over trials. However, some muscles appeared to be slightly more active in response to the first T-FZ trial compared with average T-FZ, evident by a prolonged activation of iBF and higher amplitudes of iRF. Furthermore, this figure shows that the TC trials shared characteristics of both T and T-FZ trials. Similarly to the first T-FZ trial, the first TC trial showed an early response of iGM

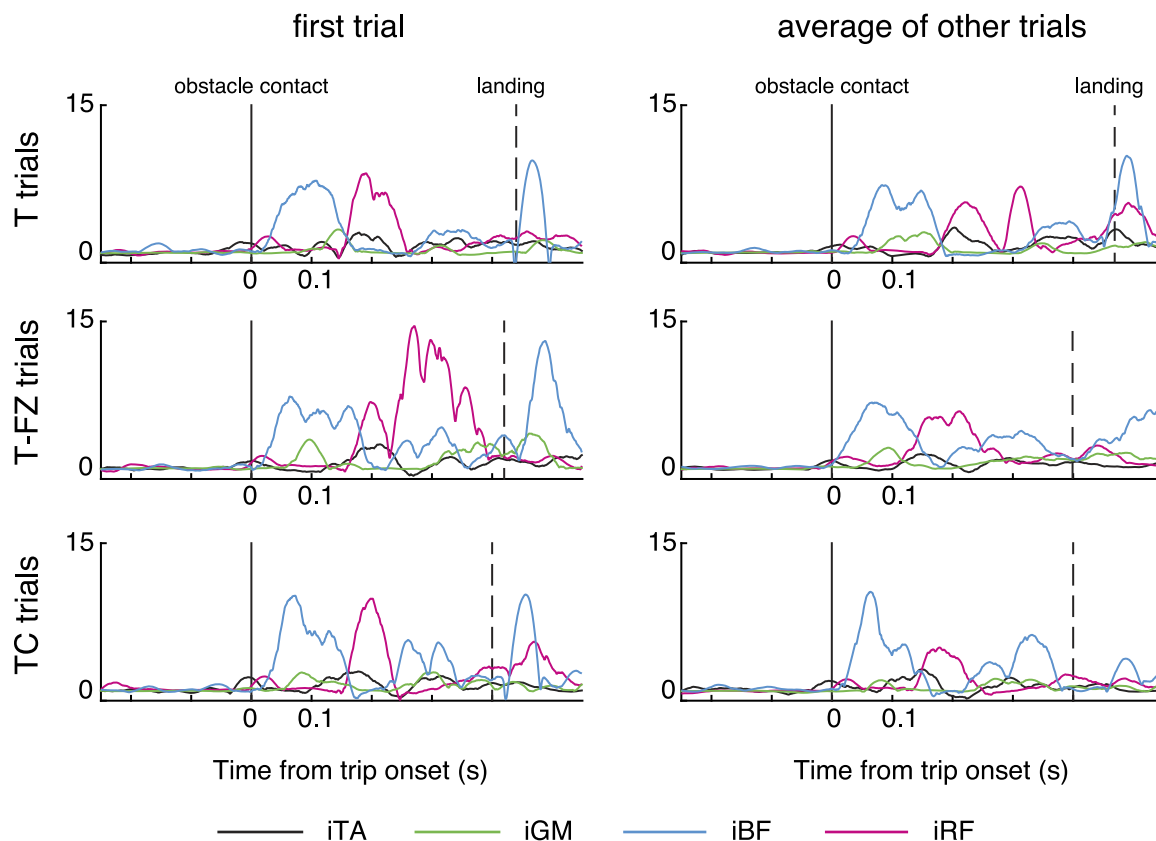


Fig. 3. Responses of ipsilateral muscles to T, T-FZ, and TC trials by a representative subject (*subject no. 11* in Fig. 3 of Potocanac et al. 2014a), for the first trial of the type (*left*) and average of remaining trials (*right*). EMG data are aligned to obstacle contact, which is indicated by a black vertical line at *time 0*. The broken black vertical line indicates recovery step landing. EMG data are normalized to average normal walking and thus are unitless.

coinciding with a reduction in iTA activity, and increased iBF activity before the recovery step landing. On the other hand, the pattern of iRF activity resembled that of T trials. Similar changes can be seen in the average responses: both T-FZ and TC trials showed an early reduction in the iTA followed by earlier activations of iGM and iTA, compared with the T trials.

Average group responses and statistical comparisons of kinematics and muscle activity. As can be seen from descriptive data presented in Fig. 4, pattern of responses was similar across subjects. From the kinematic data it can be seen that subjects landed their foot earlier during T-FZ and TC trials, compared with T trials, and exhibited a consistent pattern of vertical toe position and velocity. In response to tripping, all muscles responded shortly after trip onset, and these responses were strongest in iRF and iBF. The values of the peaks are given rather than the onset latencies to avoid subjectivity in onset detection (mean \pm SD of the first muscle activity peak is given, as calculated from individual trial peaks). During T trials, amplitude peaks occurred first in iRF (42 ± 23 ms), followed by iBF (106 ± 39 ms), iGM (120 ± 45 ms), and iTA (160 ± 49 ms). This order was slightly different during T-FZ and TC trials: activity started with iRF (32 ± 22 and 36 ± 26 ms, respectively), followed by iGM (70 ± 53 and 75 ± 45 ms, respectively), iBF (94 ± 28 and 86 ± 23 ms, respectively), and iTA (132 ± 47 and 124 ± 45 ms, respectively). These responses were consistent across subjects, although there was some variability in the magnitude of the response, especially for iRF. Finally, looking at the FZ trials, in most muscles, on average there was no activity associated with the presentation

of the FZ in the time between average trip onset and recovery step landing, meaning that the activity seen during the T-FZ trials cannot be attributed to the visual stimulus alone. The only exception was some extra iGM activity seen just before expected foot landing. This is probably related to changes in normal walking in response to the FZ, although the FZ was positioned in the expected foot landing area for tripping, which was further away from the foot liftoff position than for normal gait.

Statistically significant changes on T-FZ trials. As can be seen from Fig. 5, the main kinematic difference between T and T-FZ trials was step shortening in the T-FZ trials (to avoid the FZ). As a consequence the T-FZ steps were of shorter duration and had slightly lower peak toe elevation and velocity. Significant difference in vertical toe position at obstacle contact (0.08 m for T-FZ trials and 0.04 m for T trials) disappeared around 200 ms after contact and reversed to a maximum contrast around 400 ms after obstacle contact. At this time the vertical toe position was 0.05 m for T-FZ trials and 0.18 m for T trials, in line with the fact that the average T-FZ landing occurred around 410 ms, whereas recovery steps during the T trials lasted longer and landed around 480 ms. The same pattern was seen for vertical toe velocity; following a significant difference at obstacle contact (-0.1 m/s for T-FZ trials and -0.3 m/s for T trials), the velocities became equal around 80 ms after obstacle contact, reversed around 120 ms, and reached a maximum contrast around 320 ms after obstacle contact (-1.9 m/s for T-FZ trials and -0.8 m/s for T trials). In other words, the subjects started lowering their foot about 20 ms earlier

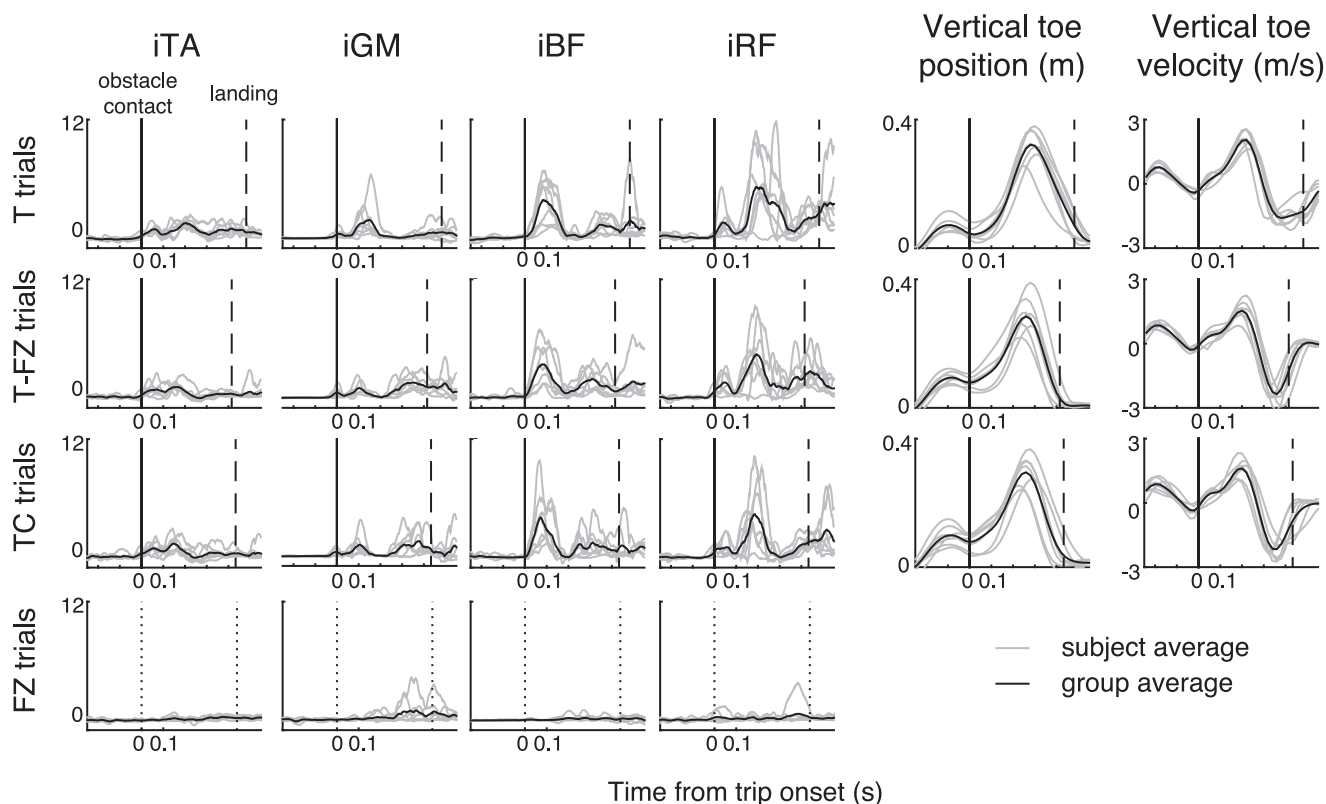


Fig. 4. Responses to T, T-FZ, TC, and FZ trials for the ipsilateral leg. Subjects' average data are shown in gray, and group averages are shown in black. T, T-FZ, and TC signals are aligned to obstacle contact, indicated by a black vertical line at *time 0*. Broken lines indicate average recovery step landing. During the FZ trials no trip occurred, and the broken vertical lines indicate expected obstacle contact and recovery step landing, based on this group average performance during tripping trials. EMG data are normalized to average normal walking and thus are unitless.

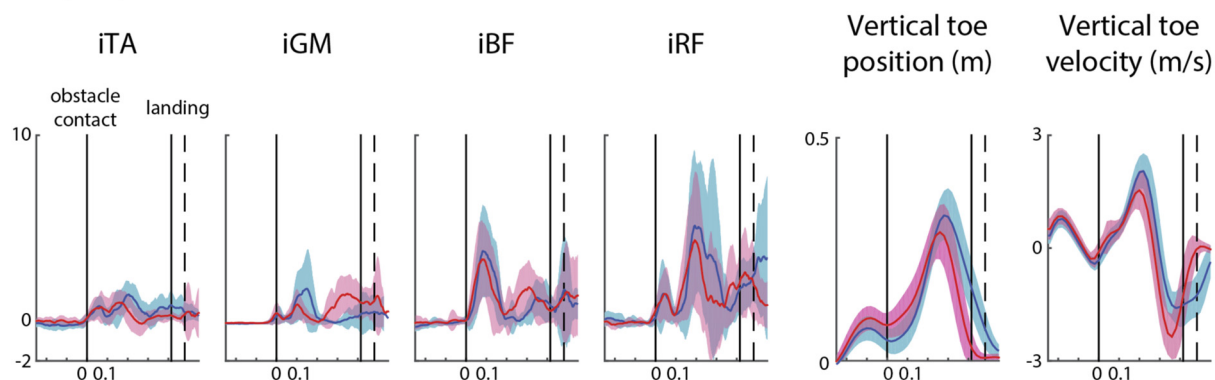
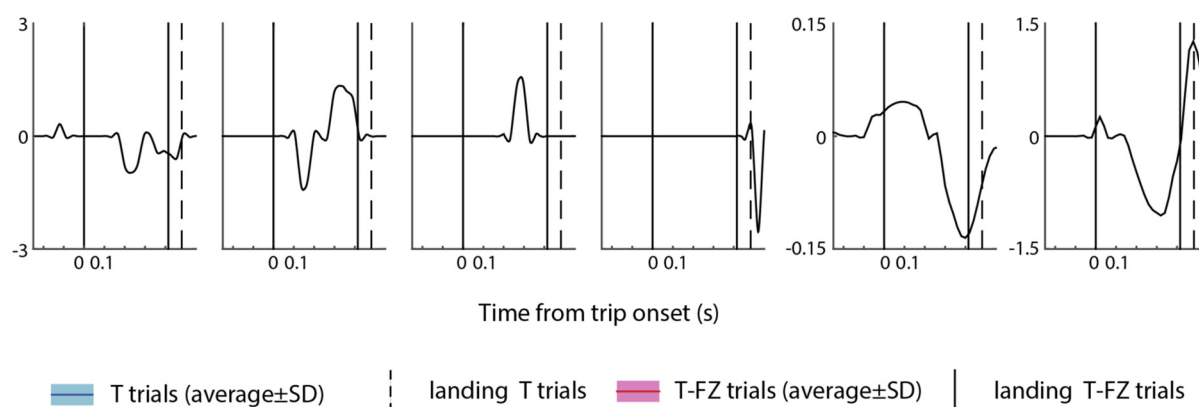
A group mean \pm SD**B** wfANOVA significant contrast T-FZ vs. T trials ($p < 0.05$)

Fig. 5. Group average responses (A) and significant contrasts (B) between normal trips (T, blue) and trips with a FZ (T-FZ, pink), for the ipsilateral leg. Group average data are shown as means \pm SD. All signals are aligned to obstacle contact, indicated by a black vertical line at time 0. Other vertical lines indicate recovery step landing for T (broken line) and T-FZ (solid line) trials. EMG data are normalized to average normal walking and thus are unitless. Contrasts are expressed in the same way, since they represent the difference in normalized EMG data between T-FZ and T trials.

during the T-FZ trials (vertical position of the toe started decreasing around 280 ms during the T trials and 260 ms during the T-FZ trials), which was preceded by a slowing down of the vertical toe velocity occurring about 60 ms earlier (T trials 220 ms, T-FZ trials 200 ms). In combination with a difference in peak toe position (T trials 0.32 m, T-FZ trials 0.28 m) this led to landing about 70 ms earlier during the T-FZ trials. In terms of muscle activity, earlier lowering of the foot was expected to require additional activity in extensors (iGM as plantar flexor and iBF as hip extensor) and a reduction of activity in flexors (such as iTA). Such activity changes indeed occurred, but not in the early phase of the recovery reaction. Changes in iGM activity started on average 107 ms following trip onset with reduced (rather than increased) activity during T-FZ trials. This reduction reached its maximum around 146 ms after trip onset (T-FZ trials 0.42 and T trials 1.83) and was followed by a period of increased activity starting at 267 ms and reaching a maximum at 323 ms (T-FZ trials 1.50 and T trials 0.14 times normal walking activity) after trip onset. The second muscle to show a change in activity was iTA, which activity was reduced during the T-FZ trials. In iTA, the earliest change was found at 171 ms after trip onset. This initial reduction in activity reached its maximum 225 ms following trip onset (T-FZ trials 0.34 and T trials 1.37 times normal walking) and was followed by another period of reduction

starting at 329 ms and reaching its peak 450 ms after trip onset (T-FZ trials 0.26 and T trials 0.82 times normal walking). Note that the recovery foot landing occurred around 410 ms during the T-FZ and 480 ms during the T trials. The third muscle to be activated differently between T and T-FZ trials was iBF. Excitation of iBF started 235 ms and reached a peak at 285 ms (T-FZ trials 1.73 and T trials 0.32 times normal walking) after trip onset. Finally, the only significant change in RF activity occurred much later, around 480 ms following obstacle contact, when the recovery steps were already completed.

Statistically significant changes on TC trials. The comparison between T-FZ and TC trials yielded no statistically significant contrast. However, TC trials significantly differed from T trials in many aspects, although the perturbation was the same (trip without the FZ) in both of these trial types (T and TC). As can be seen in Fig. 6, these differences were similar to the difference between the T and T-FZ trials. Difference in vertical toe position at obstacle contact (0.08 m for TC trials and 0.04 m for T trials) disappeared around 220 ms after contact and reversed to a maximum contrast around 380 ms after obstacle contact (0.1 m for TC trials and 0.22 m for T trials). Vertical toe velocities were not significantly different at obstacle contact and reached a maximum contrast around 280 ms after obstacle contact (-0.5 m/s for TC trials and 0.6 m/s for T trials). Overall the behavior during the TC trials was similar to

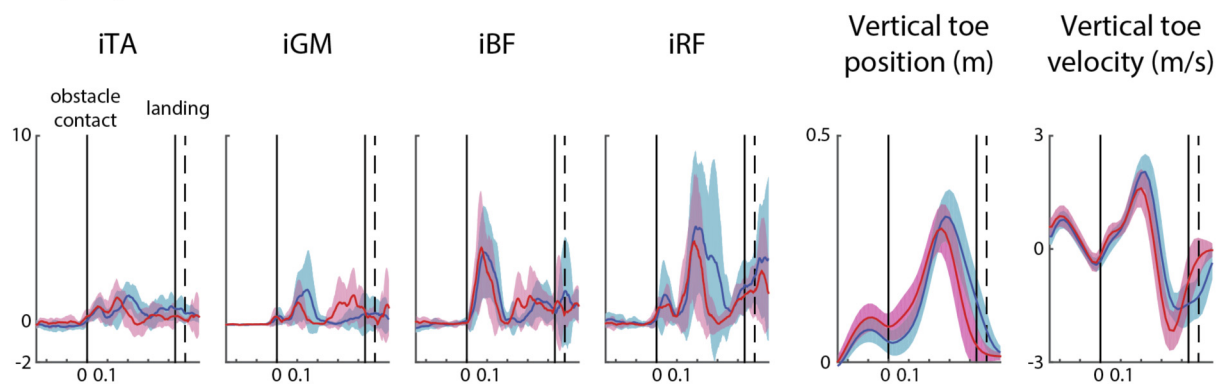
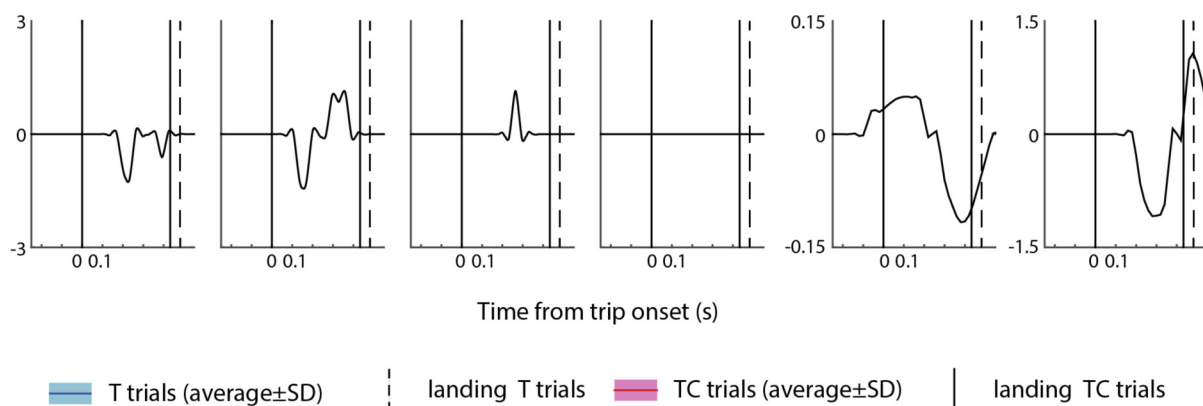
A group mean \pm SD**B** wfANOVA significant contrast TC vs. T trials ($p < 0.05$)

Fig. 6. Group average responses (A) and significant contrasts (B) between normal (T, blue) and “catch” trips (TC, pink), for the ipsilateral leg. Group average data are shown as means \pm SD. All signals are aligned to obstacle contact, indicated by a black vertical line at *time 0*. Other vertical lines indicate recovery step landing for T (broken line) and TC (solid line) trials. EMG data are normalized to average normal walking and thus are unitless. Contrasts are expressed in the same way, since they represent the difference in normalized EMG data between TC and T trials.

that during the T-FZ trials: subjects started lowering their foot about 20 ms earlier (vertical position of the toe started decreasing around 280 ms during the T trials and 260 ms during the TC trials), preceded by a decrease in the vertical toe velocity about 60 ms earlier (T trials 220 ms, TC trials 200 ms). Peak vertical toe position was 0.32 m during the T trials and 0.30 m during the TC trials, and the TC steps landed about 50 ms earlier.

Muscle activities of the TC trial also differed from the T trials and were not significantly different from activities seen during the T-FZ trials. As for T-FZ trials, the earliest change was found in iGM. The reduction in iGM activity started at 107 ms and reached a peak 156 ms after obstacle contact (TC trials 0.24 and T trials 1.76 times normal walking), before reversing to an excitation starting 267 ms and reaching a peak 356 ms (TC trials 1.16 and T trials 0.27 times normal walking) following obstacle contact. The second muscle to show a change in activity compared with the T trials was iTA, with a reduction in activity starting 171 ms after obstacle contact and reaching a peak at 225 ms after obstacle contact (TC trials 0.23 and T trials 1.37 times normal walking). This was followed by another period of reduction starting at 364 ms and reaching its peak at 392 ms after obstacle contact (TC trials 0.29 and T trials 0.79 times normal walking). Finally, activation of iBF

started at 236 ms and reached its peak at 264 ms after obstacle contact (TC trials 1.16 and T trials 0.13 times normal walking).

Foot kinematics. Because significant contrasts were mainly found in iGM and iTA muscles, which serve as ankle plantar- and dorsiflexors, respectively, we evaluated the position of the foot throughout the recovery step to evaluate the role of these muscle activations in the behavior. Given the increased iGM activation along with reduced iTA activity during the T-FZ and TC trials, one would expect that in these trials the foot would land with a toe landing (i.e., in plantar flexion). This was confirmed by the data, as can be seen from Fig. 7. Figure 7A shows the vertical distance between the toe and the heel, with a positive difference at landing indicating heel landing (toes up). Figure 7B shows subject and group-averaged ankle angles, with angles larger than 90° indicating plantarflexion. It can be seen that during T-FZ and TC trials subjects ended the recovery step by landing on their toes, which were, at landing, 0.11 m below the heel during the T-FZ trials and 0.07 m below the heel during TC trials. This was achieved by plantarflexions of 94.6° and 93.7° , respectively. In contrast, during the T trials the subjects had the toes 0.01 m above the heel, indicative of a flat foot landing, and the ankle was dorsiflexed (86.7°).

Other stepping behaviors. Finally, our subjects predominantly used step shortening for FZ avoidance, and we limited our main analysis to subjects who successfully shortened their

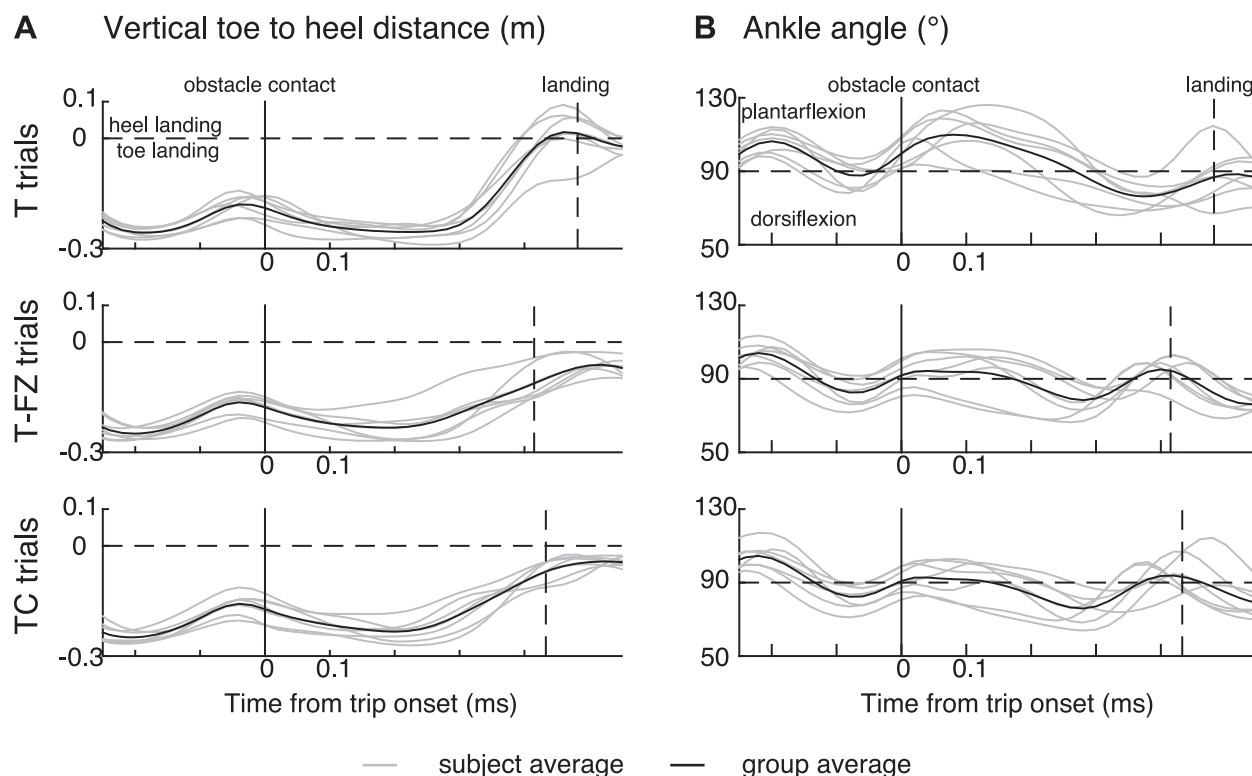


Fig. 7. Vertical distance from toe to heel (A) and ankle angle (B) for T, T-FZ, and TC trials. Subjects' average data are shown in gray, and group average is shown in black. Signals are aligned to obstacle contact, indicated by a black vertical line at *time 0*. Vertical broken lines indicate average recovery step landing. Note that positive vertical distance indicates upward direction, and 90° indicates neutral ankle position. Thus, positive distances between the toe and the heel at landing indicate heel landing, whereas negative distances indicate toe landing. Similarly, ankle angles smaller than 90° indicate dorsiflexion, whereas ankle angles larger than 90° indicate plantarflexion.

steps in all T-FZ trials. However, several subjects used side stepping and/or were unsuccessful in some of their T-FZ trials. Hence, we also analyzed muscle activity changes of their successful T-FZ avoidances to investigate whether these were in accord with the predominantly observed behavior.

Side stepping was used by three subjects, but unfortunately these subjects were not successful on all trials, and data of only seven side steps were available. These analyses revealed no statistically significant contrasts in EMG activity between the T, TC, and T-FZ trials following the wfANOVA analysis. However, looking at individual data, we observed an early reduction of iGM activity during side stepping in two of the three subjects (*subjects 5 and 12*), similar to early iGM changes observed during step shortening (Fig. 8A). This reduction was smaller than the one seen during step shortening and not statistically significant, probably due to the small sample size.

Three subjects were initially unsuccessful in their T-FZ trials, but eventually succeeded in shortening their steps to avoid the FZ. EMG data of one of these subjects were unavailable, and individual data of the remaining two are shown in Fig. 8B (*subject 7* was successful on one and *subject 8* on two T-FZ trials). Similar to side stepping, we observed a reduction in iGM activity during step shortening on successful T-FZ trials in one of these subjects.

DISCUSSION

This paper aimed at exploring the mechanisms involved in making decisions related to fast leg movement adjustments under balance threatening conditions, namely changing the

landing position after tripping (to avoid stepping in a “forbidden landing zone”). In a previous study on the same data, we had shown that such corrections can be made in a large percentage of the trials. However, because the EMG data were not yet provided, decisions underlying such fast corrections remained unknown. In the present study we addressed this issue by using wfANOVA to describe statistically significant muscle activity changes driving leg movement adjustments. We showed that the correction to avoid the FZ after tripping clearly involved a two-stage process: the first stage of the response was seemingly unrelated to the behavioral outcome, whereas the second later stage of the response consisted of muscle activity changes needed to initiate the observed step shortening.

Behaviorally, the dominant response to the FZ presented during tripping analyzed in this study was step shortening, which means the foot was placed in front of the FZ, hence requiring an earlier landing of the foot. One would predict that this requires additional activation of hip extensors (iBF) and ankle plantar flexors (iGM), along with reduced activity of dorsiflexors (iTA). This was indeed observed; the reduction in iTA activity occurred first (171 ms) and was followed by activations in iBF and iGM at relatively long latencies (235 and 265 ms, respectively). Surprisingly, the functional activation of iGM was preceded by a period of reduced activity (instead of increased, as one would expect in preparation for landing) starting at a latency of 107 ms, which can be seen in Fig. 5B. Hence the total response had two stages: it started with a nonfunctional change in iGM muscle activity and was followed

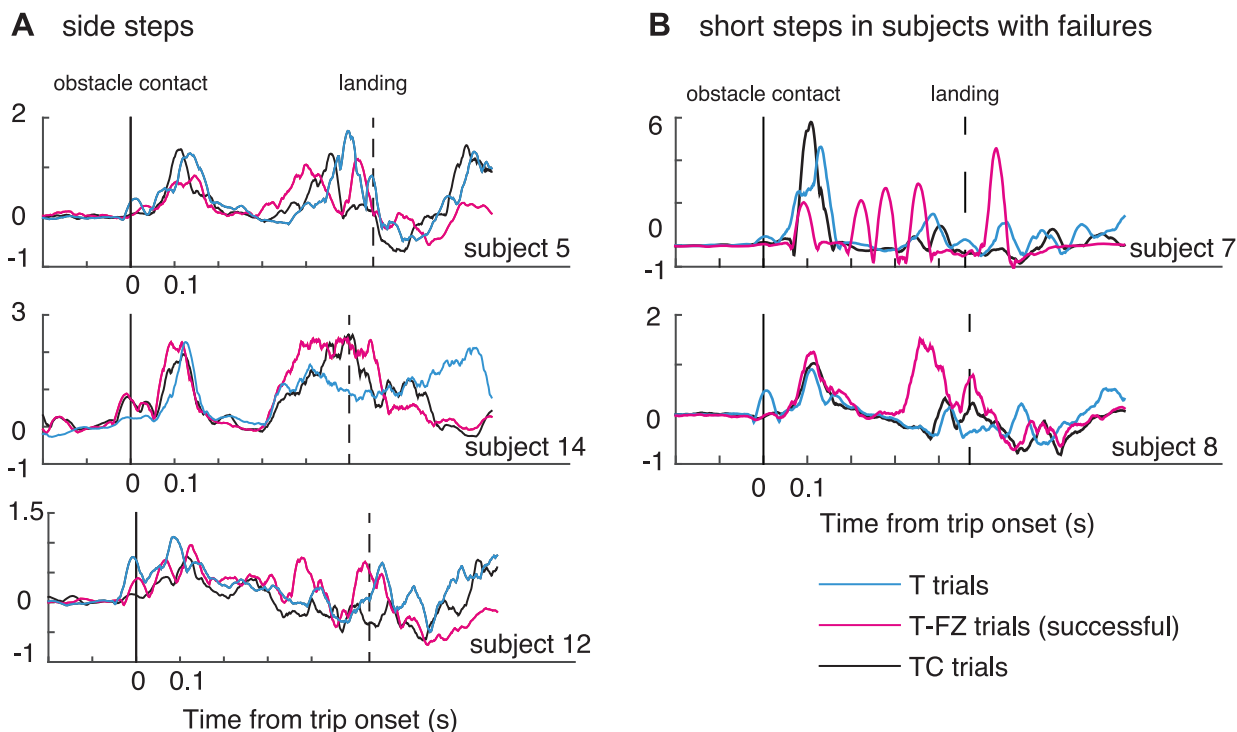


Fig. 8. iGM muscle activity of subjects using side stepping (A) and subjects using step shortening, who were initially unsuccessful in FZ avoidance (B). Subjects' average iGM responses on T (blue), successful T-FZ (pink), and TC (black) trials are shown. T, T-FZ, and TC signals are aligned to obstacle contact, indicated by a black vertical line at time 0. Vertical broken lines indicate average recovery step landing. EMG data are normalized to average normal walking and thus are unitless. Subject nos. correspond to Fig. 3 of Potocanac et al. (2014a).

by functional activity changes in iTA, iBF, and iGM, which occurred at longer latencies and led to step shortening.

To understand this two-stage decision making process, it is essential to first consider what is known about the neurophysiology of tripping. In a previous study on tripping it was shown that tripping induces a series of responses with different latencies (Schillings et al. 1999, 2000). Two of these responses had latencies below 100 ms. The earliest responses (~ 40 ms) were identified as stretch reflexes and were followed (~ 75 ms) by medium latency cutaneous and proprioceptive responses. Neither response determined the behavioral response strategy since the latter depended only on responses occurring with a latency of about 110 ms (Pijnappels et al. 2005b; Schillings et al. 2000). These types of responses were identified in the present study as well, but superimposed were two additional responses, related to the movement correction caused by the real or expected appearance of the FZ. These additional responses went along the same lines as described before, namely one initiated at a latency below 150 ms (the limit for "involuntary reactions"), followed by longer latency muscle activity changes appropriate for the behavioral response (i.e., step shortening).

Finally, we evaluated the influence of anticipation on this decision making process by analyzing performance on TC trials, which required no movement adjustment. Anticipation influenced subjects' behavior, and they shortened their steps even when the FZ was not shown, using similar movement adjustment mechanisms as used for the T-FZ trials. Because anticipation influenced the performance on TC trials it also probably influenced the T-FZ trials. However, this influence of anticipation did not fundamentally change the process by which movement adjustments occurred, and the performance

on the first trial requiring movement adjustment was similar to the performance on the ensuing trials.

The first stage: Early suppressive responses. The most puzzling new feature, seen in the present study, was the reduction of normal trip recovery iGM activity, starting at ~ 100 ms after trip onset in T-FZ and TC trials. A first explanation could be that this reduced activity was related to the increased dorsiflexion and foot clearance at trip onset, reflecting a learning effect over trials. T trials were executed first, and subjects might thus have adjusted their normal gait to make it easier to overcome the obstacle during the subsequent T-FZ and TC trials. The reduced iGM activity would fit the dorsiflexion hypothesis, but it is puzzling that it appears only after a latency of about 100 ms. Furthermore, it is not accompanied by an increased dorsiflexion compared with T trials at a latency compatible with the electromechanical delay (difference in ankle angles between T and T-FZ trials did not increase around 200 ms after obstacle contact; the foot was more dorsiflexed already before and immediately following obstacle contact during the T-FZ and TC trials). Additionally, the averaged data of individual subjects showed that the combination of increased dorsiflexion and reduced iGM activity was present only in four out of seven subjects. The remaining subjects exhibited increased dorsiflexion in combination with increased or equal iGM activity. Together with the fact that there was no concomitant increase in iTA activation and that the reduced iGM activity was present in both TC and T-FZ trials, this indicates that the reduction in iGM activity was not a functional response enabling dorsiflexion.

A second possible explanation is that the reduction of iGM activity is related to the presence of a real or expected FZ. This

reduction occurred at a latency that was too short to be consistent with a voluntary reaction (<150 ms) and was not solely dependent on anticipation of the FZ, since it was present already in the first T-FZ trial in four out of seven subjects.

Although only observed in iGM, the reduced activity could represent a suppression of activity. Such hypothetical suppression could be seen as part of a “freeze” or “pause” response, giving the system appropriate time to prepare an adequate reaction (shortened step). The seven subjects on whose performance our analysis was focused always used the same kind of movement adjustment to avoid the FZ in T-FZ trials, but this response was not necessarily their preferred trip recovery step. Hence implementing it might have required a pause during which normal trip recovery step was inhibited before step shortening could be implemented, in line with the stop-change paradigm of response inhibition (Verbruggen et al. 2008; Verbruggen and Logan 2009). Furthermore, in animals, including humans, it is common to see a freezing reaction as part of a defensive response strategy followed by appropriate reactions such as fleeing or fighting back in case of a real danger (Eilam 2005). Such suppression appears when unexpected startling stimuli are presented. For example, pronounced muscle activity suppression was found in response to a loud noise during gait with a latency of ~100 ms (Nieuwenhuijzen et al. 2000, 2006). Sometimes the freeze is also accompanied by a cocontraction of agonists and antagonists (producing joint stiffening, Nieuwenhuijzen et al. 2000), but this was not observed in the present study. The precise pathway involved in the suppressive responses is still unclear, but it is striking that loud acoustic stimuli can evoke suppression in the motor cortex as well, implying that a long loop over the cortex is a possibility (Furubayashi et al. 2000; Ilic et al. 2011; Kühn et al. 2004; Marinovic et al. 2014). The currently observed presumed suppressions were time locked to the onset of tripping; hence, one could argue that the sound of the contact with the obstacle contributed to the startling freeze. However, this sound was also present during normal tripping, indicating sound was not the determining factor. It is clear that the triggering of the response was not purely visual either, since suppression of normal walking activity was not seen during FZ trials. Hence, the brief presumed suppressions in iGM seem to be triggered by the combination of tripping and the need for step adjustment, either real or expected. In this respect, it is useful to recall that other stimuli can produce similar inhibitory effects. For example, for unexpected somatosensory stimuli such suppressions have also been noted. With electrical stimulation of cutaneous afferents from the foot, suppression of muscle activity has often been observed (for example, in TA and triceps surae muscles), with latencies in the range of 50–100 ms during plantar- and dorsiflexion (Aniss et al. 1992), running and standing (Duysens et al. 1993), and walking (Van Wezel et al. 1997; Zehr et al. 1997). Again, however, such stimuli could not have been the sole source for the observed suppression here since somatosensory stimuli were the same for all tripping trials. While the origin of this reduction in iGM activity remains unclear, such decreased activity could not contribute to step shortening, and it therefore does not belong functionally to the muscle activity changes occurring at longer latencies, which all clearly could contribute to step shortening. In support of this idea, a reduction of iGM activity around 100 ms after obstacle contact also occurred in subjects using different strategies (in 2 out of 3 subjects using side steps and in

successful T-FZ trials of 1 out of 2 subjects who initially failed to avoid the FZ; see Fig. 8). These data tentatively support our conclusion that iGM activity is not related to the observed behavioral adjustment strategy, although the suppression observed during side stepping was not statistically significant, possibly due to small sample size (only 3 subjects used side stepping and only 2 subjects exhibited a mixture of failed and successful step shortening).

The second stage: Behavioral responses (shortening strategy). Following the early suppression response (freeze period), statistically significant EMG changes were clearly related to step shortening to avoid the FZ, i.e., would lead to the observed rapid lowering and placement of the tripped foot in front of the FZ, once it had cleared the obstacle. The increase of iBF (at 285 ms) and iGM (at 320 ms) activity, along with the reduction of iTA activity (at 171 ms), are consistent with shortening of the step (resulting from increased iBF activity) and plantarflexion (resulting from increased iGM and decreased iTA activity) to prematurely lower the leg and land on the toes (Fig. 7). It is interesting to note that the latencies of movement adjustments in response to the FZ, as seen here, correspond to those reported for the hamstrings and plantarflexors in a trial in which the tripped subject started with an elevating strategy and switched to lowering due to an obstacle sticking to the foot (“delayed lowering”) (Fig. 6 in Schillings et al. 2000) and to latencies of differences in muscle activity between elevating and lowering trip recovery strategies (Fig. 3 in Pijnappels et al. 2005b).

Online adjustment or anticipation? One of the problems with studies using repeated perturbations is that only the very first perturbation trial is truly unexpected and that upcoming perturbations can influence the recovery stepping response (Pater et al. 2015) and alter the normal walking pattern (Pijnappels et al. 2001, 2006). When anticipating a trip, young subjects increase their step width and exhibit small changes in muscle activity that lead to knee stiffening, dorsiflexion, and increased foot clearance. This has led some authors to limit their study to only one unexpected tripping trial for each subject (Pater et al. 2015; Pavol et al. 2001; Troy and Grabiner 2005). To address this issue, we included a number of catch trip trials in our experimental design. These trials differed only in that the catch trials were presented in between the T-FZ trials, whereas normal trip trials occurred at the start of the experiment, before any FZ was presented. Yet, we found the performance to differ between these trial types. Behavioral changes on the TC trials were similar to those on the T-FZ trials, but of smaller magnitude. Steps were shortened both in time and distance and in 9 out of 14 trials included in this analysis would even have landed outside of the FZ, if it had been presented (see also Potocanac et al. 2014a). Muscle activity changed accordingly, showing a similar pattern of decreased iGM and iTA activity, followed by an increase in iBF and iGM activity. This clearly showed that anticipation was involved in the catch responses. Apparently, when faced with the possibility of encountering the FZ, the subjects’ responses were suitable for that situation even if no FZ was present. This behavior might stem from an adaptation of a forward model to shorten trip recovery steps irrespective of FZ appearance, resulting in co-optimization of motor behavior (Barton et al. 2014) such that an anticipated FZ could be more easily avoided if shown. Because anticipation affected the performance on catch trials it was also likely to affect most T-FZ trials. The only exception was the very

first T-FZ trial, in which subjects had no prior experience of the adjustment required.

To see the signature of a true adjustment of a balance recovery response, we looked at the very first trial with a FZ, since this is the trial in which the reaction was based on visual input mainly and not (or to a much lesser extent) on anticipation. If the influence of anticipation would be important, we would expect large changes in responses over the subsequent trials. However, the data showed that the response pattern did not differ much between the first and subsequent trials; the only observed change was a decrease in the magnitude of activity of some muscles (e.g., iRF), in line with previous work suggesting amplitude decrease with habituation (Campbell et al. 2013; Oude Nijhuis et al. 2010). This is relevant for the question whether the responses seen in the first trial are basically different from the subsequent ones or whether they are the same, but that there is mostly a scaling difference. This type of question has been investigated most thoroughly with postural perturbations (Campbell et al. 2013; Oude Nijhuis et al. 2010), and it was found that first trial responses definitely show characteristics of startle responses. However, they also differ from startle responses in some aspects, and it was therefore concluded that first trial effects are likely postural responses that are superimposed on a startle response (Campbell et al. 2013). Our experiment was somewhat different, since our subjects were already tripped before the first T-FZ trial. In the T-FZ trial, the visual stimulus was added to the trip, but this would presumably cause less of a startle than a novel balance perturbation. Therefore, it is not surprising that responses to the T-FZ trials exhibited a modest amplitude scaling, but not a major new pattern in the first trial.

Muscle activity during normal trip recovery. Because muscle activity was also recorded during normal tripping, we compared our data with those obtained in former studies on tripping responses. Muscle activity used for recovery steps during normal tripping in the present experiment was generally similar to that reported previously for elevating response recoveries from trips during overground (Eng et al. 1994) and treadmill (Schillings et al. 1999, 2000) walking. Amplitude peaks occurred first in iRF (small peak ~40 ms, large peak ~185 ms), followed by iBF (~110 ms), iGM (~120 ms), and iTA (~160), similar to previous findings either on a treadmill (Schillings et al. 2000) or overground (Eng et al. 1994). Furthermore, similar to Schillings et al. (1999) we measured very early responses to the tripping perturbation in iRF (~40 ms) and occasionally iTA (~60 ms). The main difference with these previous studies was the long latency of the late iGM activity. Such activity was either not measured (Eng et al. 1994; Schillings et al. 1996) or not found to be significant previously (Schillings et al. 2000). This large and late iGM activation might play an important role in trip recovery, when the obstacle is high and does not move (in contrast to the Schillings et al. studies). Indeed, higher foot elevation has to be compensated by increased plantar flexion at landing.

Implications and clinical relevance. Our primary goal was gaining fundamental insight into how the decision for leg movement correction is made in young adults. Yet these data are also valuable in the context of fall prevention in older adults. Tripping is one of the most common circumstances of falls (Berg et al. 1997; Overstall et al. 1977; Rao 2005; Robinovitch et al. 2013), and the ability to recover from a trip

is impaired by the physiological effects of aging (Pijnappels et al. 2005b, 2005c, 2008; Schillings et al. 2005; Van Dieën et al. 2005). Hence, adjustments to the inadequate trip recovery response of older adults might be beneficial for reduction of fall rates. Our data clearly show such adjustments are possible in young adults, occur in two stages, and can be generalized even to situations when they are not needed (TC trials). This calls for future work on whether or not the same applies to older adults, especially those at increased risk of falling. Promising results were recently reported showing adjustments of balance recovery responses in both young and older adults following exposure or anticipation of upcoming trips or slips (Bieryla et al. 2007; Pai et al. 2010; Wang et al. 2012) and reduced fall rates following training simulating tripping using treadmill accelerations (Grabiner et al. 2012; Rosenblatt et al. 2013). Furthermore, previous work in our laboratory has shown that inadequate recovery from tripping was related to deficient force production in hamstrings and that strength and power training in lower limb muscles resulted in improved trip recovery in older adults (Pijnappels et al. 2008). This suggests that, with a certain amount of strength, adjustments of strategies and therefore improvement of balance recovery responses seem possible in older adults too. In combination with our findings, this calls for future work to establish whether older adults are also able to successfully adjust their trip responses. Furthermore, the strong anticipation effect we have seen on TC trials is indicative of a feed forward movement adjustment and, if present in older adults, could indicate the possibility of replacing inadequate trip recovery responses by more appropriate responses following training. Hence, these data are a first step toward understanding the mechanisms underlying trip recovery adjustments in young adults and a basis for future work in older adults, which could inform design of training interventions for fall prevention.

Limitations. One limitation of this work lies in the fact that it was technically impossible to achieve exactly identical tripping onsets during the swing phase in all trials. As shown earlier (Pijnappels et al. 2001, 2006), subjects change their gait pattern when expecting a potential perturbation, and this is a limiting factor for these types of experiments. Although we encouraged our subjects to maintain their normal gait pattern and walking velocity and presented them with a number of normal walking trials in between the tripping trials, vertical toe position and velocity already differed slightly between the T and T-FZ trials at trip onset (toe clearance increased by 0.03 m, and velocity decreased by 0.8 m/s) because the T trials were performed earlier than T-FZ trials (for details see Potocanac et al. 2014a). Nevertheless, as mentioned in METHODS, the tripping always elicited a balance recovery response with an elevating strategy. Second, a limitation of our study was that it was not possible to systematically manipulate the timing of the FZ with respect to obstacle appearance. Based on the data available we cannot answer whether muscle activity responses found during T-FZ and TC trials would have been different or delayed if the FZ appeared later. Nevertheless, it is unlikely that priming was an important element since presenting the FZ alone (without tripping) did not cause major changes in muscle activity. Finally, we are limited in sample size, since only seven (out of 16) subjects tested exhibited consistent behavior (i.e., successfully avoided the FZ using the same strategy in each trial). For statistical comparisons, we focused our analyses on the suc-

cessful FZ avoidance trials of seven subjects using the predominant responses (step shortening). However, as described previously, other behavior was also observed; six subjects exhibited a mixture of failed and successful trials, using both short and side steps on their successful trials and even switching between step shortening and side stepping (Potocanac et al. 2014a). Unfortunately, in our experiment we could not reveal statistically significant muscle activity changes guiding other nondominant step adjustment behaviors, since we observed only seven side steps made by three subjects. We found no statistically significant contrasts in EMG activity between the T, TC, and T-FZ trials following the wfANOVA analysis, which is not surprising, since we measured the activity of iBF, iRF, iGM, and iTA, which are more important for step lengthening or shortening, whereas hip abductor activity would be expected for side stepping. Hence future research should investigate muscle activity changes over a broader range of muscles in relation to other step adjustments.

Conclusion. In line with the findings that tripping induces muscle activity responses at different latencies and only the longer latency responses are related to the balance recovery responses (elevation or lowering; Schillings et al. 2000), we found that adjustments of these recovery responses (to avoid a forbidden landing zone) also involve two stages in the decision process. The first response (decrease in iGM activity at around 100 ms after trip onset) occurred too early to be voluntary (<150 ms) and might reflect a temporary pause, enabling the system to collect information for the ensuing behavioral response. Behaviorally functional EMG responses occurred later (>230 ms) and led to appropriate movements to avoid the forbidden landing zone, in this case by shortening the recovery step. Interestingly, anticipation of the potential need for movement adjustment led to similar two-stage responses even when no forbidden zone was present during tripping.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

Author contributions: Z.P., M.P., and J.D. conception and design of research; Z.P. and M.P. performed experiments; Z.P. analyzed data; Z.P. and J.D. interpreted results of experiments; Z.P. prepared figures; Z.P. drafted manuscript; Z.P., M.P., S.V., J.v.D., and J.D. edited and revised manuscript; Z.P., M.P., S.V., J.v.D., and J.D. approved final version of manuscript.

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