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Processes of anticipatory postural adjustment and step movement of gait initiation

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ABSTRACT

The purpose of this study was to elucidate whether the anticipatory postural adjustment (APA) and focal step movement of gait initiation are produced as a single process or different processes and whether the APA receives an inhibitory drive from the ongoing stop process of gait initiation. Healthy humans initiated gait in response to a first visual cue that instructed the initial swing leg. In some trials, a switch or stop cue was also provided after the first cue. When the stop cue was provided, participants withheld gait initiation. When the switch cue was provided, participants immediately switched the initial swing leg. In both the stop and switch tasks, the APA in response to the first cue, represented by the S1 period of the displacement of the center of pressure, appeared in more than half of the trials in which the withholding of gait initiation or switching of the initial swing leg was successfully completed. These findings indicate that the APA and focal step movement of gait initiation are produced as a dual process. In trials in which the APA in response to the first cue appeared, the amplitude and duration of the APA were decreased when the participants switched the initial swing leg or withheld gait initiation. This finding indicates that the ongoing stop process of gait initiation produces an inhibitory drive over the APA. The decreases in the amplitude and duration of the APA during the switching of the initial swing leg were similar to those during the withholding of gait initiation; moreover, the decreases during the switching of the initial swing leg were positively correlated with the decreases during the withholding of gait initiation. Thus, the stop processes during switching the initial swing leg and withholding gait initiation likely share a common inhibitory mechanism over the APA.

1. Introduction

Gait initiation is referred to as the transition between an upright stance and steady-state gait (Caderby et al., 2013; Mickelborough, Van Der Linden, Tallis, & Ennos, 2004). Leg movement of gait initiation is initiated with heel off of the initial swing leg (Caderby, Yiou, Peyrot, Begon, & Dalleau, 2014; Ruget, Blouin, Teasdale, & Mouchnino, 2008). Prior to heel off of the initial swing leg, the displacement of the center of pressure (COP) occurs (Burleigh-Jacobs, Horak, Nutt, & Obeso, 1997; Mann, Hagy, White, & Liddell, 1979; Ruget et al., 2008). The COP initially moves to the initial swing side and backward (S1 period), subsequently moves to the initial stance side in the next moment (S2 period), and ultimately moves forward (S3 period)

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before gait initiation as shown in Fig. 1 (Hass, Waddell, Wolf, Juncos, & Gregor, 2008). The COP displacement in the S1 period correlates well with the momentum to the initial stance leg before gait initiation, which indicates that the medio-lateral displacement of the COP in the S1 period contributes to the shift of the center of gravity to the initial stance leg (Polcyn, Lipsitz, Kerrigan, & Collins, 1998). Based on this view, the COP displacement in the S1 period before gait initiation is considered an anticipatory postural adjustment (APA) (Caderby et al., 2014; Mouchnino, Robert, Ruget, Blouin, & Simoneau, 2012; Sun, Guerra, & Shea, 2015).

One issue to be elucidated regarding the APA that precedes gait initiation is whether the APA and focal step movement of gait initiation are produced as a single process or different processes. There are two potential models of this issue (Massion, 1992; Massion, Alexandrov, & Frolov, 2004; Stuart, 2005). One model includes a single process model in which the APA and focal step movement are produced as a single process, and the other model includes a dual process model in which the APA and focal step movement are produced as different processes (Caderby et al., 2014; Corbeil & Anaka, 2011; Hass et al., 2008; Huntley & Zettel, 2015; Leonard, Brown, & Stapley, 2009; Robert, Blouin, Ruget, & Mouchnino, 2007; Schepens & Drew, 2003; Slijper, Latash, & Mordkoff, 2002; Stamenkovic & Stapley, 2016). Several previous findings support the dual process model. There was a decoupling of the onset of the APA and that of the reaching movement in cats (Schepens & Drew, 2003). The path and kinematics of hand movement during reaching to a target was not changed by the modulation of the initial APA setting in standing (Robert et al., 2007). Moreover, the reaction time of arm movement in standing was negatively correlated with the onset of the APA (Slijper et al., 2002).

However, other findings support the single process model. Both the onset of the focal muscle activity and the onset of the postural muscle activity were similarly changed with temporal and spatial foreknowledge (Huntley & Zettel, 2015). The postural activity of the leg muscles that preceded reaching was dependent on the direction of the reaching (Leonard et al., 2009). Similarly, the trunk muscle activity during stance was dependent on the direction of reaching (Stamenkovic & Stapley, 2016). These previous findings support a view that focal movement and postural activity are produced as a single process. Moreover, there are several findings that indicate the APA and focal step movement of gait initiation are produced as a single process. Limb movement of gait initiation is delayed when the APA is mechanically perturbed, which indicates that the APA process interacts with the process of the focal step movement of gait initiation (Mille, Simoneau, & Rogers, 2014). The APA amplitude increases as the velocity of gait initiation increases (Caderby et al., 2014). The APA amplitude before stepping depends on the direction of the initial step (Corbeil & Anaka, 2011; Hass et al., 2008).

The present study was conducted to obtain further insights into the coordination between the APA and focal step movement of gait initiation by investigating the COPs in three tasks. In one task, the participants initiated gait with the leg instructed by a first cue. In the second task, the initial swing leg of gait initiation in response to a first cue was switched

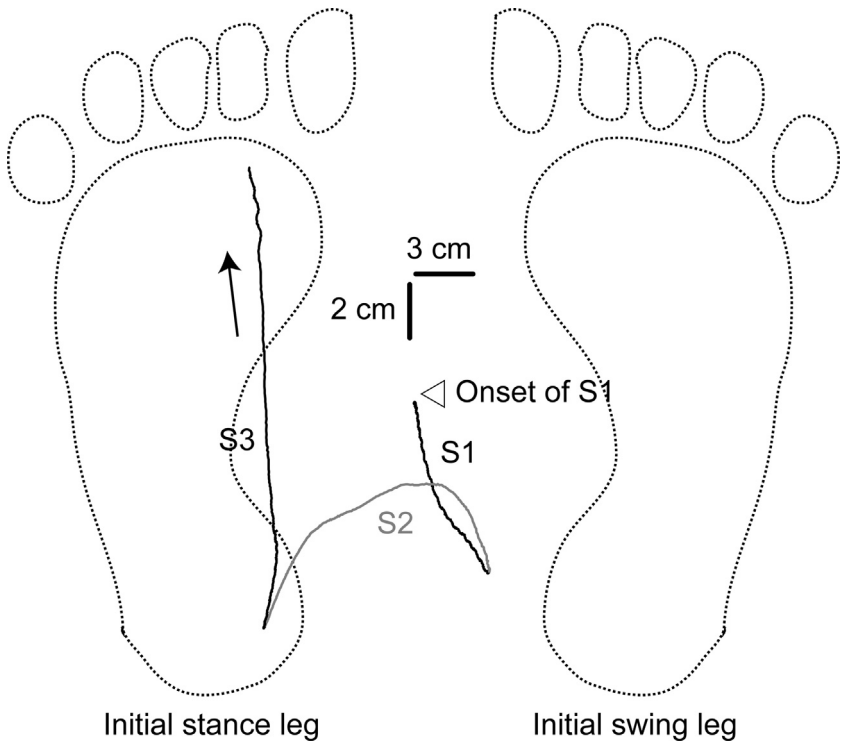

Fig. 1. Three periods of the COP displacement in response to the first cue before gait initiation in the go task of the right leg condition. An arrow indicates the direction of the COP displacement.

by the switch cue provided after the first cue. In the third task, the focal step movement of gait initiation in response to the first cue was withheld by a stop cue provided after the first cue. According to the horse race model, the go and stop processes compete when an individual attempts to withhold a motor response. When the stop process is completed before the go process, the motor response does not appear; however, if the go process is completed before the stop process, the motor response appears (Logan, Cowan, & Davis, 1984; Verbruggen & Logan, 2009). In the gait initiation tasks conducted in the present study, the go process of gait initiation must be triggered by the first cue, and the stop process must be triggered by the stop cue. Thus, the horse race model is applicable for the task in which the stop cue is provided after the go cue. In addition, the stop change process, during which the stop process occurs before the alternative response process, occurs during the switch process (Band & van Boxtel, 1999; Logan & Burkell, 1986; Verbruggen, Schneider, & Logan, 2008). A motor response is inhibited not only by the stop process but also the switch process of one motor response to another motor response (Logan & Burkell, 1986). Therefore, the stop process must be loaded not only by the stop cue but also the switch cue. Based on this view, we suppose that the go process of gait initiation triggered by the first cue competes with the simultaneously loaded stop process of gait initiation triggered by the switch or stop cue (Fig. 2).

The amplitude and duration of the startle auditory stimulus-induced APA increase as the stimulus comes closer to the imperative go cue for step initiation; however, the corticospinal excitability of the initial agonist of the focal step movement of gait initiation begins to increase 100 ms after the go cue (MacKinnon et al., 2007). This finding indicates that the APA process is initiated before the go process of the focal movement of step initiation. If this theory is true, the completion of the APA process may also be earlier than the completion of the go process of focal step movement of gait initiation. Based on this view, three hypotheses are established. The APA in response to the first cue must be absent when the focal step movement of gait initiation is successfully withheld, if the APA and focal step movement are produced as a single process (Fig. 2A). The APA in response to the first cue must also be absent when the focal step movement of gait initiation is successfully withheld, if the APA and focal step movement are produced as a dual process and the stop process is completed before the go process of the APA (Fig. 2B). The APA must be present when the focal step movement is successfully withheld by the stop process, if the APA and focal step movement of gait initiation are produced as different processes, and the stop process is completed before the completion of the focal step movement process and after the completion of the APA process (Fig. 2C).

As previously discussed, in accordance with the horse race model, the APA in response to the first cue appears when the focal step movement of gait initiation is successfully withheld in some trials, if the APA and focal step movement of gait initiation are produced as different processes, and the stop process in response to the second cue is not completed before the

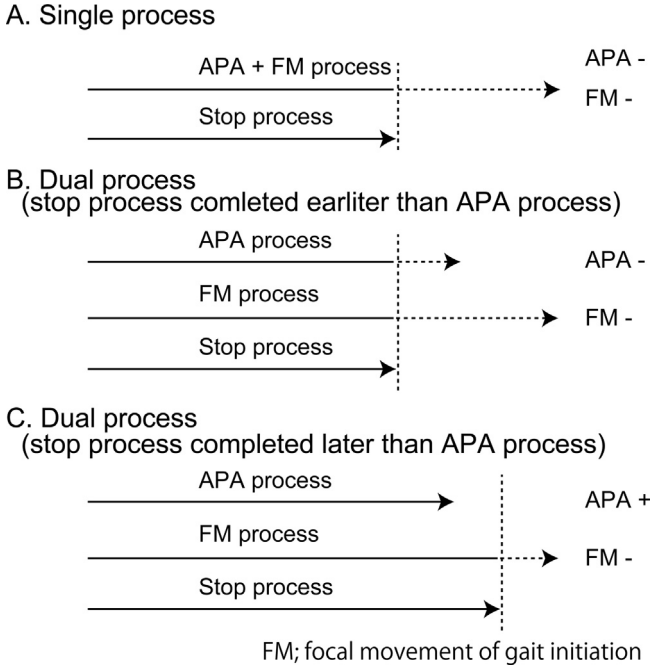

Fig. 2. Hypotheses regarding the processes of the APA and focal step movement of gait initiation when the stop process is triggered by the second cue based on the horse race model. The APA is absent if the focal step movement of gait initiation is successfully withheld and the APA and focal step movement are produced as a single process (A). The APA is absent if the focal step movement of gait initiation is successfully withheld and the APA and focal step movement are produced as a dual process, whereas the stop process is completed before the go process of the APA (B). The APA is present when focal step movement is successfully withheld by the stop process, if the APA and focal step movement of gait initiation are produced as different processes, and the stop process is completed before the completion of the focal step movement process and after the completion of the APA process (C). APA−; APA in response to the first cue is absent; APA+; APA in response to the first cue is present; FM−; focal movement is successfully cancelled.

completion of the go process of the APA in response to the first cue (Fig. 2C). In this case, another question is whether the APA in response to the first cue is modulated by the ongoing stop process of the focal step movement of gait initiation when the APA appears. It has been reported that the displacement of arm movement to the target induces online corrections of the postural adjustment in standing (Leonard, Gritsenko, Ouckama, & Stapley, 2011). An online correction of the APA is also induced by the external perturbation before stepping (Mouchnino et al., 2012). More importantly, when humans responded to a randomly presented target that instructed the stepping side accompanied by randomly directed perturbation, multiple APAs appeared in some cases; however, only one APA appeared when the side of the compensatory stepping was predetermined before perturbation was applied (Jacobs & Horak, 2007). When the stepping leg is predetermined, the step movement process must be loaded before the perturbation. In contrast, when the stepping leg is instructed and perturbation is simultaneously provided, the step movement process must be loaded after the perturbation. Based on this view, the authors of this study suggest that the multiple APAs are related to the online selection of the step movement of one leg from two competing focal step movements. If this theory is true, the APA may be modulated by the ongoing stop process that competes with the initially implemented go process of the APA. We also tested this hypothesis.

The inhibition of the APA during the stop process and the stop change process before gait initiation may share a common inhibitory mechanism. A common inhibitory mechanism of a simple motor response has been identified in some experiments. A previous study has shown that the stop and switch processes share a common neural process (Band & van Boxtel, 1999). The pre-SMA plays a role in both switching and stopping motor responses (Isoda & Hikosaka, 2007; Li, Huang, Constable, & Sinha, 2006; Mars et al., 2009). Positive electroencephalographic activity of the non-involved side of the primary motor cortex during the go trials in the choice reaction time (CRT) task and that of the involved side of the primary motor cortex during the no-go trials were similarly present (see review by Burle, Vidal, Tandonnet, & Hasbroucq, 2004). These findings indicate that the inhibition of the non-involved motor response in the go trials and the inhibition of the prepared motor response in the no-go trials in the CRT task are mediated by a common inhibitory mechanism (see reviews by Burle et al., 2004 and by Mostofsky & Simmonds, 2008). In contrast, another finding indicates that the stop and change processes of the motor response are controlled by different neural mechanisms (Krämer, Knight, & Münte, 2011). According to these contradictory previous findings, it is not certain that the APA before gait initiation is inhibited by a common mechanism when gait initiation is withheld or the initial swing side of gait initiation is switched. We investigated whether the APA that precedes gait initiation is decreased by a common inhibitory mechanism during loading of the stop process for withholding of gait initiation or loading of the stop change process for switching of the initial swing leg.

2. Methods

2.1. Participants

Ten healthy humans aged 29.7 ± 1.7 years (9 males and 1 female) participated in this experiment. They had no history of orthopedic or neurological diseases. All participants provided written informed consent for study participation prior to the experiment. All procedures were approved by the ethics committee of Osaka Prefecture University.

2.2. Apparatus

A force plate (1G06/I-B, Nihon-Denki-Sanei, Tokyo, Japan) was used to measure the COP displacements. Analog signals from the force plate were digitized at a sampling rate of 1 kHz using an A/D converter (PowerLab 800/S ADInstruments, CO, U.S.A.) and were stored in a PC. A walkway with a length of 180 cm and a width of 60 cm was placed in front of the force

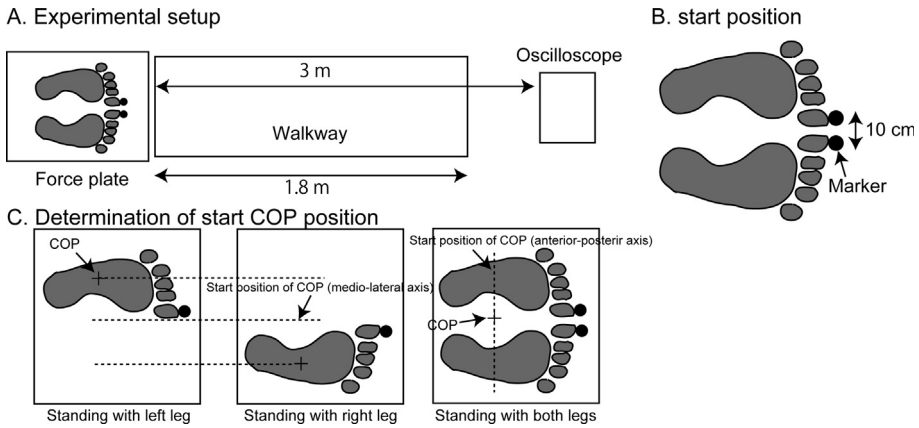

Fig. 3. Experimental setup (A), start position of the participant (B), and determination of the COP start position (C).

plate (Fig. 3A). An oscilloscope that indicated visual cues was placed 1 m beyond the end of the walkway. A video camera was placed beside the force plate so that the initial swing leg was visually determined offline.

2.3. Start position of COP and preferred initial swing leg

The participant maintained a standing position over the center of the force plate with the halluces 10 cm apart before gait initiation (Fig. 3B). The position of each hallux was preliminarily marked over the surface of the force plate, and each hallux was placed over each mark when they maintained standing over the force plate. To determine the start position of the COP on the medio-lateral axis, the participant maintained standing with the left leg when the left hallux was over the left mark and maintained standing with the right leg when the right hallux was over the right mark; the COP was recorded as shown in Fig. 3C (Procedure #1). The start position of the COP on the medio-lateral axis was the midline between the COP during standing with the left leg and the COP during standing with the right leg. The start position of the COP on the anterior-posterior axis was the average of the COPs on the anterior-posterior axis when maintaining a standing position with both legs (Fig. 3C). In the preliminary gait initiation trials, the participant initiated gait in response to a visual cue, and the initial swing side of the leg in 3 or more of 5 trials was considered to be the preferred initial swing leg (Procedure #2).

2.4. Task

Prior to gait initiation, the participant maintained standing with each hallux over each mark on the force plate (Fig. 3B) and gazed at the display placed in front of the participant (Fig. 3A). One of the six tasks was performed in response to the first and second cues. A first visual cue was provided when the COP was stable at the start position (Figs. 4 and 5). The participant initiated gait with the left leg when the first cue was presented at the position 40 mm left to the display midline (the left leg condition); gait was initiated with the right leg when the cue was presented at the position 40 mm right to the midline (the right leg condition) (Fig. 5).

In each leg condition, three types of the task were instructed by a second cue provided after the first cue (Fig. 5). When the second cue was not presented, the participant walked through the end of the walkway (go task). The correct side of the initial swing side of gait initiation in the go task was the leg ipsilateral to the side where the first cue indicated. When the second cue was presented at the side contralateral to the first cue (switch cue), the participant immediately switched the initial swing leg of gait initiation to the other leg (switch task). The correct side of the initial swing leg of gait initiation in the switch task was the side that the switch cue indicated. When the second cue was presented at the midline of the display (stop cue), they withheld gait initiation and maintained standing over the force plate (stop task).

2.5. Delay of second cue

The delay of the second cue was defined as the time between the first and second cues (Fig. 4). As indicated in Fig. 1, the COP initially moves to the initial swing side and backward (S1 period), subsequently moves to the initial stance side in the next moment (S2 period), and ultimately moves forward (S3 period) before gait initiation (Hass et al., 2008). The S1 period of the COP displacement in response to the first cue represents the APA before gait initiation (Caderby et al., 2014; Mouchnino et al., 2012; Sun et al., 2015). The delay of the second cue was provisionally determined so that the second cue preceded the onset of the S1 period of the COP displacement in response to the first cue (Fig. 4) (Procedure #3).

To provisionally determine the delay of the second cue, the participant performed 2 trials each for six tasks. The six tasks were performed in a random order to estimate the APA latency in the session to imitate the experimental session. The latency of the APA before gait initiation is approximately 300 ms in the CRT task (Hiraoka et al., 2014). Thus, in these pre-

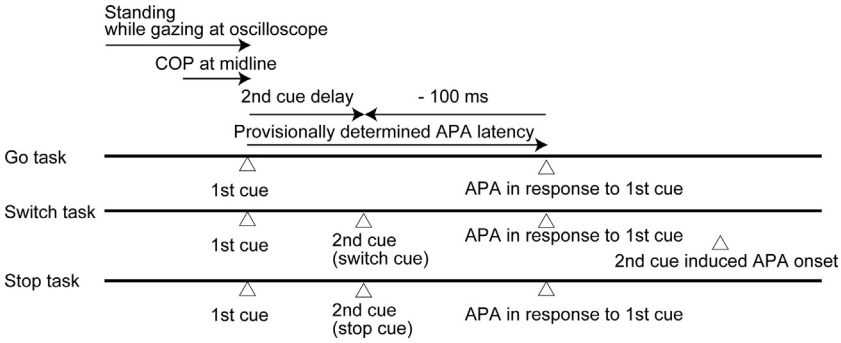

Fig. 4. Time protocol of the experimental trials. The mean APA latency presented in this figure is provisionally determined in the preliminary trials. The mean APA latency in the experimental trials was shorter than the mean APA latency provisionally determined in the preliminary trials as indicated in the text.

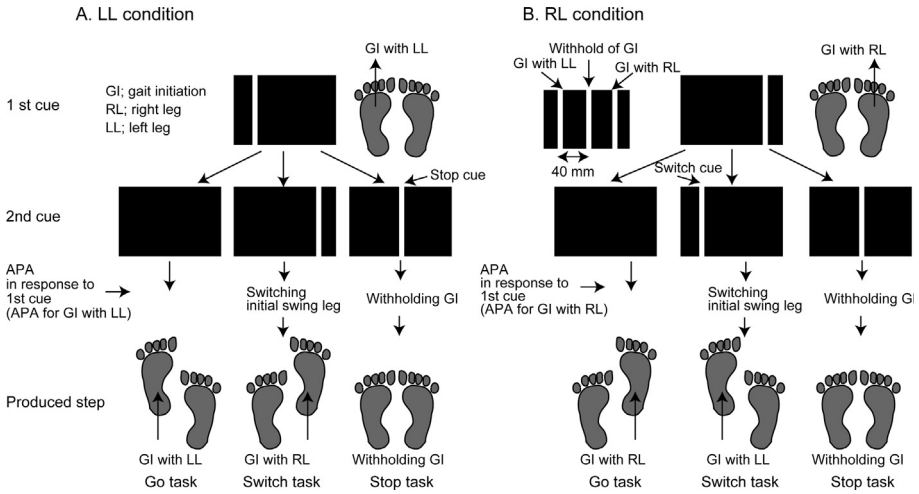

Fig. 5. Visual cues and step behaviors instructed by the cues.

liminary gait initiation trials, the second cue was provisionally presented 200 ms after the first cue. The average latency of the APA onset in response to the first cue was subsequently estimated from these 12 trials. The delay of the second cue was defined as the averaged latency of the onset of the APA in response to the first cue across the 12 trials minus 100 ms (Fig. 4). This procedure was implemented to ensure that the second cue is provided before the APA in response to the first cue, which enabled us to determine the effect of the second cue on the APA.

2.6. Procedure

In the experimental trials, 6 types of the gait initiation task, as previously described, were performed (Procedure #4). The type of the gait initiation task was randomly altered trial by trial. The recorded trials were classified into successful and unsuccessful trials during the experiment (Table 1). The trials in which the participant could not follow the instruction by the first cue, the trials in which the APA onset was earlier than the second cue (premature APA trials), the trials in which the initial swing leg was not switched in response to the switch cue (incomplete switch trials), and the trials in which gait initiation was not withheld in response to the stop cue (incomplete stop trials) were classified as unsuccessful trials. The unsuccessful trials were excluded from the APA analysis.

The trials other than the unsuccessful trials were classified as successful trials. The successful trials were classified into two types of trials: the No-APA trials, in which the COP initially moved to the initial stance side in response to the first cue, and the APA trials, in which the COP initially moved to the initial swing side in response to the first cue. Furthermore, the APA trials were classified into 2 types of trials. The trials in which the COP moved to the initial swing side first (S1 period) and subsequently moved to the forward direction and the initial stance side after the S1 period (S2 period) were classified as the S1-S2 trials. The trials in which the COP did not move forward or to the initial stance side after the S1 period, which indicates the absence of the apparent S2 period, were classified as the S1 trials.

Table 1
Classification of the trials.

	Total (N = 181 ± 20)			
	Successful (N = 171 ± 19)			Unsuccessful (N = 9 ± 2)
	APA (N = 133 ± 14)		No-APA (N = 38 ± 7)	Incomplete switch (N = 1 ± 0)
	S1-S2 (N = 114 ± 10)	S1 (N = 19 ± 4)		Incomplete stop (N = 2 ± 1)
				Premature APA (N = 7 ± 2)
Probability of No-APA	✓	✓	✓	
Probability of S1-S2	✓	✓	✓	
APA latency	✓			
APA amplitude	✓			
APA duration	✓			

In the present study, the APA in response to the first cue was examined. However, the APA in response to the first cue may be obscure in some trials because of the superimposition of the APA in response to the second cue over the APA in response to the first cue. Thus, we analyzed the amplitude, latency, and duration of the APA only in the trials in which the APA in response to the first cue was apparent. The amplitude, duration and latency of the COP displacement of the S1 were analyzed only in the S1-S2 trials because the onset and end of the S1 period were able to be identified as a result of the presence of the S1 and S2 onsets in these trials. In contrast, in the S1 trials, the estimation of these values was impossible because the end of the S1 was not obvious as a result of the lack of the S2 period. Thus, the amplitude, duration and latency of the APA were estimated from the COP traces in the S1-S2 trials (Table 1). The experimental session continued until ten of the S1-S2 trials were obtained in each type of the gait initiation task; thus, the amplitude, duration, and latency of the APA were estimated from 10 or more of trials.

2.7. Data analysis

The probabilities of the No-APA trials and the S1-S2 trials were expressed as the percentages of the numbers of successful trials. The probability of the incomplete stop trials was expressed as the percentage of the number of the trials in the stop task. The probability of the incomplete switch trials was expressed as the percentage of the number of the trials in the switch task.

The mean position of the COP in the time window from 200 to 0 ms before the first cue was estimated. The APA latency was defined as the time between the first cue and the APA onset (Fig. 6). The APA duration was defined as the time between the onset and end of the S1 period of the APA. The APA amplitude in response to the first cue was defined as the amplitude between the onset and end of the S1 period of the APA. These parameters were estimated from the COP traces in the S1-S2 trials because the identification of the COP displacement in the S1 period was possible only in the S1-S2 trials in which both the S1 and S2 periods in response to the first cue were apparent. The change in the amplitude or duration of the APA in the switch and stop tasks was expressed as the percentage of the amplitude or duration of the APA in the go task.

Two-way repeated measures ANOVA was conducted to test the two main effects: [initial swing leg * 2] and [gait initiation tasks * 3]. Another two-way ANOVA was conducted to test the other two main effects: [initial swing leg * 2] and [trial classification * 2]. When the ANOVA indicated a significant interaction between the main effects, a test of the simple main effect was conducted. Bonferroni's multiple comparison test was conducted as a post hoc test. The parameters analyzed via ANOVAs included the number of S1-S2 trials, the probability of No-APA trials, the COP position, and the latency, duration, and amplitude of the APA. A paired *t*-test was conducted to assess the difference in the probability of the incomplete stop trials and the incomplete switch trials between the leg conditions. Correlation coefficients were obtained to estimate the relationships between the probabilities of No-APA trials in the switch task and stop task, as well as the changes in the APA amplitudes or durations in the switch task and stop task. The alpha level was 0.05. Data are presented as the mean and standard error of the mean.

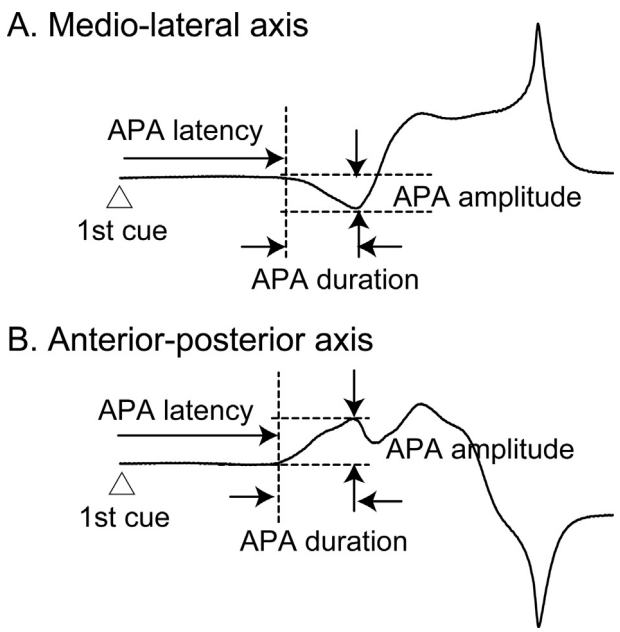

Fig. 6. Data analysis of the COP displacements on the medio-lateral axis (A) and anterior-posterior axis (B).

3. Results

In 9 of 10 participants, the preferred initial swing leg was the right leg. The delay of the second cue from the first cue was 214 ± 16 ms. The second cue was provided 69 ± 10 ms before the APA onset on the medio-lateral axis and 67 ± 10 ms before the APA onset on the anterior-posterior axis.

The probability of the incomplete stop trials in the stop task was 3.5 ± 1.1 % of the trials in the left leg condition and 3.2 ± 1.4 % of the trials in the right leg condition. There was no significant difference between the leg conditions ($p = 0.87$). The probability of the incomplete switch trials in the switch task was 2.1 ± 1.3 % of the trials in the left leg condition and 1.4 ± 0.9 % of the trials in the right leg condition. There was no significant difference between the leg conditions ($p = 0.34$).

In the left leg condition, the S1-S2 trials were in 90.8 ± 2.6 % of the successful trials in the go task, 54.1 ± 6.2 % in the switch task, and 74.0 ± 5.7 % in the stop task. In the right leg condition, the S1-S2 trials were in 79.4 ± 4.2 % of the successful trials in the go task, 47.3 ± 8.0 % in the switch task, and 69.0 ± 6.7 % in the stop task. The number of the S1-S2 trials expressed as the percentage of the number of successful trials was significantly different among the tasks [$F(2, 18) = 33.88$, $p < 0.01$]; however, it was not significantly different between the leg conditions [$F(1, 9) = 1.99$, $p = 0.19$]. There was no significant interaction between these main effects [$F(2, 18) = 0.46$, $p = 0.64$]. A post hoc test indicated that the number of S1-S2 trials expressed as the percentage of the number of successful trials in the switch task was significantly lower than that in the go and stop tasks ($p < 0.05$).

3.1. Probability of No-APA trials

No-APA trials were observed regardless of the type of task (Fig. 7). In the left leg condition, the probability of the No-APA trials was 9.2 ± 2.6 % in the go task, 16.6 ± 2.6 % in the switch task, and 23.3 ± 5.5 % in the stop task (Fig. 7b). In the right leg condition, the probability was 19.7 ± 4.0 % in the go task, 26.0 ± 4.1 % in the switch task, and 29.1 ± 6.5 % in the stop task. The probability was significantly different among the tasks [$F(2, 18) = 8.13$, $p < 0.01$]; however, it was not significantly different between the leg conditions [$F(1, 9) = 2.38$, $p = 0.16$], and there was no significant interaction between these two main effects [$F(2, 18) = 0.41$, $p = 0.67$]. A post hoc test indicated that the probability of No-APA trials in the stop task was significantly higher than that in the go task ($p < 0.05$). There was no significant difference in the COP position in the medio-lateral axis between the APA and No-APA trials [$F(1, 9) = 0.00$, $p = 1.00$] and the leg conditions [$F(1, 9) = 0.01$, $p = 0.94$]; moreover, there was no significant interaction between the main effects [$F(1, 9) = 0.06$, $p = 0.80$]. Similarly, there was no significant difference in the COP position in the anterior-posterior axis between the APA and No-APA trials [$F(1, 9) = 0.55$, $p = 0.48$] and the leg conditions [$F(1, 9) = 0.49$, $p = 0.50$]; moreover, there was no significant interaction between the main effects [$F(1, 9) = 0.74$, $p = 0.41$].

3.2. APA latency

The specimen traces of the COP in the S1-S2 trials are presented in Figs. 8 and 9. In the left leg condition, the APA latency on the medio-lateral axis was 335 ± 17 ms in the go task, 309 ± 19 ms in the switch task, and 315 ± 17 ms in the stop task (Fig. 10a). In the right leg condition, the latency was 371 ± 22 ms in the go task, 296 ± 12 ms in the switch task, and 335 ± 20 ms in the stop task. ANOVA failed to indicate a significant difference in the latency on the medio-lateral axis

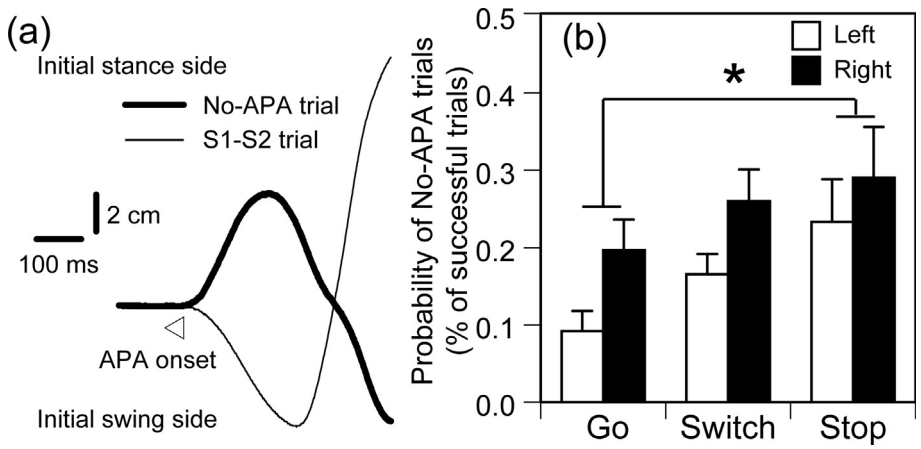

Fig. 7. Specimen record of the early period of the COP displacements in the S1-S2 and No-APA trials (a) and the probability of No-APA trials (b). Bars indicate means, and error bars indicate standard errors of the mean (b). An asterisk indicates significant difference for the post hoc test of the ANOVA ($p < 0.05$).

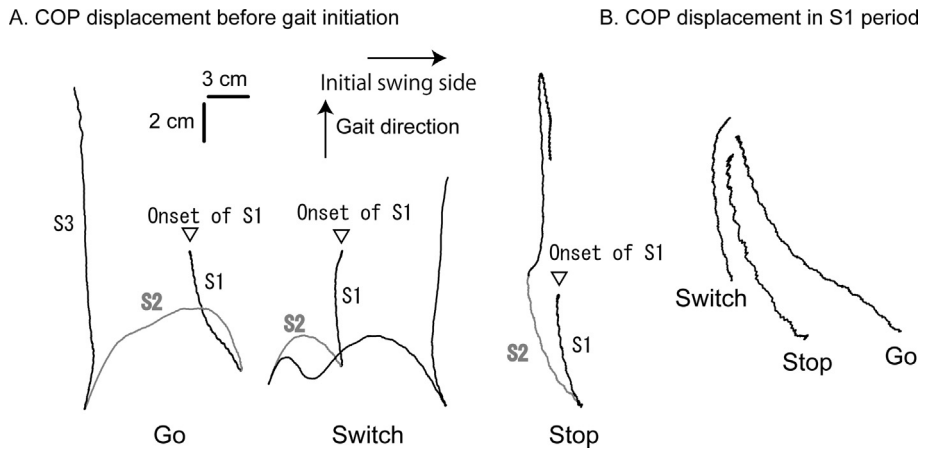

Fig. 8. Specimen records of the COP trajectories (A) and the S1 period of the trajectories in the S1-S2 trials (B).

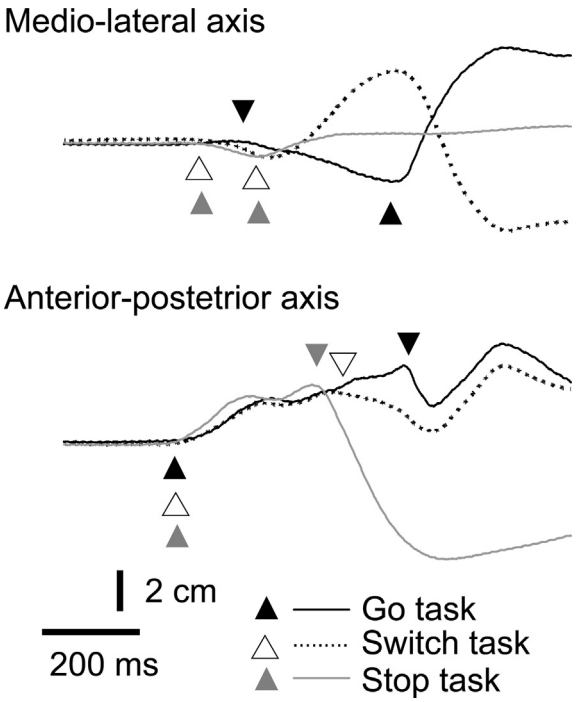

Fig. 9. Specimen records of the COP trajectories in the medio-lateral (A) and anterior-posterior (B) axes. Triangles indicate the onset and offset of the S1 period in order from left to right.

between the leg conditions [$F(1, 9) = 1.63$, $p = 0.23$]; however, there was a significant difference in the latency on the medio-lateral axis among the tasks [$F(2, 18) = 22.65$, $p < 0.01$] with a significant interaction between the two main effects [$F(2, 18) = 6.44$, $p < 0.01$]. A test of the simple main effect indicated that the APA latency in the left leg condition was significantly shorter than the APA latency in the right leg condition in the go task [$F(1, 19) = 6.96$, $p = 0.02$]. In addition, a test of the simple main effect indicated significant differences in the latency among the tasks in both the left [$F(2, 36) = 3.26$, $p < 0.05$] and right [$F(2, 36) = 26.59$, $p < 0.01$] leg conditions. A post hoc test following the simple main effect test indicated that the APA latencies in the switch and stop tasks were significantly shorter than the latency in the go task in the left leg condition ($p < 0.05$). Similarly, in the right leg condition, the APA latencies in the switch and stop tasks were significantly shorter than the latency in the go task ($p < 0.05$), and the latency in the switch task was significantly shorter than the latency in the stop task ($p < 0.05$).

The APA latency on the anterior-posterior axis in the left leg condition was 304 ± 14 ms in the go task, 286 ± 13 ms in the switch task, and 289 ± 10 ms in the stop task (Fig. 10b). In the right leg condition, the latency was 310 ± 15 ms in the go task,

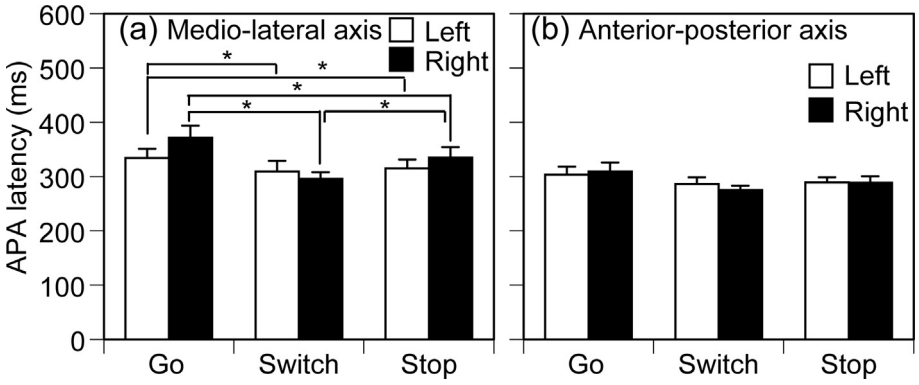

Fig. 10. APA latencies on the medio-lateral (a) and anterior-posterior (b) axes. Bars indicate means, and error bars indicate standard errors of the mean. Asterisks indicate significant difference for the post hoc test of the simple main effect test ($p < 0.05$). Detailed explanation of the statistical results is presented in the APA latency section in the Methods.

275 ± 8 ms in the switch task, and 289 ± 11 ms in the stop task. The APA latency on the anterior-posterior axis was not significantly different between the leg conditions [$F(1, 9) = 0.10$, $p = 0.76$]; however, it was significantly different among the tasks [$F(2, 18) = 7.39$, $p < 0.01$] with no significant interaction between the two main effects [$F(2, 18) = 2.61$, $p = 0.10$]. Nevertheless, a post hoc test failed to indicate a significant difference in the APA latency on the anterior-posterior axis among the tasks.

3.3. APA amplitude

The APA amplitude was decreased in the switch and stop tasks (Fig. 11). The APA amplitude on the medio-lateral axis in the left leg condition was 3.4 ± 0.2 cm in the go task, 2.1 ± 0.2 cm in the switch task, and 1.7 ± 0.1 cm in the stop task (Fig. 11a). In the right leg condition, the amplitude on the medio-lateral axis was 3.0 ± 0.3 cm in the go task, 1.8 ± 0.2 cm in the switch task, and 1.7 ± 0.2 cm in the stop task. ANOVA indicated no significant difference in the amplitudes between the leg conditions [$F(1, 9) = 4.12$, $p = 0.07$]; however, there was a significant difference among the tasks [$F(2, 18) = 37.13$, $p < 0.01$]. There was no significant interaction between the leg conditions and tasks [$F(2, 18) = 1.23$, $p = 0.32$]. A post hoc test indicated that the amplitudes in the switch and stop tasks were significantly smaller than the amplitude in the go task ($p < 0.05$). There was a significant positive correlation between the change in the APA amplitude in the switch task and the stop task both in the left ($r = 0.77$, $p < 0.05$) and right ($r = 0.79$, $p < 0.05$) leg conditions as indicated in Fig. 11c.

The amplitude on the anterior-posterior axis in the left leg condition was 6.0 ± 0.5 cm in the go task, 4.8 ± 0.5 cm in the switch task, and 4.6 ± 0.4 cm in the stop task (Fig. 11b). In the right leg condition, the amplitude was 5.8 ± 0.5 cm in the go task, 4.9 ± 0.5 cm in the switch task, and 4.8 ± 0.4 cm in the stop task. The amplitude was not significantly different between the leg conditions [$F(1, 9) = 0.11$, $p = 0.75$]; however, it was significantly different among the tasks [$F(2, 18) = 13.23$, $p < 0.01$]. There was no significant interaction between the two main effects [$F(2, 18) = 0.70$, $p = 0.51$]. A post hoc test indicated that the amplitude in the stop task was significantly smaller than the amplitude in the go task ($p < 0.05$). There was a significant positive correlation between the changes in the APA amplitude in the switch task and the stop task both in the left ($r = 0.89$, $p < 0.05$) and right ($r = 0.96$, $p < 0.05$) leg conditions as indicated in Fig. 11d.

3.4. APA duration

The APA duration was decreased in the switch and stop tasks (Fig. 12). The APA duration on the medio-lateral axis in the left leg condition was 296 ± 14 ms in the go task, 213 ± 8 ms in the switch task, and 196 ± 11 ms in the stop task (Fig. 12a). In the right leg condition, the duration was 276 ± 7 ms in the go task, 212 ± 7 ms in the switch task, and 205 ± 8 ms in the stop task. The duration was not significantly different between the leg conditions [$F(1, 9) = 0.19$, $p = 0.68$]; however, it was significantly different among three tasks [$F(2, 18) = 102.48$, $p < 0.01$]. There was a significant interaction between the leg conditions and tasks [$F(2, 18) = 3.67$, $p < 0.05$]. A test of the simple main effect indicated a significant difference in the duration among the tasks in the left leg condition [$F(2, 35) = 79.40$, $p < 0.01$]. A post hoc test indicated that the durations in the switch and stop tasks were significantly shorter than the duration in the go task ($p < 0.05$), and the duration in the stop task was significantly shorter than the duration in the switch task ($p < 0.05$). Another test of the simple main effect indicated a significant difference in the duration among the tasks in the right leg condition [$F(2, 35) = 41.59$, $p < 0.01$]. A post hoc test indicated that the durations in the switch and stop tasks were significantly shorter than the duration in the go task ($p < 0.05$). There was a significantly positive correlation between the changes in the duration in the switch task and the stop task in the left leg condition ($r = 0.86$, $p < 0.05$) and an insignificant positive correlation between the changes in the right leg condition ($r = 0.53$, $p = 0.11$) as indicated in Fig. 12c.

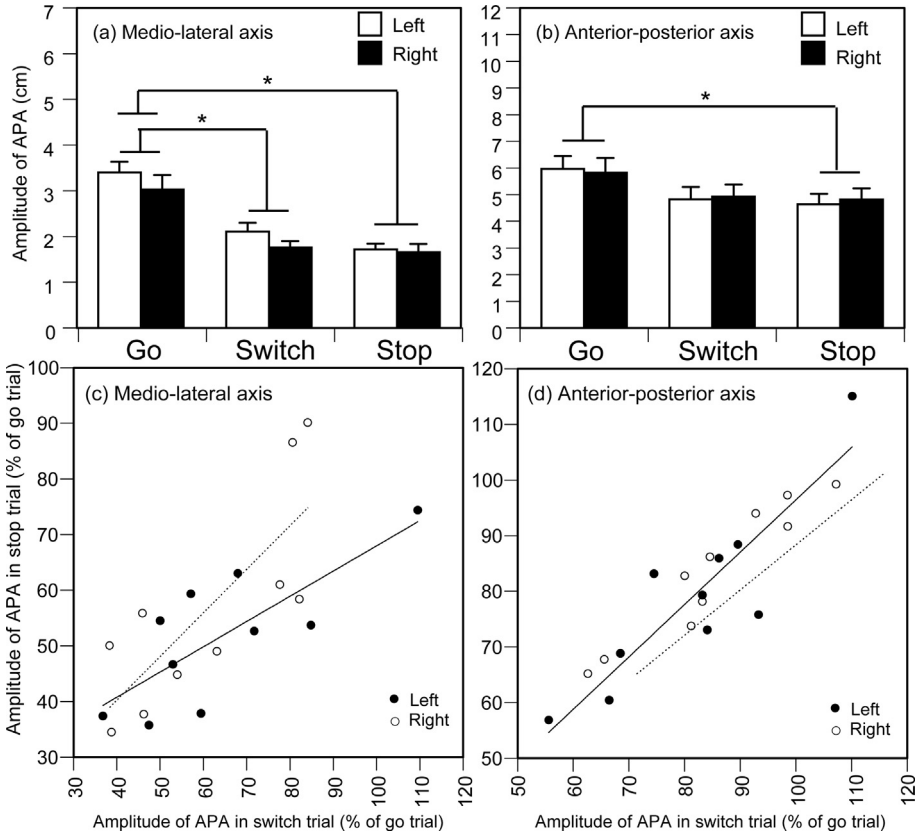

Fig. 11. Mean amplitude of the APA (a, b) and scatter plots of the change in the APA amplitude in the stop task as a function of the change in the APA amplitude in the switch task (c, d). Left panels represent medio-lateral axis (a, c) and right panels represent anterior-posterior axis (b, d). Bars indicate means, and error bars indicate standard errors of the mean (a, b). Asterisks indicate significant difference in the post hoc test of the ANOVA ($p < 0.05$). Detailed explanation of the statistical results is provided in the APA amplitude section in the Methods. Solid regression lines indicate the left leg condition, and dashed regression lines indicate the right leg condition (c, d).

The duration on the anterior-posterior axis in the left leg condition was 317 ± 15 ms in the go task, 261 ± 15 ms in the switch task, and 266 ± 13 ms in the stop task (Fig. 12b). In the right leg condition, the duration was 326 ± 17 ms in the go task, 255 ± 11 ms in the switch task, and 270 ± 10 ms in the stop task. ANOVA indicated no significant difference in the duration between the leg conditions [$F(1, 9) = 1.28$, $p = 0.29$]; however, there was a significant difference in the duration among the tasks [$F(2, 18) = 21.1$, $p < 0.01$]. There was no significant interaction between the two main effects [$F(2, 18) = 1.53$, $p = 0.24$]. A post hoc test indicated that the durations in the switch and stop tasks were significantly shorter than the duration in the go task ($p < 0.05$). There was a significantly positive correlation between the changes in the duration in the switch task and the stop task both in the left ($r = 0.94$, $p < 0.05$) and right ($r = 0.80$, $p < 0.05$) leg conditions as indicated in Fig. 12d.

4. Discussion

In the present study, the APA in response to the first cue appeared in approximately 70% of the successful trials. The probability of the disappearance of the APA in the stop task was higher than the probability in the go task. In the S1-S2 trials, the amplitude and duration of the APA similarly decreased in both the switch and stop tasks, and the amount of the decreases in the switch task was positively correlated with the amount in the stop task.

4.1. Process of APA and focal step movement

There is a controversy regarding whether the APA and focal step movement are produced as a single process or different processes (Caderby et al., 2014; Corbeil & Anaka, 2011; Hass et al., 2008; Huntley & Zettel, 2015; Leonard et al., 2009; Robert et al., 2007; Schepens & Drew, 2003; Slijper et al., 2002; Stamenkovic & Stapley, 2016). We investigated this issue in the present study. The probability of S1-S2 trials was approximately 70% of the successful trials in both the switch and stop tasks. The S1-S2 trials represent the trials in which the APA is apparently present. In addition, the successful trials represent the trials in which the initial swing leg is successfully switched in the switch task, or gait initiation is successfully withheld

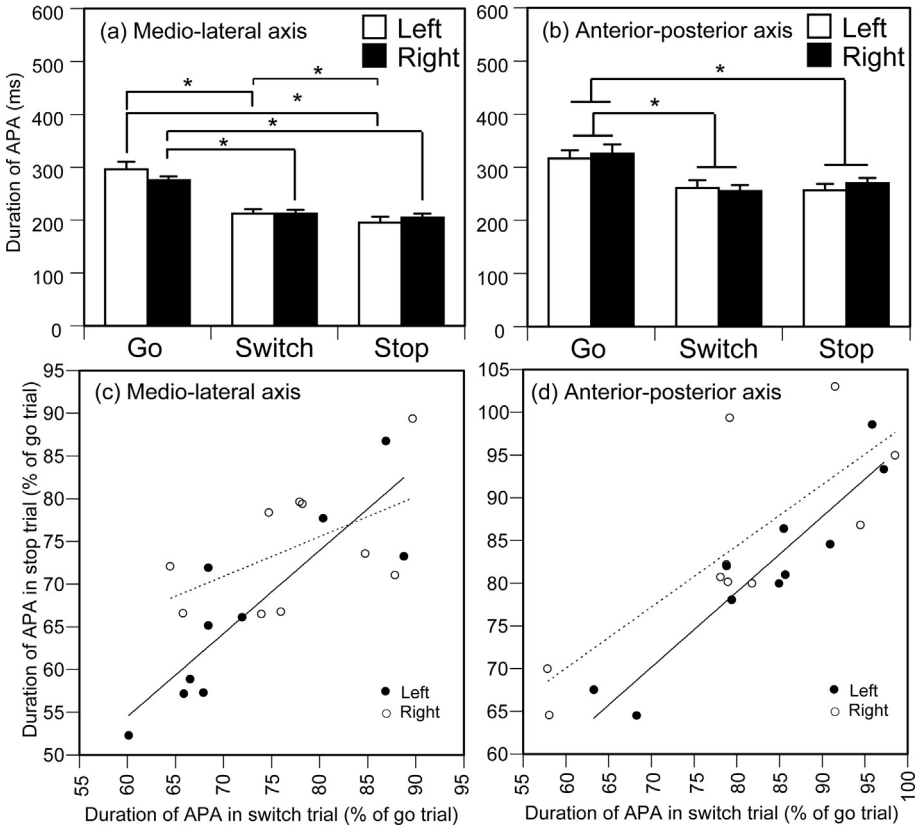

Fig. 12. Mean duration of the APA (a, b) and scatter plots of the changes in the APA duration in the stop task as a function of the changes in the APA duration in the switch task (c, d). Left panels indicate medio-lateral axis (a, c), and right panels indicate anterior-posterior axis (b, d). Bars indicate means, and error bars indicate standard errors of the mean (a, b). Asterisks indicate significant differences in post hoc tests for the simple main effect test (a) and ANOVA (b) ($p < 0.05$). Detailed explanation of the statistical results is presented in the APA duration section in the Methods. Solid regression lines indicate the left leg condition, and dashed regression lines indicate the right leg condition (c, d).

in the stop task (Table 1). Taken together, the present findings indicate that the APA in response to the first cue was not cancelled in approximately 70% of the trials even when the focal step movement of gait initiation in response to the first cue was successfully withheld. We hypothesized that in some cases, the APA appears even when the focal step movement of gait initiation in response to the first cue is successfully withheld, if the APA and focal step movement of gait initiation are produced as a dual process and the APA process completes earlier than the stop or switch process in some cases (Fig. 2C). The present findings support the view that the APA and focal step movement of gait initiation are produced as a dual process.

4.2. No-APA trials in go task

The No-APA trials were present in some successful trials of the go task. It may be speculated that the No-APA trials may be a result of the difference in the initial COP position before the first cue because the APA is predominately dependent on the initial COP position (Azuma, Ito, & Yamashita, 2007). Nevertheless, in the present study, the first cue was provided when the COP was on the midline of the base of support, and the COP position immediately before the first cue was not significantly different between the APA and No-APA trials. Thus, the initial COP position is not the direct cause of the No-APA trials in the go task in the present study. Moreover, the No-APA trials in the go task are not explained by the competition between the go and stop processes because the second cue that triggers the stop process was not provided in this task. The No-APA trial, in which the COP moves to the initial stance side in the early period of the APA, is compatible with the definition of the early period of the APA error; the initial incorrect APA was followed by the correct APA that produced correct stepping (Cohen, Nutt, & Horak, 2011). The probability of the No-APA trials in the go task was approximately similar to the probability of the APA error in the CRT task in previous studies (Cohen et al., 2011; Uemura, Oya, & Uchiyama, 2013a, 2013b). The participants initiated gait with the leg in the side indicated by the first cue in the go task, which suggests that the experimental paradigm in the go task was similar to these previous studies. Thus, the absence of the APA in the No-APA trials in the go task is well explained by the APA error.

The APA error has been considered to be a result of the initial program error (Cohen et al., 2011). An APA error prior to stepping laterally in response to an imperative cue may occur when the step side is not certain until the imperative cue is provided (Sparto et al., 2013). Moreover, the probability of an APA error when selecting the initial swing leg in response to a cue was higher than the probability when the initial swing leg was determined in advance (Cohen et al., 2011); these findings indicate that the APA error is related to the selection error of the prepared responses of gait initiation. In the present study, when responding to the first cue, one motor process was selected from the two competing processes of gait initiation; the go process of gait initiation with one leg and the process with the other leg. Thus, the absence of the APA in the No-APA trials of the go task likely reflects the selection error of the two competing APA processes: the APA process for gait initiation with the left leg and the APA process for gait initiation with the right leg.

4.3. No-APA trials in stop task

In the stop task of the successful trials, the participants successfully withheld the focal step movement of gait initiation in response to the first cue. Thus, based on the horse race model, the present finding in the successful trials is explained by the view that the stop process triggered by the stop cue is completed before the go process of the focal step movement of gait initiation (Fig. 13A). The probability of No-APA trials in the stop task was significantly higher than the probability in the go task. A previous study has indicated that the probability of an APA error prior to gait initiation was higher when the initial swing leg was instructed by an incongruent visual cue compared with when the initial swing leg was instructed by a congruent or simple visual cue (Uemura et al., 2013b). This finding indicates that an initial program error increases when the participants pay selective attention as a result of visual interference by the flanker task. In the present study, selective attention was highly required in the stop task compared with the go task because they had to discriminate whether the second cue indicated the switch or stop cue. Thus, one may speculate that an increase in selective attention is one potential cause of the higher probability of No-APA trials in the stop task. However, this view conflicts with the present findings. In the switch task, selective attention is required as the stop task; however, the probability of No-APA trials in the switch task was not significantly different from the probability in the go task.

Rather, the higher probability of No-APA trials in the stop trials is explained by the process based on the horse race model. According to the horse race model, the APA is absent when the stop process is completed before the APA process (Fig. 13A). Based on this view, in some trials, the APA process must have occurred earlier than the stop process; however, the APA process must have occurred after the stop process in other trials because both No-APA and APA trials were present in the stop

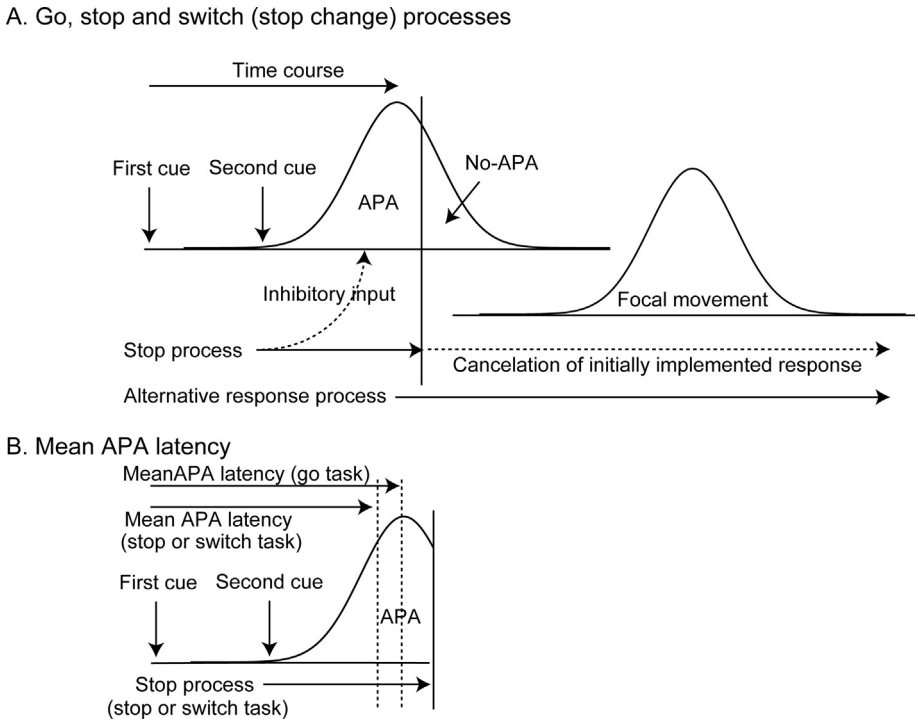

Fig. 13. Hypothetical model of the go, stop, and switch processes of the APA and focal step movement of gait initiation. Gaussian curves represent the normal distributions of the APA latency and the latency of the focal movement across trials. The focal movement in response to the first cue is always absent in the switch or stop task (A). The long latency APAs are predominantly cancelled by the stop process, which causes a shorter mean APA latency in the switch or stop task (B).

task. Moreover, long latency APAs are more likely cancelled by the stop process in the stop task because the completion of the APA process occurs later as the APA latency increases (Fig. 13B). Consequently, the number of trials with long latency APAs in the stop task was smaller than that in the go task because some trials with long latency APAs were more likely to be cancelled by the stop cue. This view is supported by a finding that the mean APA latency on the medio-lateral axis in the stop task was significantly shorter than the mean APA latency in the go task.

There are alternative explanations for the short APA latency in the stop task. A second cue was provided after the first cue in the stop task. Thus, two stimuli were provided with a short interval in this task. Based on this approach, one may speculate that the double stimulation (the first and second cues) is the cause of the decrease in the APA latency in the stop task. It has been reported that the reaction time in response to double visual stimulation is 10 ms shorter than that in response to a single stimulation (Forster, Cavina-Pratesi, Aglioti, & Berlucchi, 2002). However, the decrease in the APA latency in the stop task is not completely explained by this effect because the decrease in the APA latency on the medio-lateral axis was substantially larger than the decrease in the reaction time induced by the double stimulation; the APA latency in the stop task was 20–75 ms shorter than that in the go task. The APA is accelerated by the startling auditory stimulus (Delval et al., 2012; MacKinnon et al., 2007). Nevertheless, the shorter mean latency of the stop task compared with the mean latency of the go task is not explained by this effect because the second cue was not provided by the loud sound; instead, it was provided by the visual stimulus in the present study. Taken together, the higher probability of No-APA trials in the stop task is most plausibly explained by the cancellation of the long latency APAs by the stop process rather than the unlikely alternative explanations.

4.4. Inhibition of APA

In approximately 70% of the successful trials, the APA was present in the switch and stop tasks (S1-S2 trials). In the S1-S2 trials, the amplitude and duration of the APA were decreased during switching the initial swing leg or withholding gait initiation. This finding indicates that the APA is inhibited by the stop process even when the APA is not completely cancelled by the stop process. The amplitude and duration of the startle auditory stimulus-induced APA increase as the stimulus comes closer to the imperative go cue for step initiation; however, the corticospinal excitability of the initial agonist of the focal step movement of gait initiation begins to increase 100 ms after the go cue (MacKinnon et al., 2007). This finding indicates that the APA process is loaded before the process of the focal step movement of step initiation. Thus, the present finding is explained by a view that the stop process is completed after the completion of the go process of the APA in some successful trials, whereas the stop process is completed before the completion of the focal step movement in all successful trials in the switch and stop tasks (Fig. 13A). Thus, the decrease in the amplitude and duration of the APA are not explained by the horse race model because these decreases occurred without previous completion of the stop process relative to the APA process.

An alternative explanation for the decrease in the APA is the online correction of the APA process. Online correction of the APA is possible in accordance with previous findings that the online process of the APA is modulated by external perturbation. Tactile stimulation decreased the APA duration (Ruget et al., 2008). Moreover, pulling the body to the direction ipsilateral to the initial swing side during the APA of step initiation increased the APA amplitude and duration (Mouchnino et al., 2012). Thus, the most likely interpretation of the decrease in the amplitude and duration of the APA in the stop and switch tasks is that the APA process receives inhibitory input during loading of the stop process (Fig. 13A). A previous study indicated a reduction of the leg muscle activity during adjustment of the stepping for the trip recovery during walking (Potocanac, Pijnappels, Verschueren, van Dieën, & Duysens, 2016). The authors of this study suggest that this reduction reflects the production of the "pause" for reorganizing the neural network that mediates the adjustment of the stepping activity. The inhibitory drive over the APA during switching the initial swing leg or withholding gait initiation may also reflect this pause for reorganizing the neural network that mediates the stop process of the focal step movement of gait initiation.

4.5. Common inhibitory mechanism

In the present study, the decreases in the amplitude and duration of the APA in the switch task were similar to the decreases in the stop task. Moreover, the decreases in the amplitude and duration of the APA in the switch task were positively correlated with the decreases in the stop task. Several previous findings indicate a common neural mechanism that underlies different types of inhibitory processes (see Boecker, Gauggel, & Drueke, 2013). Positive electroencephalographic activities of the non-involved side of the primary motor cortex during the go task and the involved side of the primary motor cortex during the no-go task are similarly present in the CRT task (Burle et al., 2004). Similar cortical areas are involved in the different types of inhibitory control (Aron, Robbins, & Poldrack, 2004). The stop and change processes in the motor response activate common neural structures (Rangel-Gomez, Knight, & Krämer, 2015). Moreover, a similar activation pattern of the brain was identified during the stop and stop change tasks, with the exception of the motor area for the forthcoming alternative response (Boecker et al., 2011). In both the switch and stop tasks, the pre-supplemental motor area is the common region that contributes to the inhibition of the motor response (Isoda & Hikosaka, 2007; Li et al., 2006). The right inferior frontal gyrus, pre-supplementary motor area and midbrain are activated during both the stop and switch tasks (Kenner et al., 2010). According to these previous findings, common neural activity contributes to the online inhibition of the APA process when withholding focal step movement or switching the initial swing leg of gait initiation.

4.6. Conclusion

The APA appeared even when gait initiation was successfully withheld or the initial swing leg of gait initiation was successfully switched. This finding indicates that the APA and focal step movement of gait initiation are produced as a dual process. The amplitude and duration of the APA were decreased when gait initiation was successfully withheld or the initial swing leg of gait initiation was successfully switched, which indicates that the inhibitory input to the APA is present during stop process loading. The decreases in the amplitude and duration of the APA in the switch task were similar to those of the stop task, and the decreases in the switch task were positively correlated with the decreases in the stop task. Thus, the common inhibitory input to the APA is present during the processes of switching the initial swing leg and withholding gait initiation (Burle et al., 2004; Mostofsky and Simmonds, 2008).

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