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Cutaneous reflex modulation during obstacle avoidance under conditions of normal and degraded visual input

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Abstract

The nervous system integrates visual input regarding obstacles with limb-based sensory feedback to allow an individual to safely negotiate the environment. This latter source can include cutaneous information from the foot, particularly in the event that limb trajectory is not sufficient and there is an unintended collision with the object. However, it is not clear the extent to which cutaneous reflexes are modified based on visual input. In this study, we first determined if phase-dependent modulation of these reflexes is present when stepping over an obstacle during overground walking. We then tested the hypothesis that degrading the quality of visual feedback alters cutaneous reflex amplitude in this task. Subjects walked and stepped over an obstacle—leading with their right foot—while we electrically stimulated the right superficial peroneal nerve at the level of the ankle at different phases. Subjects performed this task with normal vision and with degraded vision. We found that the amplitude of cutaneous reflexes varied based on the phase of stepping over the obstacle in all leg muscles tested. With degraded visual feedback, regardless of phase, we found larger facilitation of cutaneous reflexes in the ipsilateral biceps femoris—a muscle responsible for flexing the knee to avoid the obstacle. Although degrading vision caused minor changes in several other muscles, none of these differences reached the level of significance. Nonetheless, our results suggest that visual feedback plays a role in altering how the nervous system uses other sensory input in a muscle-specific manner to ensure safe obstacle clearance.

Introduction

People often have to step over an obstacle, such as a child's toy, or step onto a sidewalk curb on their way to a particular destination. These scenarios require a modification to normal gait that entails careful planning and proper motor coordination (Drew and Marigold 2015). Despite our best intentions, success does not always happen. Consider the situation where one bumps one's toe on an object because of an unexpected change in its position or a poor choice in limb trajectory (a possible reflection of fatigue or not paying attention). If all goes well, a rapid withdrawal and elevated flexion of the limb ensures forward progression is maintained, thus also minimizing any perceived feeling of embarrassment. This is the so-called "stumbling corrective response" (Forssberg 1979; Schillings et al. 2000).

The stumbling corrective response, which can be elicited in the lab by mechanical perturbation to some portion of the lower limb or via electrical stimulation of nerves transmitting cutaneous information from the foot, is seen in cats (Forssberg 1979) and humans (Eng et al. 1994; Schillings et al. 2000; van Wezel et al. 1997; Zehr et al. 1997). In humans, the recovery responses to mechanically induced tripping vary depending on the phase of the gait cycle (Eng et al. 1994; Schillings et al. 2000). When tripped early in swing phase, subjects adopt an elevating strategy, whereas when tripped late in swing phase, subjects typically employ a lowering strategy (Eng et al. 1994; Schillings et al. 2000). This phase-dependency is also evident in cutaneous reflex responses elicited via electrical stimulation (Duysens et al. 1990; van Wezel et al. 1997; Yang and Stein 1990; Zehr et al. 1997). Interestingly, when postural threat is increased by having subjects cross their arms as well as mechanically perturbing the foot dorsum, this leads to changes in cutaneous reflex amplitude in ankle muscles evoked by electrical stimulation of the superficial peroneal (SP) nerve (Haridas et al. 2008). Taken together, these results suggest that the nervous system is primed to respond as a function of the phase of walking and the context of

the task. However, in these and similar studies, the tripping object is usually presented at unexpected times and/or positions. Furthermore, electrical stimulation or mechanical contact to the foot to elicit a cutaneous reflex is most often performed during normal gait. In contrast, stepping over an obstacle like a sidewalk curb imposes different biomechanical constraints and represents a different, albeit common, type of task. Whether a similar phase-dependent modulation of cutaneous reflexes is seen in this case remains unresolved.

Vision plays an important role in planning how to negotiate obstacles. People tend to fixate an obstacle as they approach but not while stepping over it (Patla and Vickers 1997). In this latter phase, peripheral visual information from the lower visual field is important (Marigold 2008). Since visual input regarding the environment is obtained in advance, the nervous system can predictively modify the weighting given to incoming muscle and cutaneous feedback from the limbs to deal with potential hazards. This may result in changes to reflex gains. For instance, Llewellyn et al. (1990) found attenuated soleus H-reflexes when walking under visual guidance on a narrow elevated beam compared to regular treadmill walking. Recently, we demonstrated that the amplitudes of cutaneous reflexes are modulated when visual feedback regarding the terrain is critical for walking (Ruff et al. 2014). In separate experiments, we constrained where subjects could place their foot using narrow rungs of a horizontal ladder or narrow flat targets. We found changes in the amplitude of lower limb cutaneous reflexes between these and control conditions predominantly during late swing phase, a time when the control of precise foot placement is paramount (Ruff et al. 2014). However, it is not clear the extent to which cutaneous reflexes are modified based on the quality of visual input.

Understanding how the quality of vision affects how non-visual feedback is integrated during walking is an important avenue of research given the increasing prevalence of debilitating eye diseases (Klein and Klein 2013), and their potential impact on mobility performance

(Alexander et al. 2014; Heasley et al. 2004; Timmis et al. 2014; Timmis and Pardhan 2012). Cutaneous input may play an even greater role when vision is not available (Perry et al. 2001) or is severely degraded. These situations may also increase perceived threat, which is thought to influence the modulation of cutaneous reflexes (Haridas et al. 2005, 2008).

In the current study, we had two objectives. First, as our primary objective, we determined whether the quality of visual feedback alters cutaneous reflex amplitude when stepping over an obstacle during overground walking. Second, we tested whether phase-dependent modulation of cutaneous reflexes is preserved in this task. To this end, we electrically stimulated the SP nerve (a nerve at the level of the ankle that transmits cutaneous input from the foot dorsum) at different phases of the step over an obstacle. To test how the quality of visual input alters cutaneous reflexes, we had subjects perform the walking task with and without degraded vision induced by special glasses.

Methods

Subjects

Twelve, healthy university-aged subjects (7 males, 5 females; mean ± SD age = 22.3 ± 2.8 years; all right leg dominant) underwent electrical stimulation of the SP nerve while walking and stepping over an obstacle, as described below. Exclusion criteria included uncorrected visual deficit (e.g., loss of visual field in one or both eyes), neurological disorder (e.g., stroke), or musculoskeletal impairment (e.g., chronic instability of a joint due to sprain) that affected movement. We also excluded subjects if they had metal (e.g., orthopedic screws) in their legs or feet and/or electronic implants anywhere in their body. The Office of Research Ethics at Simon Fraser University approved the study, and subjects gave written informed consent prior to testing.

Protocol

Subjects performed an obstacle avoidance task that required them to walk and step over a 21-cm high (10-cm wide and 80-cm long) wooden obstacle with their right leg first (Fig. 1). This height is similar to the size of the rise of many stairs and sidewalk curbs. In this experiment, subjects walked without visual manipulation (i.e., normal vision) in one condition and while wearing special custom-made glasses that reduced the quality of vision (i.e., degraded vision) in the other condition. To degrade vision, we covered the lenses of the glasses with 12 sheets of clear plastic wrap. We blocked the lower visual field below the bottom edge of the glasses with black fabric such that subjects could not see their feet or ground unless they looked through the blurry lenses. We randomly varied the subject's start position relative to the obstacle on a trial-to-trial basis, thus increasing the need to use visual feedback to precisely guide foot placement before stepping over the obstacle. Subjects experienced 90 walking trials in each condition. We counterbalanced the order of conditions (i.e., normal versus degraded vision) across subjects.

To determine the effect of the glasses on visual function, we assessed habitual binocular visual acuity and contrast sensitivity. We assessed binocular visual acuity using ETDRS eye charts (5 letters per line) on a SIFIMAV Vision Tester (Mav-III; SIFI, Italy). The smallest line where there were fewer than two incorrectly read letters represented the acuity, which we subsequently converted to a logMAR score, with higher values representing worse visual acuity. We measured binocular contrast sensitivity using the Melbourne Edge Test (chart 1, version 2.4.1) at a 40 cm distance. In this test, subjects had to indicate the orientation of an edge within a series of round test patches of varying contrast. We employed a four-alternative forced choice method to determine the lowest contrast test patch correctly identified. We scored this test as dB

= -10log$_{10}$(Michelson contrast), where lower values represent worse contrast discrimination. We measured the illumination at eye level from overhead lighting during these tests as ~600 lux.

Electrical Nerve Stimulation

We electrically stimulated the right SP nerve using a Digitimer constant current stimulator (model: DS7A, Digitimer Ltd., Hertfordshire, England) attached to disposable bipolar silver/silver-chloride electrodes (GS27, Bio-Medical Instruments Inc., Warren, MI) located at the talo-navicular junction of the ankle. We applied the stimulation in trains of 5 x 1.0 ms pulses at 300 Hz and at a current of 2.5x the subject's radiating threshold (RT) (Bagna and Bouyer 2011; Haridas et al. 2005; Ruff et al. 2014; Zehr et al. 1997). We defined the RT as the point at which a sensation spread across the skin distal to the electrode. We tested this threshold while subjects sat and again while they stood. We re-assessed the RT between the conditions. If the threshold differed, we increased or decreased the current accordingly to maintain the 2.5x RT value.

We manually triggered SP nerve stimulation via LabVIEW software at different times between left heel contact (which occurred before the right foot stepped over the obstacle) and left toe-off of the same step (see Fig. 1) for a total of 60 stimulation trials. Specifically, we applied the nerve stimulation once during the step over the obstacle in each walking trial. Across trials, an experimenter randomly targeted the stimulation to coincide with a specific phase of this step. Thus, subjects could not predict the precise timing of the nerve stimulation on a given trial. Ten non-stimulation (control) walking trials occurred before stimulation trials began, and then an additional 20 control trials were randomly interspersed amongst the 60 stimulation trials. This produced 90 walking trials for each condition.

Data collection and analysis

We recorded muscle activity at 2,000 Hz with a MA300 EMG system (Motion Lab Systems Inc., Baton Rouge, LA) from the tibialis anterior (TA), medial gastrocnemius (MG), vastus lateralis (VL), and biceps femoris (BF) bilaterally. We recorded kinematic data at 200 Hz with an Optotrak Certus camera system (Northern Digital Inc., Waterloo, Ontario, Canada). We placed infrared emitting diodes bilaterally and facing laterally on the top of the feet, the toes (the head of the fifth metatarsal), and the heels. On the right leg (the one stepping over the obstacle first), we also placed these diodes on the femur, head of the fibula, and the lateral malleolus. We also collected foot-switch data from one foot at 200 Hz to use for binning reflex data (described later). We synchronized EMG, kinematic, and foot switch data using LabVIEW software (National Instruments, Austin, TX). We determined foot contact and toe-off of the left leg (i.e., the leg opposite to the one that received electrical stimulation) using two foot-switches attached to the plantar surface of the foot under the head of the second metatarsal and under the heel.

To determine cutaneous reflexes, we used a method similar to that reported in the literature (e.g., Haridas et al. 2005, 2006, 2008; Hoogkamer et al. 2012, 2015; Lamont and Zehr 2006). First, we full-wave rectified the EMG data and then filtered it using a zero-lag, 4^{th}-order Butterworth algorithm with a low-pass cut-off of 50 Hz. Next, for each walking trial, we windowed the data between heel contact and toe-off of the left foot as the right foot stepped over the obstacle (see Fig. 1). For each muscle, we time-normalized the EMG data of the non-stimulated walking trials based on this data window, and then calculated the mean (control) activity. We divided the data window into six equal bins. We then sorted trials in which nerve stimulation occurred into one of these bins based on the manual timing of stimulation. This resulted in an average of 9.2 ± 3.7 and 8.9 ± 3.7 stimulation trials per bin in the normal and degraded vision conditions, respectively. Once sorted into bins, we aligned the stimulation trials to stimulation onset and then calculated the mean activity. We subtracted the mean control EMG

at the same relative phase of the step cycle for each bin from the mean stimulation trial activity to generate a net reflex for each bin. This allowed us to determine cutaneous reflexes from this net reflex trace for each muscle and bin. Specifically, we calculated the mean amplitude of the middle latency time period (70 to 120 ms after stimulation onset); during walking, this middle latency cutaneous reflex is most frequently studied (Baken et al. 2006; Haridas et al. 2006, 2008; Lamont and Zehr 2006; van Wezel et al. 1997; Yang and Stein 1990). Positive amplitudes indicate facilitatory reflex responses whereas negative amplitudes indicate suppressive reflex responses. We amplitude-normalized these reflexes by the maximum control EMG activity in the normal vision condition. We separated the background EMG activity into bins and amplitude-normalized the signals in a similar way.

To filter the kinematic data, we used a zero-lag, 4^{th}-order Butterworth algorithm with a low-pass cut-off of 6 Hz. We determined vertical toe clearance of the right foot at the time of obstacle crossing (Fig. 1, middle panel). We also calculated relative knee joint angle during the step over the obstacle (i.e., from right foot toe-off until right foot heel contact after the obstacle). To allow averaging across subjects and to compare between conditions, we subsequently time-normalized knee joint angle. Finally, we calculated gait speed using the chest marker during stance phase of the left foot to capture the period of stepping over the obstacle with the right foot.

Statistical Analysis

We used JMP 12 software with an alpha level of 0.05 for all statistical analyses. We used paired t-tests to determine differences in habitual binocular visual acuity and contrast sensitivity between normal and degraded vision conditions. Since, to our knowledge, no one has studied cutaneous reflexes when stepping over an obstacle during overground walking (except in the context of tripping), we first used one-sample t-tests for each phase bin (n = 6) to determine

significant differences from zero for cutaneous reflex amplitudes in this experiment. This method is similar to previous research (Ruff et al. 2014; van Wezel et al. 1997). Subsequently, we performed separate two-way repeated measure ANOVAs (Phase x Condition) for each muscle to compare cutaneous reflex amplitude across phase (averaged reflex activity in each bin) and condition (normal vision and degraded vision). When warranted, we used Tukey's post hoc tests for significant phase main effects. We compared background EMG amplitude in a similar manner. To determine differences in toe clearance between conditions, we used a paired t-test.

Results

Cutaneous reflex modulation during obstacle avoidance: normal vision

Given that the strength of cutaneous reflexes change depending on the phase of the gait cycle during level walking, it is likely that a so-called phase-dependent modulation also occurs when stepping over an obstacle. To confirm this idea, we first examined cutaneous reflexes in the normal vision condition. The ipsilateral BF and TA (responsible for flexing the knee and ankle joint, respectively) are most important for stepping over an obstacle (Carrière and Beuter 1990; Lajoie et al. 2012; Patla et al. 1991; Patla and Rietdyk 1993). The net cutaneous reflex responses in ipsilateral (i) BF of a representative subject are shown in Fig. 2a, and group data across the six phase bins in the normal vision condition for all ipsilateral muscles are illustrated in Fig. 2b. We found facilitatory reflex responses for iBF during and immediately after push-off (bins 1 and 2; $p < 0.05$). During the rest of the movement, including the limb going over the obstacle, reflexes were largely absent. While the ipsilateral leg prepared for toe-off to step over the obstacle (bin 1), we found a suppressive reflex in iTA. This reversed to a facilitatory reflex in early swing phase (bin 2). Suppressive reflexes returned as the foot prepared to land on the ground on the other side

of the obstacle and continued into the initial limb loading phase following heel contact (bins 5 and 6). We also observed increasingly facilitatory reflexes in iVL (bins 1, 3 and 4) as the ipsilateral limb elevated to step over the obstacle. In contrast, we found suppressive reflexes in iMG at the approximate time the toe approached the leading edge of the obstacle (bin 3) and again as the foot prepared to land on the ground afterwards (bin 5).

Contralateral (c) muscle cutaneous reflex amplitude (bars) and background EMG activity (lines) across the six phase bins in the normal vision condition are illustrated in Fig. 3. This limb provides body support while the ipsilateral limb steps over the obstacle first. We found small-amplitude cutaneous reflexes in cVL, with only the suppressive response in bin 2 statistically significant ($p < 0.05$). However, we found large facilitatory reflex responses for cMG in early and mid stance phase (bins 1 – 3) as well as a small facilitatory reflex in bin 5 before reversing to a small suppressive reflex response in bin 6. Although the cBF had a facilitatory reflex response in bin 3 and suppressive response in bin 6, we found no statistically significant reflexes for the cTA.

The effects of degraded visual input on cutaneous reflex modulation during obstacle avoidance

The blurring glasses used in the degraded vision condition significantly reduced habitual binocular visual acuity (normal vision = -0.05 ± 0.14 logMAR vs. degraded vision = 1.13 ± 0.11 logMAR; paired t-test, $p < 0.0001$) as well as habitual binocular contrast sensitivity (normal vision = 21.5 ± 1.3 dB vs. degraded vision = 4.7 ± 3.6 dB; paired t-test, $p < 0.0001$). Despite the visual deficits, we found no difference in gait speed between conditions (normal vision = 1.44 ± 0.48 m/s; degraded vision = 1.42 ± 0.53 m/s; paired t-test, $p = 0.189$). However, we observed a significant increase in toe clearance over the obstacle in the degraded vision condition ($p = 0.002$), as illustrated in Figure 4a. Not surprisingly, there is greater peak knee flexion in the degraded

vision condition (Fig. 4b). In both the normal and degraded vision conditions, four subjects each hit the obstacle with their foot once.

Although background muscle activity varied as a function of phase bin, degraded vision had no effect on it. Figure 4d illustrates the group ipsilateral leg cutaneous reflex data for the two vision conditions. Specifically, we found no significant main effect of condition or condition x phase interaction for background muscle activity in any ipsilateral or contralateral muscle ($p > 0.05$). In ipsilateral flexor muscles (Fig. 4d, left side), elevated background activity occurred in the earliest phase bin, in preparation for withdrawing the foot from the ground and into early swing phase, and again in the later phase bins, in preparation for foot placement. This is supported by significant phase main effects for iBF ($F_{5,110} = 9.5$, $p < 0.0001$) and iTA ($F_{5,110} = 25.7$, $p < 0.0001$). Post hoc tests for iBF showed greater background activity in bins 1 and 5 compared to bins 2 to 4, and greater activity in bin 6 compared to bins 3 and 4. For iTA, we found greater background activity in bins 1 and 5 compared to the rest, and in bin 6 compared to bin 3. In the ipsilateral extensor muscles (Fig. 4d, right side), greater background activity occurred in the later phase bins, corresponding to late swing phase and into the swing-to-stance transition (iVL, phase main effect: $F_{5,110} = 20.3$, $p < 0.0001$; iMG, phase main effect: $F_{5,110} = 25.6$, $p < 0.0001$). Specifically, we found greater background muscle activity in bins 5 and 6 compared to the rest for iVL. For iMG, we found greater activity in bin 5 compared to the rest, in bin 6 compared to bins 1 to 3, and in bin 4 compared to bin 2. Phase-dependent modulation of background muscle activity also occurred in contralateral muscles (data not shown; see Fig. 3 for normal condition though).

Overall, degraded vision had minimal impact on cutaneous reflex modulation during the obstacle avoidance task. However, in the iBF, we found greater amplitude cutaneous reflexes regardless of phase bin (condition main effect: $F_{1,68} = 8.3$, $p = 0.005$). This is evident in the group

data (Fig. 4d) as well as the representative subject (Fig. 4c). Yet, we found no significant effects of condition, whether as a condition main effect or condition x phase interaction, on cutaneous reflex amplitude for any other ipsilateral leg muscle ($p > 0.05$).

Cutaneous reflex amplitude depended on the phase bin in all ipsilateral leg muscles (Fig. 4d). For instance, we found a significant main effect of phase bin for the iBF ($F_{5,110} = 10.9$, $p < 0.0001$) in which cutaneous reflex amplitude was greater in bin 1 than the rest. This phase bin corresponds to the time when iBF is strongly activated to initiate knee flexion to lift the leg off the ground. Although we also found a significant main effect of phase bin for iVL ($F_{5,110} = 3.0$, $p = 0.014$), post hoc tests did not separate the bins. As is typical for walking, we found a significant main effect of phase bin for iTA ($F_{5,110} = 19.1$, $p < 0.0001$). For this muscle, we observed a large facilitatory cutaneous reflex in bin 2 that differed significantly from the suppressive reflex responses in bins 1 and 4 – 6. Post hoc tests also revealed that the suppressive cutaneous reflex responses in bins 1, 5, and 6 differed from bin 3, and that bins 1 and 5 differed from bin 4. For iMG, post hoc tests based on a phase main effect ($F_{5,110} = 7.0$, $p < 0.0001$) showed that the strong suppressive cutaneous reflex response in bin 5 differed from bins 1, 2, and 6. The small facilitatory reflex response in bin 1 also differed from the suppressive reflex response in bin 4.

In terms of the contralateral leg muscles, we found no main effects of condition or condition x phase interactions on cutaneous reflex amplitudes ($p > 0.05$). However, we did find phase main effects for cBF, cTA, and cMG ($p < 0.05$). These data are not shown.

Discussion

The nervous system integrates sensory feedback from multiple sources—regardless of the quality of this input—to facilitate the planning and execution of a variety of movements. In the context of walking, this allows an individual to accommodate changes in terrain, to avoid objects, and if the need arises, to rapidly respond to unforeseen events like an unexpected collision. In our study, with SP nerve stimulation, we found phase-dependent modulation of lower limb cutaneous reflexes while stepping over an obstacle. In addition, we discovered that degrading the quality of visual feedback led to greater reflex amplitude in the ipsilateral BF muscle regardless of the phase of the movement. We suggest that the nervous system alters the gain of this reflex circuit to ensure task success based on visual feedback. In contrast, degrading vision had little impact on cutaneous reflexes in other muscles. Our results add to the growing literature demonstrating context-dependent cutaneous reflex modulation during walking (Baken et al. 2006; Haridas et al. 2005, 2008; Hoogkamer et al. 2015; Ruff et al. 2014).

Cutaneous reflex modulation during obstacle avoidance

The iBF plays a critical role in stepping over an obstacle, as it is responsible for flexing the knee (Carrière and Beuter 1990; Lajoie et al. 2012; Patla et al. 1991; Patla and Rietdyk 1993). Given this action, and its contribution to hip extension due to its biarticular nature, the relatively large facilitatory cutaneous reflexes in the iBF that we observed in the stance-to-swing transition and early swing phase may allow an individual to extend the leg away from an obstacle and/or flex the knee to step over it to a greater extent. The facilitatory response seen in bin 2 for the iTA muscle may help prepare for elevating the toe to clear the obstacle through ankle dorsiflexion. Albeit small, the suppressive response in iMG during bin 3—a time when the toe is clearing the leading edge of the obstacle—can prevent unwanted plantarflexion and possible toe contact. The

large facilitatory cutaneous reflex responses present in cMG when the contralateral foot is in contact with the ground to provide body support (and throughout ipsilateral limb swing phase) may provide additional propulsion through plantarflexion to aid in forward progression over the obstacle. Together, these responses contribute to successfully avoiding the obstacle.

The act of stepping over an obstacle differs from normal unobstructed walking. Nonetheless, we can compare cutaneous reflex modulation in our experiment with past research. One of the most striking similarities between the responses elicited during obstacle avoidance in this study and normal walking is the large facilitatory iBF cutaneous reflexes at the stance-to-swing transition and into early swing phase (Haridas et al. 2008; Ruff et al. 2014; van Wezel et al. 1997; Zehr et al. 1997). This is not surprising given this muscle's role described above and its involvement in the stumbling corrective reaction. However, we did not find the typical facilitatory iBF cutaneous reflex responses towards mid to late swing phase. It is possible that this relates to the fact that the preparation for landing after clearing the obstacle is quite different than the regular placing of the foot action with normal walking.

At the level of the ankle, we found an initial suppressive response in iTA for bin 1 (the stance-to-swing transition) similar to previous research (Haridas et al. 2008; Zehr et al. 1997). This response likely occurs so that ankle plantarflexion can proceed and aid in push-off of the limb about to step over the obstacle. The late swing phase iTA suppressive responses in our study are also compatible with other studies (Ruff et al. 2014; van Wezel et al. 1997; Zehr et al. 1997). However, the facilitatory iTA response in early swing phase is in contrast with this other work (Haridas et al. 2008; Zehr et al. 1997), albeit congruent with a burst of activity in this muscle in response to contact with an actual obstacle during this phase (Eng et al. 1994). Although the MG muscle is measured less frequently in studies on cutaneous reflexes, similar to walking overground in the absence of an obstacle (Ruff et al. 2014), we found large facilitatory responses

in cMG during swing phase of the ipsilateral limb. Taken together with the findings for the iBF, many of the same cutaneous reflex responses observed during normal unobstructed walking are also present when stepping over a visible, expected obstacle. This supports the notion that similar reflex circuits are involved in both walking tasks.

The effects of degraded vision on cutaneous reflexes when stepping over an obstacle

Our blurring glasses significantly degraded vision in all of our subjects. Specifically, they reduced visual acuity and contrast sensitivity to a similar level as people with severe vision loss caused by the advanced stages of macular degeneration or cataracts (Alexander et al. 2014; Chua et al. 2004). We found that larger facilitatory cutaneous reflex responses in iBF accompanied the decreased visual function compared to the normal vision condition. Although we did not find an effect of degraded vision on iVL cutaneous reflexes (discussed below), in a post hoc analysis, we performed a two-way (Condition x Phase) ANOVA on the ratio of iBF:iVL net reflexes. We found a larger positive ratio in the degraded vision condition compared to the normal vision situation (condition main effect: $F_{1,95} = 4.0$, $p = 0.049$), indicating a greater modulation of net facilitatory iBF reflex amplitude relative to iVL. Since subjects are less able to properly determine the obstacle height relative to their foot with degraded vision, this exaggerated reflex response provides an extra margin of safety. Specifically, a combination of knee flexion and hip extension caused by the iBF would provide an efficient action to overcome the obstacle. Therefore, this strategy serves a functional purpose.

We did not find, however, changes to reflex amplitudes with degraded vision in any other muscle. It is possible that inter-subject variability may have masked any small changes. A second more likely explanation is the fact that these other muscles play a less critical function in stepping over an obstacle relative to the iBF. Importantly, the single-muscle effect suggests that the

nervous system does not alter the overall state of cutaneous reflex circuits in a generalized manner in response to changes in the quality of visual information. Muscle-specific and functionally relevant context-dependent modulation of cutaneous reflexes is also evident in other studies related to walking (Haridas et al. 2005, 2006, 2008; Lamont and Zehr 2006; Ruff et al. 2014).

Completely removing vision, rather than degrading it, also appears to alter reflex gains when standing and walking. For example, Forero and Misiaszek (2014, 2015) recently demonstrated that cutaneous reflexes in the upper and lower limbs evoked by median and radial nerve stimulation differ when walking on a treadmill with eyes closed compared to eyes open. In fact, they showed larger amplitude cutaneous reflexes in ankle muscles with eyes closed. Furthermore, Taube et al. (2008) demonstrated that soleus H-reflex amplitude is increased (and center of pressure displacement decreased) when standing on an unstable surface and having subjects point a laser at a target in front of them to enhance visual feedback. On the other hand, two studies showed that standing soleus H-reflex gain is reduced when vision is removed by closing the eyes (Hoffman and Koceja 1995; Pinar et al. 2010). Taken together with our findings, visual feedback plays a role in altering how the nervous system uses other sensory input.

What are the neural mechanisms responsible for the changes in cutaneous reflex amplitude in our task? Changes in motoneuron pool excitability are unlikely to have contributed to the facilitated iBF cutaneous reflex amplitudes with degraded vision since we found no differences in background muscle activity between vision conditions. This is further supported by the fact that other studies show little relationship between reflex amplitude and background activity during walking (Lamont and Zehr 2006; Ruff et al. 2014; van Wezel et al. 1997).

The visually guided nature of the task and the need to modify gait to step over the obstacle implies cortically driven control of the lower limbs. This is substantiated by the fact that neurons

in the posterior parietal and motor cortices of the cat discharge in advance of, or during, respectively, a step over an approaching obstacle (Drew 1991; Drew and Marigold 2015). Middle-latency cutaneous reflexes of the type studied in this report are thought to use a transcortical pathway, as appropriately timed electrical stimulation of cutaneous afferents of the foot facilitates motor evoked potentials caused by transcranial magnetic stimulation (Christensen et al. 1999; Nielsen et al. 1997; Pijnappels et al. 1998). Thus, changes in cortical excitability due to the visual demands of the task and quality of vision might affect cutaneous input that reaches this level and subsequently modify cutaneous reflex amplitude. Alternatively, or in addition, descending commands originating in the motor cortex, which are thought to act through interneuronal circuits comprising the locomotor central pattern generators (Drew and Marigold 2015), may combine with cutaneous feedback utilizing these same interneuronal circuits (Bretzner and Drew 2005). Either way, our results support the involvement of supraspinal centers in modulating cutaneous reflexes.

In conclusion, our results suggest that degrading vision in a visually demanding task leads to muscle-specific gating of cutaneous feedback such that the gain of cutaneous reflexes is enhanced to ensure success. These results also suggest that individuals with visual impairment may have larger cutaneous reflexes and/or use cutaneous feedback to a greater extent. Further research on the effects of simulated degraded vision on cutaneous reflex amplitude in other visually guided walking tasks is warranted. In addition, testing people with visual impairment is recommended.

Conflict of interest: The authors declare that they have no conflict of interest.

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Figure Legends:

Fig. 1 Experimental set-up. Inset shows obstacle dimensions. Electrical stimulation to the right (ipsilateral) superficial peroneal (SP) nerve occurred at different time periods between heel contact of the left, contralateral foot and toe-off of the same foot while stepping over the obstacle with the right leg. We randomly applied the nerve stimulation once during the step over the obstacle in each walking trial

Fig. 2 SP nerve evoked cutaneous reflexes in the normal vision condition. **a** Net cutaneous reflexes (averaged non-stimulation trial EMG signal subtracted from averaged stimulation trial EMG signal) in the ipsilateral (i) biceps femoris muscle across the six bins for a representative subject. Data aligned to stimulation onset. Shaded boxes represent middle latency reflex component (70 to 120 ms post-stimulation onset) that we used to quantify cutaneous reflex amplitude. **b** Cutaneous reflex amplitude (bars) and background EMG activity (lines) in ipsilateral muscles in the normal vision condition (mean ± SE). The horizontal bar in the upper left panel shows approximate times for stance (solid black) and swing (open white) phases, and the arrow denotes the approximate time of ipsilateral toe clearance relative to the bins. Muscle abbreviations: BF = biceps femoris; VL = vastus lateralis; TA = tibialis anterior, and MG = medial gastrocnemius. Asterisk (*) indicates significant one-sample t test (different than zero, $P < 0.05$) for cutaneous reflex amplitude (bars)

Fig. 3 SP nerve evoked cutaneous reflex amplitude (bars) and background EMG activity (lines) in contralateral (c) muscles in the normal vision condition (mean ± SE). The black horizontal bar in the lower left panel shows that the contralateral limb remains in stance phase throughout the time period analyzed. Muscle abbreviations: BF = biceps femoris; VL = vastus lateralis; TA = tibialis anterior, and MG = medial gastrocnemius. Asterisk (*) indicates significant one-sample t test (different than zero, $P < 0.05$) for cutaneous reflex amplitude (bars)

Fig. 4 a Ipsilateral limb toe clearance over the obstacle for the normal and degraded vision conditions. Asterisk (*) indicates significant paired t test ($p < 0.05$). **b** Mean knee joint angles for the normal and degraded vision conditions from contralateral limb heel contact until toe-off while the ipsilateral limb steps over the obstacle. **c** Net cutaneous reflexes (averaged non-stimulation trial EMG signal subtracted from averaged stimulation trial EMG signal) in the ipsilateral (i) biceps femoris muscle across the six bins for a representative subject. Normal condition is shown in grey (also shown in Fig. 2A) and degraded vision condition is shown in black. Data aligned to stimulation onset. Shaded boxes represent middle latency reflex component (70 to 120 ms post-stimulation onset) that we used to quantify cutaneous reflex amplitude. **d** SP nerve evoked cutaneous reflex amplitude (bars) and background EMG activity (lines) in ipsilateral (i) muscles in the normal vision (grey lines/bars) and degraded vision (black lines/bars) walking conditions (mean ± SE). The horizontal bar in the upper left portion of this panel shows approximate times for stance (solid black) and swing (open white) phases, and the arrow denotes the approximate time of ipsilateral toe clearance relative to the bins. Muscle abbreviations: BF = biceps femoris; VL = vastus lateralis; TA = tibialis anterior, and MG = medial gastrocnemius. Significant main effects are indicated in each figure panel (see text for specific details)

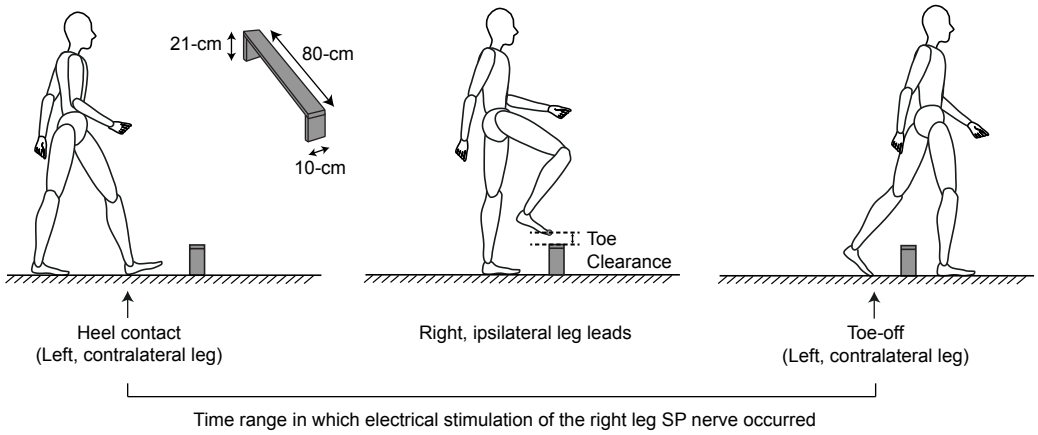
21-cm
80-cm
10-cm
Toe
Clearance
Heel contact
(Left, contralateral leg)
Right, ipsilateral leg leads
Toe-off
(Left, contralateral leg)
Time range in which electrical stimulation of the right leg SP nerve occurred

Figure 1

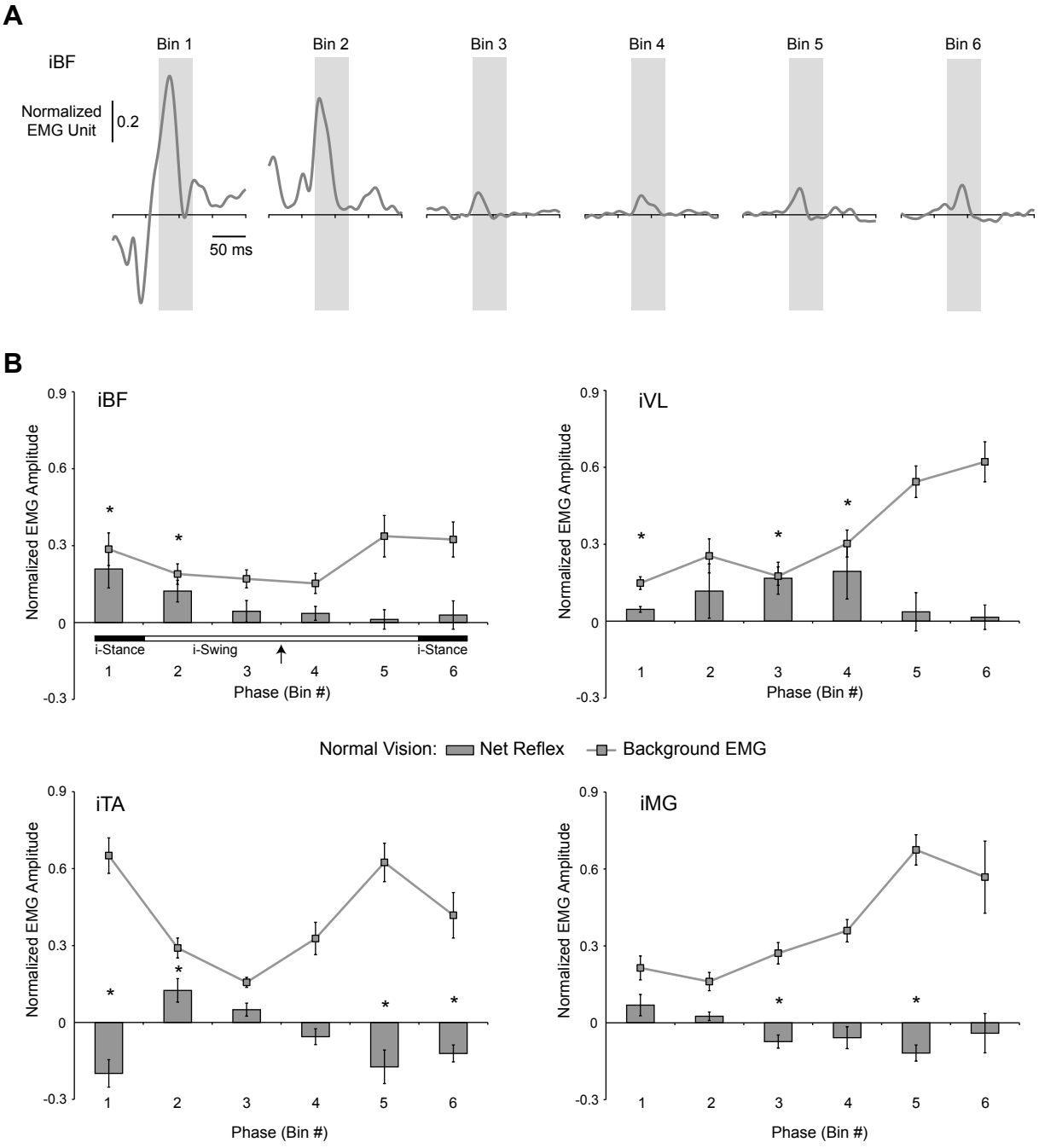
A
Bin 1
Bin 2
Bin 3
Bin 4
Bin 5
Bin 6
iBF
Normalized EMG Unit
0.2
50 ms
B
iBF
iVL
iTA
iMG
Normalized EMG Amplitude
0.9
0.6
0.3
0
-0.3
i-Stance
i-Swing
i-Stance
1
2
3
4
5
6
Phase (Bin #)
Normal Vision: Net Reflex Background EMG

Figure 2

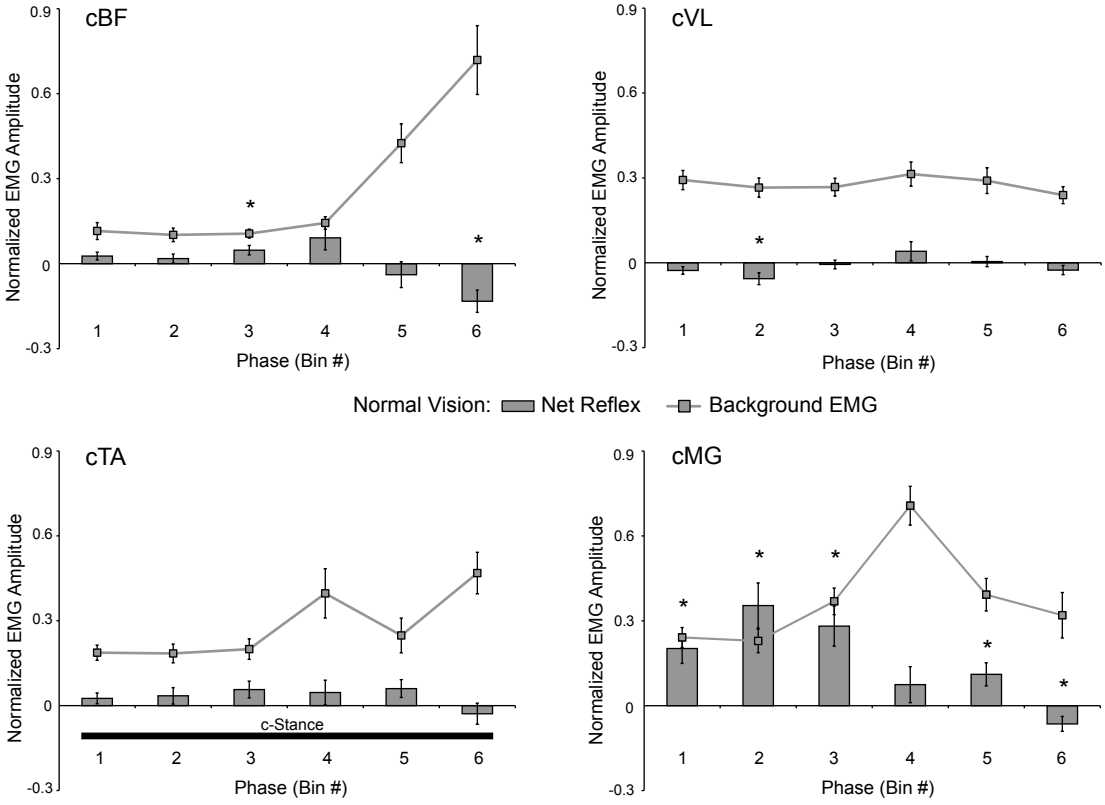
cBF
cVL
cTA
cMG
Normalized EMG Amplitude
Phase (Bin #)
0.9
0.6
0.3
0
-0.3
1
2
3
4
5
6
*
Normal Vision: Net Reflex Background EMG
c-Stance

Figure 3

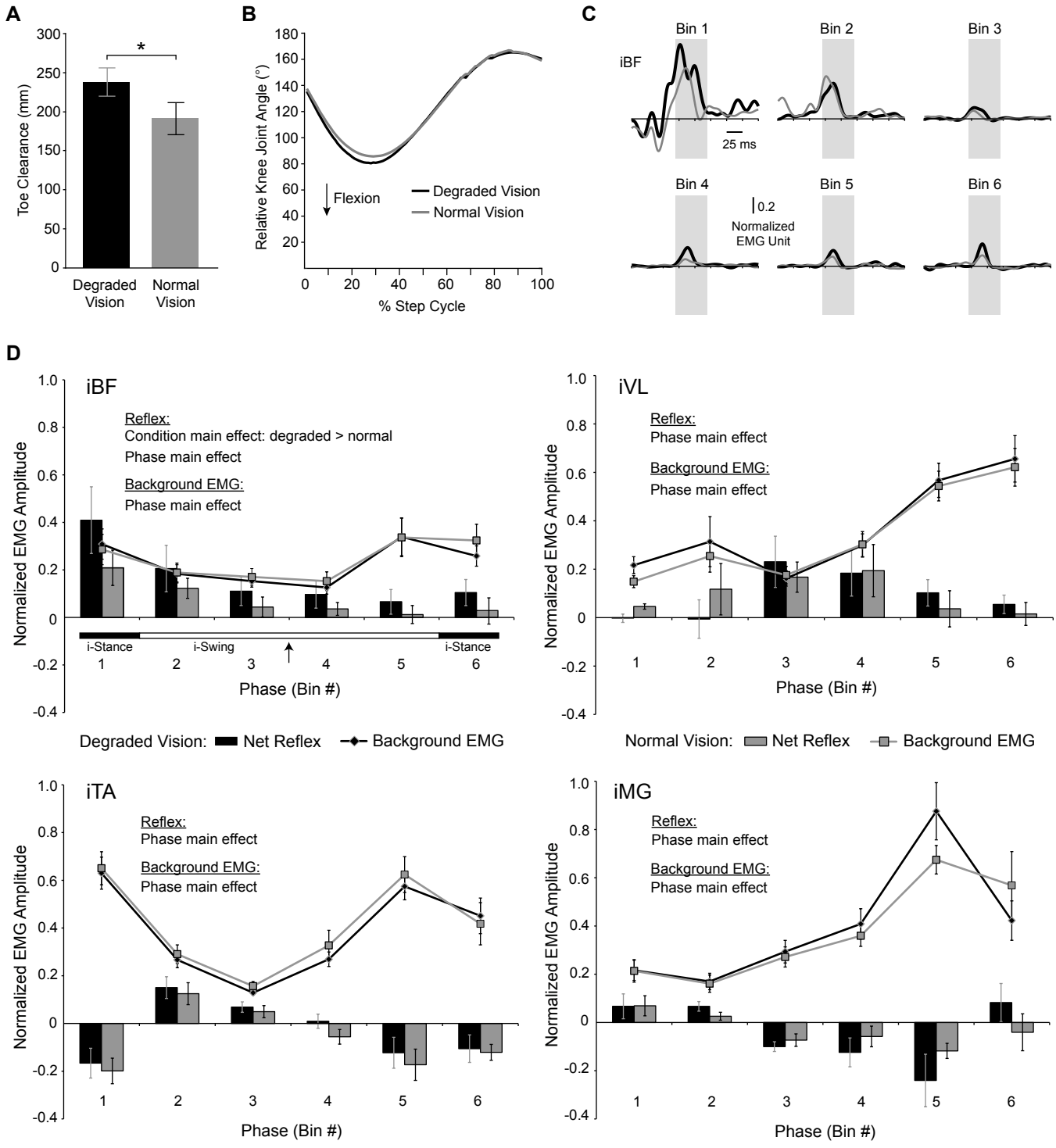
A
Toe Clearance (mm)
Degraded Vision
Normal Vision
B
Relative Knee Joint Angle (°)
Flexion
Degraded Vision
Normal Vision
% Step Cycle
C
Bin 1
Bin 2
Bin 3
iBF
25 ms
Bin 4
Bin 5
Bin 6
0.2
Normalized EMG Unit
D
iBF
Reflex:
Condition main effect: degraded > normal
Phase main effect
Background EMG:
Phase main effect
i-Stance
i-Swing
i-Stance
Phase (Bin #)
Normalized EMG Amplitude
Degraded Vision: Net Reflex Background EMG
iVL
Reflex:
Phase main effect
Background EMG:
Phase main effect
Normal Vision: Net Reflex Background EMG
iTA
Reflex:
Phase main effect
Background EMG:
Phase main effect
iMG
Reflex:
Phase main effect
Background EMG:
Phase main effect

Figure 4