Disturbance of neural coupling between upper and lower limbs during gait transition

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ABSTRACT

Humans spontaneously alternate between walking and running with a change in locomotion speed, which is termed gait transition. It has been suggested that sensory information in the muscle is a factor that triggers the gait transition; however, direct evidence for this has not been presented. In addition, it has been suggested that upper limb movement during human gait facilitates leg muscle activity due to the neural coupling between the upper and lower limbs. We hypothesized that a disturbance of afferent inputs in the neural coupling between the upper and lower limbs suppressively act on the gait transition. Here, we aimed to deepen the understanding of contribution of the afferent inputs in neural coupling between the upper and lower limbs to the gait transition. Eight participants performed spontaneous walk-to-run and run-to-walk transitions under two different conditions: Normal (arms swinging normally); and TIS (partial blocking of afferent inputs from the arms by inducing tourniquet ischemia). We compared the preferred gait transition speeds (PTS), joint angles, muscle activities, and muscle synergies between the two conditions. Control of coordinated muscle activities can be investigated by analyzing muscle synergies, which are groups of muscles that activate together. The PTS, joint angle profiles, muscle activity profiles, and muscle synergies were nearly identical between conditions (walk-to-run PTS at Normal and TIS: 6.9 ± 0.4 and 6.9 ± 0.4 km/h; run-to-walk PTS at Normal and TIS: 6.6 ± 0.4 and 6.5 ± 0.4 km/h; p = 0.869 and p = 0.402, respectively). Therefore, we conclude that the control of gait transition is little affected by disturbing the neural coupling between the upper and lower limbs by reducing afferent inputs from the forearms and distal upper arms. Our findings might reflect robustness of the neural coupling between the upper and lower limbs during locomotion against neural perturbations or disturbances.

1. Introduction

Humans select an appropriate mode of locomotion to move efficiently. A walk-to-run transition (WRT) occurs with increasing locomotion speeds, while a run-to-walk transition (RWT) occurs as the locomotion speed decreases. Investigating the gait transition helps to better understand the control of selection of efficient locomotion modes. Many studies have investigated the factors that act as triggers for gait transition. The preferred gait transition speed (PTS) has consistently been reported to occur within a narrow range of speeds (approximately 7 km/h) in healthy adults [1]. Scientists [2,3] have suggested that gait transition is triggered by metabolic costs. However, the metabolic cost cannot completely explain the WRT in humans [4] because it occurs at speeds slower than those predicted by the metabolic cost hypothesis.

Studies have proposed several alternative triggers of the WRT, including the muscle-specific overexertion [5] or muscle force-velocity-length relationships [6]. In addition, Kung et al. (2018) supposed that the proprioceptors in the muscles, which provide feedback about how hard the muscles are working, might be the determinants of gait transition [7]. This is derived from the evidence that the WRT speeds become faster when the muscular effort required by the hip flexors, ankle plantar-flexors, and dorsi-flexors are reduced by assistive devices [8]. However, direct evidence that the sensory information contributes to gait transition is not proposed.

Although the profiles of joint angles, angular velocities, and most joint torques are similar for walking with and without arm swinging [9], we cannot ignore the benefits of arm swinging for locomotion. For example, arm swinging during locomotion reduces vertical
displacement of the center of mass [10], offsets the generation of angular momentum [11], and reduces angular displacement [12]. In addition, active arm movement has been found to significantly increase activation in leg muscles during combined arm/leg recumbent stepping [13]. It might indicate that the arm swinging during human gait affects the leg muscle activity due to the neural coupling between the upper and lower limbs [14]. Muscle activation durations or levels might not be optimized when the neural coupling between arms and legs is disturbed, and the PTS might be decreased by unoptimized muscle activations. However, how disturbance of the neural coupling between the upper and lower limbs affects the PTS remains unclear.

Our purpose was to deepen the understanding of afferent information in the neural coupling between the upper and lower limbs and its contribution to gait transition. For that purpose, we compared the PTS, joint angles, muscle activities, and coordinated muscle activation patterns among two different conditions (normal arm swinging and partial blocking of the afferent inputs from the arms). Hagio et al. (2015) revealed that muscle activities during the gait transition can be explained by nine coordinated muscle activation patterns, and they suggested that the specific patterns are regulated by the afferent information or changing the descending neural input. Our speculation is that the factor for decreased PTS by partial blocking of the afferent inputs from the arms can be described by the viewpoint of coordinated muscle activation patterns. We hypothesized that the PTS decreases and coordinated muscle activation patterns are modulated when the afferent inputs from the arms are partially blocked.

2. Methods

2.1. Participants

Eight healthy men participated in this study (age: 24 ± 2 years, height: 176 ± 10 cm, body mass: 68 ± 10 kg [average ± standard deviation]). Participants had no musculoskeletal or neurological disorders. The participants provided written informed consent to participate in the study after receiving a detailed explanation of the purpose, potential benefits, and risks associated with participation. The experimental procedures were conducted in accordance with the Declaration of Helsinki and were approved by the Local Ethics Committee of the Graduate School of Human and Environmental Studies at Kyoto University (30-H-28).

2.2. Experimental setup

The experiments were conducted on a treadmill (SA-T652, SportsArt, Tainan, Taiwan). The walking surface of the treadmill was 1.55 m long and 0.55 m wide. All the participants walked or ran on the treadmill at 5.0–7.5 km/h to familiarize themselves with treadmill walking and running before the measurement. Participants were asked to choose their own gait pattern—either walking or running—including a natural gait transition depending on the treadmill speed (set to steadily increase or decrease) [1]. Participants started walking at a speed of 4.0 km/h, and the treadmill speed was continuously increased by 0.1 km/h every 1 s. After the WRT, the treadmill speed was increased to 7.5 km/h; the participants ran for 10 s at this speed. Then, the speed was decreased to 4.0 km/h by 0.1 km/h every 1 s, and the RWT occurred similarly. Participants performed one WRT and RWT in a trial. We asked participants to start running with the right leg.

Participants walked or ran with arms swinging normally (Normal) and arms with tourniquet ischemia (TIS). TIS induces partial blocking of the sensory afferent inputs in humans when standing or walking [15,16]. A tourniquet with 10 cm width (AG-101 CUFF INFLATOR, AIR SOURCE, E20 Rapid Cuff Inflator, Hokanson, Bellevue, USA) was placed around both middle of upper arms to block the afferent inputs from the arms and inflated for 20 min at 200 mmHg [15]. To reduce the kinematic and kinetic changes in arm swinging while utilizing the tourniquet, the tourniquet was placed around the middle of the upper arms. We verified ischemia of the arms by enquiring the participants about the presence or absence of sensation in their arms. Participants experienced dysesthesia in the upper arm (e.g., in the biceps brachii, coracobrachialis, and triceps brachii), forearm, and hand muscles induced by tourniquet ischemia. We confirmed that all participants lost their sensation at their forearms after 20 min of tourniquet ischemia application. In the case of the TIS condition, the cuff pressure was maintained at 200 mmHg during walking and running.

2.3. Data collection

Reflective markers were attached to 30 anatomical landmarks in the whole body [17]. Those position coordinate values were measured by a three-dimensional motion capture system with 18 cameras (OptiTrack V100:R2, NaturalPoint, Inc., Corvallis OR, USA) operating at 100 Hz.

EMG data of the following 16 muscles in the right lower limb and trunk were recorded: the gastrocnemius medialis (MG), gastrocnemius lateralis (LG), soleus (SOL), tibialis anterior (TA), vastus lateralis (VL), rectus femoris (RF), biceps femoris (BF), adductor longus (AL), gluteus medius (Gmed), gluteus maximus (Gmax), erector spinae at L5 (ES), abdominal external oblique (EO), anterior deltoid muscle (DeltA), posterior deltoid muscle (DeltP), superior trapezius (TrapSup), and latissimus dorsi (LatDors). The electrode placement locations were carefully chosen using an ultrasonic device to minimize crosstalk from the adjacent muscles. The electrodes were placed based on recommendations from the SENIAM project (seniam.org). The EMG signals were amplified (SX230-1000, Biometrics, Gwent, UK) and bandpass filtered between 20 and 450 Hz [17]. All electrical signals were recorded at a sampling frequency of 1,000 Hz and stored in the hard disk of a personal computer using a 16-bit analog-to-digital converter (PowerLab/16SP; AD Instruments, Sydney, Australia).

One gait cycle was the time from right heel contact to the next. Walking and running were generally determined by whether a double stance phase was present or absent. Walking has a double stance phase, and running is characterized by a flight phase. Hence, we judged walking and running by whether or not the left toes were in contact with the treadmill surface when the right heel was in contact. The transition step, also termed the zero step, was defined as the step initiating a flight phase (WRT) or the step initiating a double stance phase (RWT).

2.4. Analysis of the joint angle and muscle activities

To identify the gait-related events, a velocity-based algorithm, proposed by O’Connor and colleagues [18], was implemented [19]. The times of heel contacts and toe-offs were defined as the local minima and maxima of the vertical velocity of the center of mass of the foot segments, respectively, as measured via motion analysis.

We compared the profiles of the joint angles, muscle activities, and coordinated muscle activation patterns between the Normal and TIS conditions. We analyzed the kinematics and EMG data of 8 gait cycles before and after gait transition. The position coordinate values of the reflective markers were smoothed using a low-pass digital Butterworth filter. The cutoff frequency (4–20 Hz) was selected per a position coordinate value based on the residual analysis [20].

The EMG signals were high-pass filtered (40 Hz) with a zero lag fourth-order Butterworth filter to remove the noise. Thereafter, the EMG signals were demeaned, digitally rectified, and low-pass filtered at 15 Hz with a zero lag fourth-order Butterworth filter [1]. The low-pass filtered EMG signals were time interpolated over one gait cycle motion to fit a normalized 200-point time base. Each muscle activity was normalized to the peak activity for each muscle among all conditions [17].

2.5. Analysis of muscle synergies

The coordinated muscle activation patterns are modeled as a muscle
synergy [21], which are groups of muscles that activate together. The muscle synergies were extracted by using a non-negative matrix factorization (NMF) algorithm [21]. We extracted muscle synergies from a 16 muscle \times 34 gait cycle-sized matrix (16 muscles \times 6800 time steps) for each participant. The muscle activation pattern for a condition (\( M \)) is represented by the following equation:

\[
M = \sum_{i=1}^{N} w_i c_i + \epsilon \quad w_i \geq 0 \quad c_i \geq 0
\]

where \( N \) is the number of synergies, \( w_i \) is the weighting of a muscle in a muscle synergy \( i \), \( c_i \) denotes an activation that involves a relative contribution of the muscle synergy, and \( \epsilon \) is the residual. The composition of the muscle synergy, \( w_i \), does not change within a condition, but the activation, \( c_i \), changes within a condition. The weightings of each muscle synergy and activation coefficient were normalized such that the individual muscle weighting vector was a unit vector.

To determine the number of synergies, we calculated the variability accounted for (VAF) as an indication of the goodness of fit. The VAF was calculated as follows: 100 \times the coefficient of determination from the uncentered Pearson correlation coefficient. The number of muscle synergies in all participants and conditions was defined as the minimum number of synergies at which the average VAF exceeded 90% [22].

We classified muscle synergies across all participants and conditions into a set of clusters using an unsupervised classification (k-means clustering) according to the similarity of coordination patterns in the 16-dimensional Euclidean space [23]. We calculated the silhouette values of each classification while changing the number of the clusters from 2 to 16 to estimate the optimal number of clusters. We defined the optimal number of clusters as the one that yielded the largest mean silhouette value across all possible muscular coordination patterns; optimal number of clusters was found to be nine. Thereafter, we classified the muscle synergies of all participants and conditions into nine clusters using the following MATLAB functions: pdist (Minkowski option, \( P = 3 \)), linkage (Ward option), and cluster [24].

3. Results

3.1. PTS, joint angle, and EMG

We observed no significant difference in PTS among the different conditions and the moderate evidence for the H0 (Table 1). The cosine similarities in joint angles between the Normal and TIS conditions exceeded 0.95 (see Supplementary material). The cosine similarities in EMGs between the Normal and TIS conditions exceeded 0.92 (see Supplementary material).

3.2. Muscle synergies

There was no significant difference in VAF between the Normal and TIS conditions (\( p > 0.38 \)). The weightings of muscle synergies and their activation levels are illustrated in Fig. 1. The cosine similarities in the average weightings and activations exceeded 0.82 (see Supplementary material).

Synergy-1 was mainly composed of ankle plantar flexors (MG, LG, and SOL), and this synergy activated during the propulsion phase. Synergy-2 mainly included the shoulder extensors (DeltP and LatDors) and scapular elevator (TrapSup). Synergy-2 was activated at the time of left heel contact. Synergy-3 mainly comprised the hip adductors (AL), lumber extensors (ES), and shoulder flexors (DeltA). Activation levels of Synergy-3 were relatively low as compared with the other two synergies. Synergy-4 mainly comprised the hip flexors (RF) and hip adductors (AL). Like Synergy-3, the activation levels of Synergy-4 were relatively small. Synergy-5 mainly included the hip extensors (BF). Synergy-5 activated during the swing phase. Synergy-6 mainly comprised the hip adductors (AL), lumber extensors (ES), and trunk rotators (EO). Synergy-6 activated during walking and running (left heel contact and the swing phase, respectively). Synergy-7 predominantly comprised the ankle dorsiflexors (TA) and hip extensors (BF) and activated during the swing phase. Synergy-8 predominantly consisted of the ankle dorsiflexors (TA) and hip extensors (BF) and activated during the swing phase. Synergy-9 mainly comprised the knee extensors (VL and RF), hip abductors (Gmed), and hip extensors (Gmax). Synergy-9 activated at the time of right heel contact.

4. Discussion

Our purpose was to deepen the understanding of afferent input in neural coupling between the upper and lower limbs and its contribution to gait transition. Contrary to our hypothesis, we observed that partial blocking of afferent input from the arms did not affect the PTS. This finding suggests that the neural coupling between the upper and lower limbs during locomotion robustly acts during gait transition against disturbances, and is notable evidence to explain the flexible locomotion control.

Our results revealed that the joint angle profiles, EMG profiles, muscle synergy weightings and activations were nearly identical between the Normal and TIS conditions (range of cosine similarities: 0.82–0.99), suggesting that the CNS can appropriately regulate muscle activations and joint angles in the case where the afferent input from the arms is weakened. Such robustness of the neural coupling between the upper and lower limbs was also seen in a previous study revealing that passively imposed upper limb movements in incomplete cervical spinal cord injury patients acted to modulate locomotor-like muscle activity [27]. Thus, humans have the robustness of the neural coupling between the upper and lower limbs during locomotion, and such robustness might contribute to flexible control of locomotion. However, invasive disturbances or disconnection of the neural coupling would affect the muscle activity. Cheung et al. (2005) investigated muscle synergies during swimming and jumping in bullfrogs before and after deafferentation. They speculated that few synergies, specific to the intact states, might represent afferent-specific modules [24]. Moreover, another study reported that both the weightings and activations of synergies were severely affected in mice that lacked sensory feedback from muscle spindles [28]. Therefore, muscle synergies during gait...
transition might be affected by invasive disconnection of afferent inputs in the neural coupling, and such modification of the neuromuscular system might act suppressively on the PTS.

This study includes some limitations. We did not quantitatively estimate the sensory loss. However, it has been reported that a period of 15–25 min of ischemia was required to block the Ia afferents to the level at which the H-reflex and stretch reflex amplitudes had decreased to <10% of the baseline amplitude [16]. In addition, we verified that the tactile sensation of participants at their fingertips disappeared after 15–20 min of tourniquet ischemia application in our previous study [15]. In this study, the cuff pressure was maintained at 200 mmHg during walking and running. Therefore, we suppose that the afferent inputs from the arms were reduced.

Loss of afferent inputs from the arm flexor and extensor muscles was incomplete as the deltoid and pectoralis major muscles were not ischemic. To achieve complete loss, invasive blocking is required as tourniquet application is difficult for the pectoralis major muscles due to its location. In case of applying the tourniquet application to the shoulders, ischemia of certain trunk segments is required as some shoulder muscles have their origins in the trunk segment. This would affect the kinematic or kinetic of the arm swinging. In this study, although the deltoid or pectoralis major muscles were not ischemic, the biceps brachii, coracobrachialis, and triceps brachii were ischemic. Besides, the participants experienced substantial arm dysesthesia. Therefore, we concluded that disturbance of neural coupling between the upper and lower limbs occurred.

In this study, although the number of participants was small, it was relatively larger than those in previous studies (5–7 participants) [1,5]. Moreover, we verified that the p-values for PTS between the Normal and TIS conditions were high and that the evidence for the H0 was moderate (Table 1). Therefore, the average PTS would not differ significantly even if the number of participants increased.

![Fig. 1. Weightings and activation levels of the muscle synergies. (A) The average weightings of the muscle synergies among participants. Green bars represent the Normal condition, red bars denote the TIS condition. (B) The ensemble average activation levels of the muscle synergies among participants are indicated as color maps. The vertical axis shows the gait transition step (defined as the gait transition ± 8 gait cycles), and the horizontal axis indicates the phase of one gait cycle (from the onset of the right leg to the next; normalized to 200 time bins). The white dotted area indicates the gait transition cycle. The red and blue lines denote average left heel contact and right toe off timing, respectively.](image-url)
We cannot discuss the effect of partial blocking of afferent input from the lower limbs on gait transition. We applied TIS to the upper arms because we judged that applying TIS to the lower limbs during high walking speeds is dangerous for the participants. However, it has been reported that afferent input from the feet can be a substantial factor in the motor control of gait [29]. Therefore, the influence of disturbing the neural coupling between the upper and lower limbs by partially blocking afferent input from the lower limbs might be large. In future studies, we must investigate the effect of partially blocking afferent input from the lower limbs on the PTS after designing a safe experimental setup. It would reveal the significance of the lower limbs in the neural coupling between the upper and lower limbs during gait transition.

5. Conclusion

We conclude that the control of gait transition is little affected by disturbing the neural coupling between the upper and lower limbs by reducing afferent input from the forearms and distal upper arms. Our findings might reflect robustness of the neural coupling between the upper and lower limbs during locomotion against neural perturbations or disturbances.

6. Data availability

The datasets analyzed in the current study are available from the corresponding author upon reasonable request.

7. Cord availability

The custom cords in the current study are available from the corresponding author upon reasonable request.

CRediT authorship contribution statement

Benio Kibushi: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing.
Naoto Kihira: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft.
Toshibo Moritani: Conceptualization, Funding acquisition, Project administration, Supervision, Validation.
Motoki Kouzaki: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neulet.2021.136100.

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