Preparatory state and postural adjustment strategies for choice reaction step initiation

Authors:

Tatsunori Watanabe[a], Kazuto Ishida[a], Shigeo Tanabe[b], Ippei Nojima[a]

Affiliations:

[a]Department of Physical Therapy, Nagoya University Graduate School of Medicine, Aichi, 461-8673 Japan

[b]Faculty of Rehabilitation, Fujita Health University School of Health Sciences, Aichi, 470-1192 Japan

Corresponding author:

Ippei Nojima
Department of Physical Therapy
Nagoya University Graduate School of Medicine
1-1-20 Daiko-Minami, Higashi-ku, Nagoya-shi, Aichi
461-8673 JAPAN
Tel/Fax: +81-(0)52-719-1365
Email: nojima@met.nagoya-u.ac.jp

Abbreviations

RT, reaction time; APAs, anticipatory postural adjustments; COP, center of pressure; EMG, electromyogram; LAS, loud auditory stimulus; SRT, simple reaction time; CRT, choice reaction time; GNG, go/no-go; TA, tibialis anterior; SCM, sternocleidomastoid; SD, standard deviation; SEM, standard error of the mean; ANOVA, analysis of variance.

Abstract

A loud auditory stimulus (LAS) presented simultaneously with a visual imperative stimulus can reduce reaction time by automatically triggering a movement prepared in the brain and has been used to investigate a movement preparation. It is still under debate whether or not a response is prepared in advance in reaction time tasks involving choice responses. The purpose of the present study was to investigate the preparatory state of anticipatory postural adjustments (APAs) during a choice reaction step initiation. Thirteen young adults were asked to step forward in response to a visual imperative stimulus in two choice stepping conditions: i) the responding side is not known and must be selected and ii) the responding side is known but whether to initiate or inhibit a step response must be selected. LAS was presented randomly and simultaneously with the visual imperative stimulus. LAS significantly increased the occurrence rates of inappropriately initiated APAs while reducing the reaction times of correct and incorrect trials in both task conditions, demonstrating that LAS triggered the prepared APA automatically. This observation suggests that APAs are prepared in advance and withheld from release until the appropriate timing during a choice reaction step initiation. The preparatory activity of APAs might be modulated by the inhibitory activity required by the choice tasks. The preparation strategy may be chosen for fast responses and is judged most suitable to comply with the tasks because inappropriately initiated APAs can be corrected without making complete stepping errors.

Key words:

anticipatory postural adjustments; choice stepping; gait initiation; preparation; loud auditory stimulus

Introduction

Initiation of gait, the transition period from standing to walking, is a seemingly simple but challenging task. This process leads an individual to an unstable posture as she/he stands on a single leg while concurrently swinging the other leg forward to generate the momentum to take a step. The ability to initiate a step quickly and efficiently is a fundamental human skill required for maintaining an upright position and to avoid losing balance and falling. Indeed, recent evidence suggests that a slow stepping reaction time (RT) is related to future falls in the elderly (Lord and Fitzpatrick, 2001, Pijnappels et al., 2010).

Anticipatory postural adjustments (APAs) that occur before the step initiation are the strategies to minimize the postural disturbances and maintain balance (Massion, 1992, Malouin and Richards, 2000, Kaminski and Simpkins, 2001, Timmann and Horak, 2001). APAs include consecutive muscle activations that generate a backward displacement of the center of pressure (COP) toward the swing leg, followed by a forward COP displacement toward the stance leg. This consecution of postural movements unloads the swing leg and creates the forces that propel the body mass into forward motion (Burleigh et al., 1994, Elble et al., 1994). Although the precise neural origin of APA generation is unknown, they are known to be controlled by subcortical mechanisms (Massion, 1992, Schepens and Drew, 2003, 2004) and can be modulated by several cortical mechanisms (e.g., Tard et al., 2013, 2016).

Recently, several studies have indicated that errors in the initial direction of weight transfer, known as APA errors, could occur when there is uncertainty regarding the direction of step initiation and that these may slow the stepping reaction time, conceivably increasing the risk of falls (e.g., Cohen et al., 2011). As the number of errors increases when performing a stimulus–response incompatibility task, inhibitory control is related to APA errors (Sparto et al., 2013, Uemura et al., 2013, Watanabe et al., 2015). Likewise, in choice RT (CRT) tasks involving hand responses (e.g., button-push tasks), subthreshold electromyogram (EMG) activity of an incorrectly responding hand muscle, known as partial errors, can be detected in trials where the incorrect EMG response precedes the execution of the correct response (e.g., Vidal et al., 2000, Burle et al., 2002, 2008, Masaki et al., 2012). Although these two types of errors seem similar in that neither of them is complete or overt, the error rates are quite different and generally more than two times higher in APA errors than in partial errors (e.g., Schreiber et al., 2011, Masaki et al., 2012, Uemura et al., 2013, Watanabe et al., 2015). This observation led us to suspect that the difference in error rates is caused by pre-programming or preparation of APA. In other words, even though a required stepping leg is not known in advance (i.e., a CRT task), individuals are likely to prepare APA beforehand, with the prepared APA required to be withheld or inhibited until it needs to be released. Thus, disinhibition of the incorrect APA preparation during the CRT task would make the individuals more liable to APA errors.

The preparation of movements can be assessed using a loud auditory stimulus (LAS). A number of studies have reported, using a simple RT (SRT) paradigm in which the appropriate response is known in advance and thus can be fully prepared before the presentation of an imperative stimulus, that the prepared movements, stored in the subcortical region, are triggered unintentionally by LAS at short latency (e.g., Carlsen et al., 2004b). Based on an activation model, where a movement is initiated when activation of neural network responsible for the movement reaches a threshold (Carpenter and Williams, 1995, Hanes and Schall, 1996), the neural activity develops over time during preparation to a level below the movement threshold, and LAS drives the already elevated neural activity beyond the threshold, resulting in a dramatic reduction of RT (Tresilian and Plooy, 2006, Marinovic et al., 2013, 2014). Accordingly, RT would indicate the time required to reach the movement threshold from the preparatory level (Maslovat et al., 2015). That means, when the preparatory activity is higher, LAS triggers the prepared movement with a shorter latency.

In contrast to SRT tasks, there have been discrepancies in results regarding CRT tasks. Some studies found that the response may be prepared in advance (Kumru et al., 2006, Nijhuis et al., 2007, Maslovat et al., 2011) while others did not (Carlsen et al., 2004a, 2008). In the field of step initiation, it has been shown that APAs are prepared in advance when stepping leg is known beforehand (i.e., a SRT task) and possibly even when the stepping leg selection is required (i.e., a CRT task) (MacKinnon et al., 2007). However, as there was an unequal probability of left and right responses (i.e., there were more right responses) and EMG electrodes were attached only to the right leg, a possible response bias toward the right side was postulated by the authors (MacKinnon et al., 2007). Thus, their study may have unintentionally treated the CRT task as a SRT task, and would, thus, not have been able to properly examine the effects of response conflicts created by the choice task on the APA preparation. Furthermore, the authors failed to examine RTs for error trials, even though reduced RTs are crucial not only in the correct trials but also in the incorrect trials to conclude the preparation of a movement (Carlsen et al., 2008). Surprisingly, no other studies have evaluated the preparatory state during a choice reaction step initiation, although Delval et al. (2012) extended the research on simple step initiation and revealed possible modulation of the APA initiation by the cortex.

In the present study, we examined using LAS whether APAs are prepared during a choice reaction step initiation and how the inhibitory process contributes to APA initiation when the response requires a choice. We replicated the CRT study by MacKinnon et al. (2007) without the response bias and extended the data analysis to provide additional information. We further applied a different type of choice reaction step initiation task, namely, a go/no-go (GNG) task, in which the responding side is known but whether to initiate or inhibit a step response must be selected. Due to the advance information about the responding side, this task may be treated as a SRT task. At the same time, it involves the inhibition of a response, providing more pertinent information about the involvement of an inhibitory process in APA initiation. To compare our results with two previous studies (MacKinnon et al., 2007, Delval et al., 2012), we used the same intensity (115 dB) for LAS. We also focused specifically on the state of APA preparation and not on the effects of APA errors and LAS on the stepping performance, because these were clearly characterized in those and other previous studies (e.g., Cohen et al., 2011). We hypothesized that if an APA is prepared in advance and required to be inhibited from release until the response conflict is resolved during a choice reaction step initiation, then a LAS would trigger the prepared APA unintentionally and possibly inaccurately, increasing the rate of APA errors in the CRT task and inappropriate APA initiations in the no-go trials of the GNG task, shortening the latency of APA in both correct and incorrect trials.

Experimental procedures

Participants

Thirteen subjects (6 males, 7 females, mean age ± SD = 22 ± 1.94) from Nagoya University School of Health Sciences and Graduate School of Medicine participated in this study. They had no reported history of hearing, neurological, or orthopedic disorders that could influence the balance function. All had normal or corrected-to-normal vision and were right-leg dominant. The study was approved by the Ethics Committee of Nagoya University, and written informed consent was obtained from each participant before participation.

Protocol

Participants with their feet bare maintained a stationary standing posture on a force plate. The initial standing position was the same for all participants; each foot was placed 5 cm apart from a centerline, vertical to the frontal plane, drawn on the force plate. The participants were instructed to step forward as quickly as possible in response to a visual imperative stimulus that appeared on a computer screen set just below eye level at a distance of 1.0 m from the participant. They stepped forward with the leg specified by the stimulus onto a wood plate placed right front of the force plate and brought the other leg alongside. LAS (1000 Hz, 115 dB) was also delivered randomly and simultaneously with the visual stimuli from two speakers set just behind the head of the participants; we told participants to ignore this. They were instructed to balance the weight of their feet evenly before each trial, and this was confirmed by monitoring the COP position online. After each trial, the participants were required to move back to the same starting position and prepare for the next trial. At the end of the experiment, the participants were asked about their perception of their movements.

Apparatus

The data regarding ground reaction forces during step executions were collected from a force plate (Tech Gihan, Kyoto, Japan). Using silver–silver chloride surface electrodes, surface EMG data were collected from the bilateral tibialis anterior (TA) as well as the right sternocleidomastoid (SCM); the data of SCM EMG activity was used to evaluate startle responses. Unilateral SCM measurement was chosen due to there being no reported differences in startle response between the left and right SCM (Brown et al., 1991). The EMG signals were amplified and band-pass filtered (1–1000 Hz) using a conventional EMG machine (Nihon Kohden, Tokyo, Japan). The ground reaction forces and EMG signals were recorded at a sampling rate of 1000 Hz. Visual and auditory stimulus generation and the signal acquisitions were performed using customized LabVIEW programs (National Instruments, Austin, TX, USA).

Visual and auditory stimuli and task

The duration of each trial was 10 s. All the visual stimuli were presented in black on a white-screen background. The trial started with a plus-shaped fixation point presented in the center of a computer screen. A circle serving as the forewarning for the imperative stimulus followed the fixation after a random period of 6–7 s and was presented for 500 ms. The visual imperative stimulus (an arrow) then appeared for 500 ms after a random period of 3–4 s. For 25 % of the trials, a LAS was presented simultaneously with the visual imperative stimulus. In the CRT task, either a left- or a right-pointing arrow was randomly displayed in the center of the screen. In the GNG task, an arrow pointing either upward or downward was randomly presented in the center of the screen (Fig. 1).

Each participant performed four blocks of the CRT task, four blocks of the GNG task with the left leg, four blocks of the GNG task with the right leg, and one control block in which the participants did not respond to the visual imperative stimuli. Each task block consisted of 20 trials in total. In the CRT task, 10 left- and 10 right-pointing arrows were randomly presented, and the participants were required to step forward with the leg that corresponded to the direction of the arrow. In the GNG task, 10 upward and 10 downward arrows were randomly presented, and the participants were required to step forward in response to the upward arrow and not to move in response to the downward arrow. In the control block, 20 upward arrows were presented, and the participants were required not to respond. The control block was conducted to confirm that LAS triggered movement only when it was prepared and that TA EMG activity in trials with LAS was not due to the startle reaction. The order of tasks was interchanged randomly among the participants.

Data analysis

We performed the data analysis using customized programs written in Matlab (MathWorks, Natick, MA, USA). In this study, only the trials with an APA present during stepping sequence were analyzed; that is, we excluded trials at which the participants successfully withheld APA in the no-go trials. We considered that an APA was present when a TA EMG burst, a COP movement toward the swing leg, and a posterior COP movement all occurred prior to the lift-off of the swing leg. The amplified EMG signals were full-wave rectified and band-pass filtered with a fourth-order zero phase lag Butterworth filter with cut-off frequencies of 50–250 Hz. RTs of

SCM EMG signals were determined as the time at which the EMG amplitude increased above 3 SD from the mean value over the baseline period from -500 to 0 ms with respect to the imperative visual stimulus. The RTs of TA EMG signals were detected as the time in which the EMG amplitude increased above 3 SD for at least 5 ms from the mean value over the same baseline. These were further visually verified and manually adjusted when obviously inaccurate RTs were indicated as this has been reported to be more accurate than automated algorithms (Vanboxtel et al., 1993, Hodges and Bui, 1996). For each trial, we calculated RTs of EMG signals from left and right TAs and chose the shorter latency as RT of TA EMG for the trial (Lin and Yang, 2011), as the bilateral TA muscles are reported to co-activate when initiating APA (Assaiante et al., 2000, Mickelborough et al., 2004, Delval et al., 2012), and also because it was confirmed that RTs of the left and right TAs were not different ($p > 0.05$). The COP data obtained from the force plate were low-pass filtered at a cutoff frequency of 50 Hz using a fourth-order zero phase lag Butterworth filter, and the COP RT was determined by its movement speed (Delval et al., 2012). A threshold was set at which the COP movement speed exceeded 100 mm/s for at least 3 ms. APA errors during the CRT tasks were identified by the mediolateral deviation of the COP toward the stance leg at the time of reaction, and inappropriate APA initiations during the GNG tasks were identified by the presence of an APA in no-go trials (Fig. 2).

Statistical analysis

Prior to statistical analysis, the following trials were excluded: those in which excessive TA EMG activity or mediolateral COP sway was observed during the baseline period, and those where COP RTs were faster than 50 ms (1.01 % of the trials). The data obtained in right and left step trials as well as trials from different blocks were combined for each task and participant. First, we examined the effects of LAS on APA errors during the CRT tasks and inappropriate APA initiations during the GNG tasks by comparing the LAS and non-LAS trials using paired Student *t*-tests. To investigate the possible existence of default APA preparation for the dominant-leg step, the APA error rates for the right step and left step in the CRT task were compared using paired Student *t*-tests, after dividing the combined trials into right step and left step trials. Next, TA and COP RTs were subjected to a two-factor repeated-measures analysis of variance (ANOVA) with LAS (presence/absence) and inappropriate APA initiations/APA errors (presence/absence) as within-subject factors for both tasks. The Greenhouse–Geisser correction was applied to the degrees of freedom when the sphericity assumption was violated. Bonferroni post-hoc analyses were performed to test interaction effects and to determine the locus of the difference when this was necessary. All statistical analyses were performed using SPSS (IBM, Armonk, NY, USA), and the alpha level was set at $p < 0.05$ for all tests.

Results

All participants completed the entire experiment without any difficulties. Stepping movements were all accompanied by the TA EMG burst, posterior COP movement, and mediolateral COP movement toward the swing leg. APA errors and inappropriate APA initiations occurred in both LAS and non-LAS trials. Activation of SCM was detected in all the participants. However, the SCM activation was inconstant and variable, as in previous studies (MacKinnon et al., 2007, Delval et al., 2012). No participant was aware of the shortening of onset latencies, and no one mentioned that LAS helped her/him to react quickly. Most participants further insisted that they could *not* stop themselves from initiating a movement when LAS was present in the no-go trials of the GNG task.

Error rates

One complete error was observed in the current experiment. The participant did not step when a “go” sign was presented during the GNG task. No other complete errors were detected. APA errors and inappropriate APA initiations were observed in all the participants, and presentation of LAS increased their occurrence rates. Figure 3 shows the mean occurrence rate of APA errors and inappropriate APA initiations for LAS trials and non-LAS trials. The mean APA error rate (mean ± SE) for the CRT task was 16.4 ± 2.1 % in the non-LAS trials and 27.8 ± 3.4 % in LAS trials. The mean inappropriate APA initiation rate for the GNG task was 18.8 ± 3.4 % in the non-LAS trials and 75.6 ± 2.9 % in LAS trials. A paired *t*-test indicated that the occurrence rate of APA errors and inappropriate APA initiations was higher in trials with LAS than in those without LAS in the CRT task ($p = 0.007$) as well as in the GNG task ($p < 0.001$). In the CRT task, the mean APA error rate (mean ± SE) for the right step was 20.5 ± 2.9 % and that for the left step was 18.1 ± 2.9 %; these were not significantly different ($p = 0.55$), indicating there was no default APA preparation for the dominant-leg step.

Reaction times

The TA activity or COP movement was not observed in any of the participants in the control block. That indicated the application of LAS did not trigger APA or stepping sequence when a step had not been planned. During the other tasks, however, APA and the following stepping movement were triggered early by LAS. A summary of the mean latencies of TA EMG signals and COP movements is given in Table. 1.

Figure 4 shows the mean TA and COP RTs of the trials in the CRT and GNG tasks. In the CRT task, there were significant main effects of LAS ($F_{(1, 12)} = 85.29$, $p < 0.001$) and APA errors ($F_{(1, 12)} = 10.02$, $p = 0.008$) but no interaction on TA RTs. Post-hoc analysis showed that LAS reduced TA RTs for the trials with and without APA errors ($p < 0.001$). In addition, TA RTs for the trials with APA errors were significantly shorter than for trials without APA errors when LAS was absent ($p = 0.033$), and there was the tendency for this to be the case when it was present ($p = 0.054$). In addition, there were significant main effects of LAS ($F_{(1, 12)} = 84.64$, $p < 0.001$) and APA errors ($F_{(1, 12)} = 36.58$, $p < 0.001$) on COP RTs. Post-hoc analysis demonstrated that LAS reduced the COP RTs for the trials with and without APA errors ($p < 0.001$) and that the COP RTs for the trials with APA errors were shorter than for trials without APA errors when LAS was present ($p = 0.019$) and absent ($p < 0.001$).

In the GNG task, the two-factors repeated-measures ANOVA revealed a significant main effect of LAS ($F_{(1, 12)} = 98.56$, $p < 0.001$) but not inappropriate APA initiations or their interaction on TA RTs. Post-hoc analysis revealed that TA RTs for the trials with LAS were significantly shorter than for trials without LAS, regardless of the presence of the inappropriate APA initiations ($p < 0.001$). Also, there was a significant main effect of LAS ($F_{(1, 12)} = 95.76$, $p < 0.001$) on COP RTs in the GNG task, and post-hoc analysis showed that LAS significantly reduced the COP RTs ($p < 0.001$). There was no significant main effect of inappropriate APA initiation or interaction with LAS on the COP RTs.

Discussion

The present study examined the state of preparation during a stepping task requiring choice responses. A LAS presented simultaneously with a visual imperative stimulus increased the APA error rate in the CRT task and the inappropriate APA initiation rate in the GNG task. That is, incorrectly prepared APAs were unintentionally triggered by LAS in the CRT task, and prepared APAs were automatically triggered by LAS in the no-go trials of the GNG task. The absence of the TA EMG burst or COP movement during the control block implies that APAs were released only when a stepping sequence was pre-planned and that TA EMG bursts were not due to the startle reflex. In addition, LAS dramatically reduced the latencies of APAs in correct and incorrect trials in the CRT and GNG tasks. These observations suggest that APAs are prepared in advance and has to be inhibited until the proper timing during a choice reaction step initiation.

In a simple step initiation paradigm, it has been reported that TA RT was dramatically reduced by the presentation of a LAS, suggesting advanced preparation of APAs when required stepping leg is known beforehand (MacKinnon et al., 2007, Delval et al., 2012). The underlying nature of the findings proposed by the authors was that LAS triggered APAs prepared and stored in the subcortical region. Similarly, the current findings of an increase in the inappropriately initiated APAs as well as a dramatic reduction in TA and COP RTs with the presentation of a LAS in two choice tasks plausibly demonstrate that LAS unintentionally and automatically triggered the subcortically prepared APA. It is, therefore, suggested that APAs are prepared in advance even during a choice reaction step initiation; the prepared APA would have to be inhibited from release until the response conflict in choice reaction is resolved, indicating that neural activation for APA preparation and neural inhibition for withholding APA release are simultaneously operating. Substantial studies have indicated that postural responses, including APAs, can be modified by cortical mechanisms (Jacobs and Horak, 2007a, Jacobs et al., 2009, Yakovenko and Drew, 2009, Chang et al., 2010, Tard et al., 2013, 2016). As choice tasks require the prepotent response inhibition (Brunia et al., 2003), the prefrontal cortex, which was activated by the inhibitory processes needed for the tasks (Aron et al., 2004, Sumner et al., 2007), may have inhibited APA release until the appropriate timing. Furthermore, as compared to TA RTs reported in previous studies using a simple step initiation paradigm (i.e., about 100 ms) (MacKinnon et al., 2007, Delval et al., 2012), TA RTs for CRT and GNG tasks in the present study are quite prolonged. Given that the distance to the movement threshold from the preparatory level determines the preparatory activity, this finding conceivably implies that subcortical preparatory activity of APAs is reduced during a choice reaction step initiation, potentially by activity of the prefrontal cortex in the similar way as mentioned above. Indeed, there are ample neural projections from the prefrontal cortex to the pedunculopontine nucleus (which is related to APA) in monkeys, and more so in humans (Schmahmann and Pandya, 1997, Ramnani et al., 2006, Fling et al., 2013). We, hence, propose that the subcortically prepared APAs may be modulated by inhibitory activity of the prefrontal cortex during a choice reaction step initiation, although confirmation of this mechanism will require further investigation.

In contrast to the previous study by MacKinnon et al. (2007), our results did not indicate default APA preparation for the dominant-leg step. Although those authors found that the incidence of the APA errors for non-dominant-leg step was low (MacKinnon et al., 2007), the APA error rates for the dominant and non-dominant leg steps were similar and not significantly different in the present study. The dominant-step bias induced by their experimental design (EMG electrodes attached only on the dominant leg and a greater number of dominant-leg steps) may have contributed to their finding. Also, when performing a RT task, the preceding trial can influence the current trial in terms of, for instance, attention, priming, or guessing strategy (for review, see Fecteau and Munoz, 2003). Thus, APA preparation appears to depend more on the environmental context and the previous experiences.

In addition to the factors discussed already, the upright position required to perform the stepping task may affect the performance strategy. More specifically, the strategies used for the choice reaction step initiation could differ from those for a CRT task performed in a sitting position. Previous studies in reactive stepping have repeatedly shown that individuals tend to select the postural response before a perturbation is triggered (Burleigh and Horak, 1996, Zettel et al., 2002a, b). Particularly in a study by Jacobs and Horak (2007b), withholding information regarding which leg to step with until the onset the perturbation (so that this is a CRT task-like condition) produced not only multiple APAs but also a quick step initiation with one APA at the cost of an increase in incorrect error stepping. Along with other studies (Pai et al., 1998, Rogers et al., 2003), the authors concluded that the stepping sequence was initiated with the pre-selected leg. Likewise in the voluntary choice reaction step initiation investigated in the present study, it is feasible and may in some cases be appropriate to preselect and prepare postural responses prior to the presentation of the imperative stimulus, especially when a controlled fast response is mandatory. Preselection of the responding leg in CRT tasks further unlikely results in a complete stepping error as inappropriate APAs started by incorrect preselection can be corrected within the duration of APA by producing multiple APAs, that is, APA errors. In a similar way in GNG tasks, inappropriately initiated APA can be withheld without making a step. The APA preparation strategy may, therefore, be chosen and judged to be the most suitable to comply with the tasks. Taken together, during a choice reaction step initiation APA is to a certain extent prepared in advance in order to respond quickly while efficiently maintaining balance; this may not be the case for other CRT tasks that are performed in a sitting position (Carlsen et al., 2004a, 2008), although the postural response components, if examined, may be prepared in advance even in those tasks (Slijper et al., 2002).

With regard to the increase in the APA error rates and inappropriate APA initiation due to the presentation of LAS, the considerable difference in their occurrence rates for LAS trials (27.78 % for the CRT task and 75.59 % for the GNG task) may be due to the following reason: the APA error occurs only when an inappropriate APA is prepared in a CRT task, whereas inappropriate APA initiation could occur whenever APA is prepared in the no-go trials of a GNG task. It may also be argued that LAS could just have interfered with the cognitive execution process. Indeed, in a study involving hand responses, Carlsen and colleagues attributed the LAS-induced increase in the error rates to an interference effect of LAS as the LAS failed to reduce latencies for both correct and incorrect trials and further induced such an error as a failure to perform a task and a considerably late response (2004a, 2008). In the present study, however, latencies were reduced regardless of the response correctness, and above-mentioned errors were absent, suggesting that LAS triggered the prepared APAs.

We would like to mention here that in the CRT task, RTs of trials with APA errors were shorter than those of trials without APA errors both with and without LAS (Fig. 4). The results without LAS were consistent with those of previous reports (Cohen et al., 2011, Uemura et al., 2013, Watanabe et al., 2015). When there was a LAS, there may have been correct-response trials where incorrectly prepared APAs were inhibited cognitively without making any incorrect movements (TA EMG activity or COP movement), and this initial cognitive inhibition process could have slowed TA and COP RTs. The finding that LAS did not trigger APAs in some of the no-go trials in the GNG task supports this view.

Consistent with previous studies (MacKinnon et al., 2007, Delval et al., 2012), a startle reaction was not consistently observed. The lower stimulus intensity (115 dB) than the previous reports (120–130 dB) may have influenced the magnitude of the startle reaction. Although the intensity was chosen to be comparable with previous studies, this may have been a limitation of the present study. However, the mean RTs of TA EMG signals in a participant who consistently showed SCM bursts (in 95 % of the trials) were similar to those of another participant with inconsistent SCM bursts. For instance, the mean TA EMG RTs of the trials without inappropriately initiated APAs in the CRT and GNG tasks for the participant with the consistent SCM bursts were 156 ms and 173 ms, respectively, and those of the participant with the inconsistent SCM bursts were 152 ms and 175 ms, respectively. In addition, accumulating evidence supports that a LAS reduces RTs irrespective of any startle reaction, (e.g., Valls-Solé et al., 1995, Reynolds and Day, 2007, Nonnekes et al., 2013, 2014), warranting further investigation of its necessity.

Intersensory facilitation, where the presentation of multiple sensory stimuli results in RTs that are shorter than those resulting from a single sensory stimulus (Nickerson, 1973, Schmidt et al., 1984), may have partially accounted for the shortening of RTs. However, our previous study, which examined the effects of an auditory stimulus (80 dB) presented occasionally and concurrently with a visual imperative stimulus on a stepping response, revealed that an auditory stimulus of 80 dB had no effect on APA errors in a CRT task (Watanabe et al., 2015). This is inconsistent with the results of the present study and conceivably indicates that different mechanisms underlie these two observations. Along with the startle reaction being potentially unnecessary, whether or not the stimulus intensity is large enough to push the preparatory activity beyond the movement threshold may be an important factor underlying the present phenomenon. The exact mechanism should be clarified in future studies.

Our incentive for studying the preparatory state of APAs during a choice reaction step initiation was to clarify the mechanisms behind APA errors, which are related to slowed stepping reaction and, thus, to fall risks. It has been hypothesized that deficits in the inhibitory function would lead to an increase in APA errors (Cohen et al., 2011, Sparto et al., 2013, Uemura et al., 2013, Watanabe et al., 2015). The question was whether individuals prepare APA before the presentation of an imperative stimulus even during a choice reaction step initiation. In the context of the serial processing model (Sternberg, 1969) and the conflict monitoring theory (Botvinick et al., 2001), response conflict, defined as co-activation of the possible responses, occurs only after stimulus detection and identification. The response therefore would not be prepared in advance, and an individual would commit an error because of the failure to inhibit incorrect instances of the co-activated responses. Our results, however, did not support this view. APAs appear to be prepared in advance to a certain extent at the cost of making APA errors rather than complete errors, which may be a compensatory strategy for a fast response. Consequently, avoiding unnecessary preparation while keeping RT to a minimum could reduce the fall risk and, thus, be the target for preventative intervention, in addition to the inhibitory function. Older individuals, however, tend to use a cautious response strategy with prolonged RTs to avoid errors (Beste et al., 2009, Hoffmann and Falkenstein, 2011). Therefore, how aging affects the preparatory activity of APAs during a choice reaction step initiation may need to be clarified in future studies. It could also be interesting to evaluate preparation and decision-making strategies during a choice reaction step initiation in the cortical level using neurophysiological tools such as electroencephalography and near infrared spectroscopy.

In summary, this study demonstrated that APAs are prepared prior to the presentation of an imperative stimulus and during a choice reaction step initiation, are required to be inhibited from release until the response conflict is resolved. When it is not known beforehand which leg to make a step response with (i.e., the CRT task), individuals tend to preselect a stepping leg and prepare its associated APA. Furthermore, when making a step response with the preselected leg and occasionally having to inhibit the step response (i.e., in a GNG task), individuals tend to prepare APAs in advance. The preparatory activity of APAs also appears to be modulated by the inhibitory processes required for the choice task. Employing this strategy is unlikely result in a complete error but may cause an APA error or inappropriate APA initiation and, thus, may provide compensation for a quick response with maintained balance. The current findings could provide new insight into the features and strategies of postural adjustments.

Acknowledgements

This work was partly supported by Grant-in-Aid for Young Scientists (B) 25750203 (to I.N.) from the Japan Society for the Promotion of Science. We would like to thank

Yamada Osamitsu Scholarship Foundation for the support (to T.W.) and also thank our participants for their time and effort.

References

Aron AR, Robbins TW, Poldrack RA (2004) Inhibition and the right inferior frontal cortex. Trends Cogn Sci 8:170-177.

Assaiante C, Woollacott M, Amblard B (2000) Development of postural adjustment during gait initiation: kinematic and EMG analysis. Journal of motor behavior 32:211-226.

Beste C, Willemssen R, Saft C, Falkenstein M (2009) Error processing in normal aging and in basal ganglia disorders. Neuroscience 159:143-149.

Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD (2001) Conflict monitoring and cognitive control. Psychol Rev 108:624-652.

Brown P, Rothwell JC, Thompson PD, Britton TC, Day BL, Marsden CD (1991) New observations on the normal auditory startle reflex in man. Brain 114 (Pt 4):1891-1902.

Brunia CHM, Ullsperger M, Falkenstein M (2003) How is stopping realized? In: Errors, Conflicts, and the Brain Currect Opinitions on Performance Monitoring, pp 96-103.

Burle B, Possamaï CA, Vidal F, Bonnet M, Hasbroucq T (2002) Executive control in the Simon effect: An electromyographic and distributional analysis. Psychol Res 66:324-336.

Burle B, Roger C, Allain S, Vidal F, Hasbroucq T (2008) Error negativity does not reflect conflict: a reappraisal of conflict monitoring and anterior cingulate cortex activity. J Cogn Neurosci 20:1637-1655.

Burleigh A, Horak F (1996) Influence of instruction, prediction, and afferent sensory information on the postural organization of step initiation. J Neurophysiol 75:1619-1628.

Burleigh AL, Horak FB, Malouin F (1994) Modification of postural responses and step initiation: evidence for goal-directed postural interactions J Neurophysiol 72:2892-2902.

Carlsen AN, Chua R, Dakin CJ, Sanderson DJ, Inglis JT, Franks IM (2008) Startle reveals an absence of advance motor programming in a Go/No-go task. Neurosci Lett 434:61-65.

Carlsen AN, Chua R, Inglis JT, Sanderson DJ, Franks IM (2004a) Can prepared responses be stored subcortically? Exp Brain Res 159:301-309.

Carlsen AN, Chua R, Inglis JT, Sanderson DJ, Franks IM (2004b) Prepared movements are elicited early by startle. Journal of motor behavior 36:253-264.

Carpenter RH, Williams ML (1995) Neural computation of log likelihood in control of saccadic eye movements. Nature 377:59-62.

Chang WH, Tang PF, Wang YH, Lin KH, Chiu MJ, Chen SH (2010) Role of the premotor cortex in leg selection and anticipatory postural adjustments associated with a rapid stepping task in patients with stroke. Gait Posture 32:487-493.

Cohen RG, Nutt JG, Horak FB (2011) Errors in postural preparation lead to increased choice reaction times for step initiation in older adults. The journals of gerontology Series A, Biological sciences and medical sciences 66:705-713.

Delval A, Dujardin K, Tard C, Devanne H, Willart S, Bourriez JL, Derambure P, Defebvre L (2012) Anticipatory postural adjustments during step initiation: elicitation by auditory stimulation of differing intensities. Neuroscience 219:166-174.

Elble RJ, Moody C, Leffler K, Sinha R (1994) The initiation of normal walking. Mov Disord 9:139-146.

Fecteau JH, Munoz DP (2003) Exploring the consequences of the previous trial. Nat Rev Neurosci 4:435-443.

Fling BW, Cohen RG, Mancini M, Nutt JG, Fair DA, Horak FB (2013) Asymmetric pedunculopontine network connectivity in parkinsonian patients with freezing of gait. Brain 136:2405-2418.

Hanes DP, Schall JD (1996) Neural control of voluntary movement initiation. Science 274:427-430.

Hodges PW, Bui BH (1996) A comparison of computer-based methods for the determination of onset of muscle contraction using electromyography. Electromyography and Motor Control-Electroencephalography and Clinical Neurophysiology 101:511-519.

Hoffmann S, Falkenstein M (2011) Aging and error processing: age related increase in the variability of the error-negativity is not accompanied by increase in response variability. PLoS One 6:e17482.

Jacobs JV, Horak FB (2007a) Cortical control of postural responses. Journal of neural transmission (Vienna, Austria : 1996) 114:1339-1348.

Jacobs JV, Horak FB (2007b) External postural perturbations induce multiple anticipatory postural adjustments when subjects cannot pre-select their stepping foot. Exp Brain Res 179:29-42.

Jacobs JV, Lou JS, Kraakevik JA, Horak FB (2009) The supplementary motor area contributes to the timing of the anticipatory postural adjustment during step initiation in participants with and without Parkinson's disease. Neuroscience 164:877-885.

Kaminski TR, Simpkins S (2001) The effects of stance configuration and target distance on reaching I. Movement preparation. Exp Brain Res 136:439-446.

Kumru H, Urra X, Compta Y, Castellote JM, Turbau J, Valls-Sole J (2006) Excitability of subcortical motor circuits in Go/noGo and forced choice reaction time tasks. Neurosci Lett 406:66-70.

Lin SI, Yang WC (2011) Effect of plantar desensitization on postural adjustments prior to step initiation. Gait Posture 34:451-456.

Lord SR, Fitzpatrick RC (2001) Choice stepping reaction time: a composite measure of falls risk in older people. The journals of gerontology Series A, Biological sciences and medical sciences 56:M627-632.

MacKinnon CD, Bissig D, Chiusano J, Miller E, Rudnick L, Jager C, Zhang Y, Mille M-L, Rogers MW (2007) Preparation of anticipatory postural adjustments prior to stepping. J Neurophysiol 97:4368-4379.

Malouin F, Richards CL (2000) Preparatory adjustments during gait initiation in 4-6-year-old children. Gait Posture 11:239-253.

Marinovic W, de Rugy A, Lipp OV, Tresilian JR (2013) Responses to loud auditory stimuli indicate that movement-related activation builds up in anticipation of action. J Neurophysiol 109:996-1008.

Marinovic W, Tresilian JR, de Rugy A, Sidhu S, Riek S (2014) Corticospinal modulation induced by sounds depends on action preparedness. J Physiol 592:153-169.

Masaki H, Murphy TI, Desjardins JA, Segalowitz SJ (2012) The error-related negativity associated with different strength of stimulus-response interference. Clin Neurophysiol 123:689-699.

Maslovat D, Drummond NM, Carter MJ, Carlsen AN (2015) Reduced motor preparation during dual-task performance: evidence from startle. Exp Brain Res 233:2673-2683.

Maslovat D, Hodges NJ, Chua R, Franks IM (2011) Motor preparation and the effects of practice: evidence from startle. Behav Neurosci 125:226-240.

Massion J (1992) Movement, posture and equilibrium: interaction and coordination. Prog Neurobiol 38:35-56.

Mickelborough J, van der Linden ML, Tallis RC, Ennos AR (2004) Muscle activity during gait initiation in normal elderly people. Gait Posture 19:50-57.

Nickerson R (1973) Intersensory facilitation of reaction time: energy summation or preparation enhancement. Psychol Rev 80:489-509.

Nijhuis LB, Janssen L, Bloem BR, van Dijk JG, Gielen SC, Borm GF, Overeem S (2007) Choice reaction times for human head rotations are shortened by startling acoustic stimuli, irrespective of stimulus direction. J Physiol 584:97-109.

Nonnekes J, Oude Nijhuis LB, de Niet M, de Bot ST, Pasman JW, van de Warrenburg BP, Bloem BR, Weerdesteyn V, Geurts AC (2014) StartReact restores reaction time in HSP: evidence for subcortical release of a motor program. J Neurosci 34:275-281.

Nonnekes J, Scotti A, Oude Nijhuis LB, Smulders K, Queralt A, Geurts AC, Bloem BR, Weerdesteyn V (2013) Are postural responses to backward and forward perturbations processed by different neural circuits? Neuroscience 245:109-120.

Pai YC, Rogers MW, Patton J, Cain TD, Hanke TA (1998) Static versus dynamic predictions of protective stepping following waist-pull perturbations in young and older adults. J Biomech 31:1111-1118.

Pijnappels M, Delbaere K, Sturnieks DL, Lord SR (2010) The association between choice stepping reaction time and falls in older adults-a path analysis model. Age Ageing 39:99-104.

Ramnani N, Behrens TE, Johansen-Berg H, Richter MC, Pinsk MA, Andersson JL, Rudebeck P, Ciccarelli O, Richter W, Thompson AJ, Gross CG, Robson MD, Kastner S, Matthews PM (2006) The evolution of prefrontal inputs to the cortico-pontine system: diffusion imaging evidence from Macaque monkeys and humans. Cereb Cortex 16:811-818.

Reynolds RF, Day BL (2007) Fast visuomotor processing made faster by sound. The Journal of physiology 583:1107-1115.

Rogers MW, Hedman LD, Johnson ME, Martinez KM, Mille ML (2003) Triggering of protective stepping for the control of human balance: age and contextual dependence. Brain Res Cogn Brain Res 16:192-198.

Schepens B, Drew T (2003) Strategies for the integration of posture and movement during reaching in the cat. J Neurophysiol 90:3066-3086.

Schepens B, Drew T (2004) Independent and convergent signals from the pontomedullary reticular formation contribute to the control of posture and movement during reaching in the cat. J Neurophysiol 92:2217-2238.

Schmahmann JD, Pandya DN (1997) Anatomic organization of the basilar pontine projections from prefrontal cortices in rhesus monkey. J Neurosci 17:438-458.

Schmidt RA, Gielen SC, van den Heuvel PJ (1984) The locus of intersensory facilitation of reaction time. Acta Psychol (Amst) 57:145-164.

Schreiber M, Pietschmann M, Kathmann N, Endrass T (2011) ERP correlates of performance monitoring in elderly. Brain Cogn 76:131-139.

Slijper H, Latash ML, Mordkoff JT (2002) Anticipatory postural adjustments under simple and choice reaction time conditions. Brain Res 924:184-197.

Sparto PJ, Fuhrman SI, Redfern MS, Jennings JR, Perera S, Nebes RD, Furman JM (2013) Postural adjustment errors reveal deficits in inhibition during lateral step initiation in older adults. J Neurophysiol 109:415-428.

Sternberg S (1969) The discovery of processing stages: Extensions of Donders' method. Acta Psychol (Amst) 30:276-315.

Sumner P, Nachev P, Morris P, Peters AM, Jackson SR, Kennard C, Husain M (2007) Human medial frontal cortex mediates unconscious inhibition of voluntary action. Neuron 54:697-711.

Tard C, Dujardin K, Bourriez JL, Derambure P, Defebvre L, Delval A (2013) Stimulus-driven attention modulates the release of anticipatory postural adjustments during step initiation. Neuroscience 247:25-34.

Tard C, Dujardin K, Girard A, Debaughrien M, Derambure P, Defebvre L, Delval A (2016) How does visuospatial attention modulate motor preparation during gait initiation? Exp Brain Res 234:39-50.

Timmann D, Horak FB (2001) Perturbed step initiation in cerebellar subjects: 2. Modification of anticipatory postural adjustments. Exp Brain Res 141:110-120.

Tresilian JR, Plooy AM (2006) Effects of acoustic startle stimuli on interceptive action. Neuroscience 142:579-594.

Uemura K, Oya T, Uchiyama Y (2013) Effects of visual interference on initial motor program errors and execution times in the choice step reaction. Gait Posture 38:68-72.

Valls-Solé J, Solé A, Valldeoriola F, Muñoz E, Gonzalez LE, Tolosa ES (1995) Reaction time and acoustic startle in normal human subjects. Neurosci Lett 195:97-100.

Vanboxtel GJM, Geraats LHD, Vandenberglenssen MMC, Brunia CHM (1993) Detection of EMG onset in ERP research. Psychophysiology 30:405-412.

Vidal F, Hasbroucq T, Grapperon J, Bonnet M (2000) Is the 'error negativity' specific to errors? Biol Psychol 51:109-128.

Watanabe T, Koyama S, Tanabe S, Nojima I (2015) Accessory stimulus modulates executive function during stepping task. J Neurophysiol 114:419-426.

Yakovenko S, Drew T (2009) A motor cortical contribution to the anticipatory postural adjustments that precede reaching in the cat. J Neurophysiol 102:853-874.

Zettel JL, McIlroy WE, Maki BE (2002a) Can stabilizing features of rapid triggered stepping reactions be modulated to meet environmental constraints? Exp Brain Res 145:297-308.

Zettel JL, McIlroy WE, Maki BE (2002b) Environmental constraints on foot trajectory reveal the capacity for modulation of anticipatory postural adjustments during rapid triggered stepping reactions. Exp Brain Res 146:38-47.

Competing Interests

None.

Author Contributions

T.W. and I.N. designed experiments. T.W., K.I., and S.T. performed experiments and analyzed data. T.W. wrote the manuscript. All authors approved the final version of the manuscript.

Figure Captions

Figure 1. Visual imperative stimuli and the temporal layout of one example trial
Left side: The choice reaction time (CRT) task comprised an arrow pointing either left or right, and the go/no-go (GNG) task comprised an arrow pointing either upward or downward. Right side: Visual stimuli were presented in the following sequence: fixation (random interval of 6–7 s), forewarning (0.5 s), fixation (random interval of 3–4 s), imperative stimulus (IS, 0.5 s). The total duration was kept constant at 10 s.

Figure 2. Examples of tibialis anterior (TA) electromyographic (EMG) activities and center of pressure (COP) movements
Rectified TA EMG (top) and mediolateral COP movement data (bottom) for an anticipatory postural adjustment (APA) error trial of the choice reaction time task (A) and for a no-go trial with an inappropriate APA initiation of the go/no-go task (B).

Figure 3. Effects of loud auditory stimuli (LAS) on anticipatory postural adjustment (APA) error rate (top) and inappropriate APA initiation rate (bottom)
CRT: forced choice reaction time; GNG: go/no-go. Error bars show standard error of the mean.

Figure 4. Effects of loud auditory stimuli (LAS) and anticipatory postural adjustment (APA) errors or inappropriate APA initiations on reaction times
The mean reaction times of the electromyographic (EMG) activity recorded in the tibialis anterior (TA) (A) and mediolateral center of pressure (COP) movements (B) are shown separately. The left side represents the choice reaction time (CRT) task and right side represents the go/no-go (GNG) task. Error bars show standard error of the mean.