Biological Cybernetics (2021) 115:207–217
https://doi.org/10.1007/s00422-021-00873-x

Biological Cybernetics

ORIGINAL ARTICLE

Perceptual adaptation during a balancing task in the seated posture and its theoretical model

Satoshi Ito[1] · Kazuya Tomabechi[2] · Ryosuke Morita[1]

Received: 29 August 2020 / Accepted: 29 March 2021 / Published online: 10 May 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

This paper proposes a theoretical model of the control and perception mechanism in human balance. Human balance perception is evaluated by the subjective upright posture, the posture at which a person does not feel he/she is at an incline. Our balance experiments in the seated posture showed that the subjective upright posture changed after the balancing task where the participants needed to incline to maintain their balance. This paper aimed to explain this adaptive phenomenon by reproducing the experimental results using computer simulations. Hypothesizing that "humans gradually come to recognize the posture they need to take to maintain their balance as being upright," an adaptation rule for subjective upright posture is defined, so that it approaches the averaged posture in the period of the balancing task. For the balance control, center of pressure feedback is adopted. As a result, the similar changes in subjective upright posture are simulated with a two-link model with a base link, implying that our hypothesis is one possible explanation on the mechanism for human balance control and perception.

Keywords Perceptual adaptation · Motor learning · Seated balance · Upright perception · Theoretical model

1 Introduction

Motion generation adaptation to various environmental conditions is one form of intelligence in biological systems. Understanding the motion control mechanism in humans is important not only from a medical point of view, such as to propose effective rehabilitation methods (MacKay-Lyons 2002; Barbeau 2003; Oña et al. 2018), but also from an engineering point of view, such as realizing the substitution of human tasks with robotic behaviors. Previous research has mostly investigated motor control mechanisms in humans using arm reaching movements (e.g., Kawato 1996). One of the most important contributions of studies on reaching movements is the establishment of the motor learning paradigm: force field learning has provided lots of new insights on human motor learning (Shadmehr and Mussa-Ivaldi 1994).

Studies using force field learning discovered that motor learning not only affects the motor system, such as hand trajectories, but also the sensory system, especially the somatosensory perception of hand positions. Ostry et al. (2010) demonstrated that the hand positional perception, i.e., perceptual boundary dividing the left and right side of the right-hand position got shifted to the opposite direction of the force during force field learning.

Then, is this phenomenon in which the sensory system is affected by the motor system limited to arm reaching movements? Can the effects of motor learning be observed only in the somatosensory system? To answer these questions, we predicted that perceptual changes accompanying motor learning also work for the other kind of motor tasks. Particularly, we focused on the balance maintenance of the body, because it contains a form of perception other than somatosensory perception.

For balancing tasks, the effect of visual perturbation has been reported in several studies. Changes in balance perception are also found in sway or un-stabilization from visual

Communicated by Benjamin Lindner.

A part of this work was supported by Grant-in-Aid for Scientific Research(B) (No. 16H02879) of Japan Society for the Promotion of Science.

✉ Satoshi Ito
satoshi@gifu-u.ac.jp

1 Faculty of Engineering, Gifu University, Tokai National Higher Education and Research System, Yanadigo 1-1, Gifu, Japan

2 Graduate School of Information Science and Technology, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-8656, Japan

stimuli. For example, the compensating body sways when seeing a train start moving on the next line from the window of the stopping train, because this visual information causes us to perceive our balance as disturbed. Owing to its relation to visual information, the subjective upright has sometimes been assessed by an index, the subjective visual vertical (SVV). Mittelstaedt (1983) introduced the concept of idiotropic vector to explain why, depending on tilted head posture, the SVV can be overestimated in comparison with the physical vertical. Afterward, the fact that there are separate cases in which SVV is overestimated in some and underestimated in others, depending on head tilt angle, was reported, and researchers aimed to provide a theoretical explanation (e.g., based on the Bayesian method Mittelstaedt 1983).

The subjective haptic vertical (SHV) was proposed as another index (Luyat et al. 2001), and the effects to the SHV as well as the SVV from posture and visual stimuli were recently studied from the aspect of the decay time of their adaptive effect (Wedtgrube et al. 2020). However, few papers have considered the direct effect to balancing perception, in the sense that it is neither visual nor haptic, from motor learning; thus, this paper aims to address this issue. Ramadan et al. (2017) evaluated human balance in the seated posture within the lateral plane as this paper will do; however, their study aimed to propose a reliable balance assessment method, and thus differed from this paper, which focus on the perceptual changes accompanying motor learning.

To detect the effects of motor learning, some novel environments should be conducted repeatedly, so that the humans can identify another posture to maintain balance in those situations. Thus, the objectives of this research project are as follows:

1. To establish an experimental protocol that can detect changes in balancing perception;
2. To theoretically explain control mechanisms that include perceptual changes as the dynamical process;
3. To replay or realize the adaptive behavior as the robotic motions.

This paper mainly addresses the second objective. For the first objective, a protocol we proposed (Kumagai et al. 2015) was our original and thus novel. Its result, i.e., the change of the balance perception accompanying the balance motor learning, has not yet been explained mathematically. This paper attempting to propose its theoretical model will contribute to help us with understanding the control mechanism of the human balance.

This paper is organized as follows. In Sect. 2, the evidence of human perceptual changes is described based on our previous study (Kumagai et al. 2015), corresponding to the first objective above. Our subgoal is to reproduce the results in Fig. 5 via computer simulations based on our modeling for a human control mechanism. Section 3 addresses our hypothesis our modeling is based and proposes a balance control law and an updated rule of balance perception. Our modeling is simulated in Sect. 4 to demonstrate the validity of our hypothesis by reproducing the results shown in Sect. 2. Section 5 concludes the paper.

2 Measurement of human behavior

2.1 Scenario of perceptual changes

For the adaptation, a new steady environment is required, so that the acquired motion pattern, or the posture, adjusts to the environment. To create such an environment, our experimental plan (Kumagai et al. 2015)[1] produces periodic disturbances, so the exactly upright posture is not always advantageous for maintain balance. To achieve this condition, we have manufactured a special stool with a seat that rotates in the pitch as well as rolls, so that the whole stool slides to either the left or right; because of the symmetry, the disturbance application, as well as the perceptual test, is conducted in a lateral direction. Considering safety, the balance experiment was designed for a seated, not standing, position to avoid the risk of easy falls.

In the experiments, participants are asked to maintain their balance with keeping the slowly rotatable seat as horizontal as possible; however, participants do not take an exactly upright posture. Participants are required to learn a new suitable posture to adjust to the periodic disturbance. Thus, our prediction is that the direction the participants perceive exactly upright will change toward the one being taken to maintain the balance.

In the following sections, we establish the experimental protocol that achieves this scenario.

2.2 Experimental setup

Here, we mention the experimental setup we originally manufactured first, before we explain the experimental design, to make it easier to understand the actual content of the experiments. The whole system is shown in Fig. 1.

The main device of the experimental setup is the stool. This stool can slide in lateral directions, and its seat surface turns to the left or right around the roll axis. The surface can also tilt to the back and front; however, this motion is not used during the experiments, and thus, the pitch angle of the seat surface is always fixed parallel to the floor.

Four load cells are installed at the corner of the seat to detect the position of the center of pressure (CoP) of partic-

[1] The experimental method and its result in Sect. 2 have been already reported in Kumagai et al. (2015).

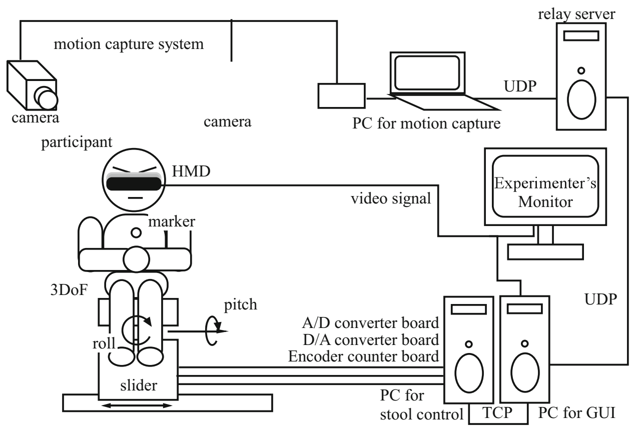


Fig. 1 Experimental setup

ipants in a seated posture. To detect head and torso position, a motion capture system was introduced. Additionally, a head-mounted display (HMD) is used to block outside visual information and provide visual instruction to participants.

Three computers operate during the experiments. One is for the motion capture system to calculate the marker position and send it to the relay server, the second computer. The second computer is used for stool control, and has an A/D converter, a D/A converter, and encoder counter boards, and controls the stool motions in 1ms cycles. The third computer provides the graphical user interface to both the participant and experimenter. It can obtain the markers position through the UDP connection and the stool state through the TCP connection in 20 ms cycles. These states can be provided by computer graphics to help the participant maintain balance. This computer also displays the stool's control panel and helps the experimenter with commanding to the controller PC.

2.3 Motor learning in the balancing task

The purpose of this task is to force the participants to keep their balance while not in the exact upright posture. Particularly, as our interest is in the learning of the motion, i.e., not static but dynamic posture, we apply periodic disturbances to create the balancing task dynamics.

Two kinds of disturbances are applied: a slide disturbance and a rotational disturbance, as illustrated in Fig. 2a.

The former is produced just by repeatedly moving the stool in a lateral direction. It is symmetrical and thus has no directionality.

However, to characterize directionality in the latter, we introduced a concept called virtual rotation axis. Figure 3 illustrates how it works. Physically, the rotation direction is decided by the relative CoP position with respect to the mechanical rotation axis. Here, we replace this role with the virtual rotation axis by controlling the stool's roll axis motor.

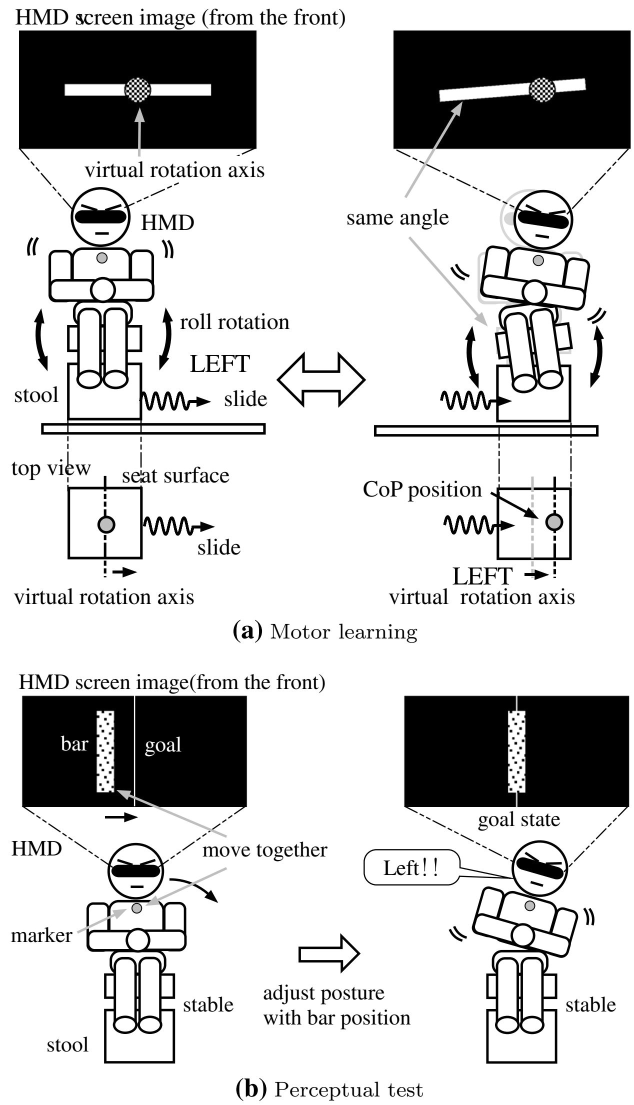


Fig. 2 Two phases in the human measurement experiment

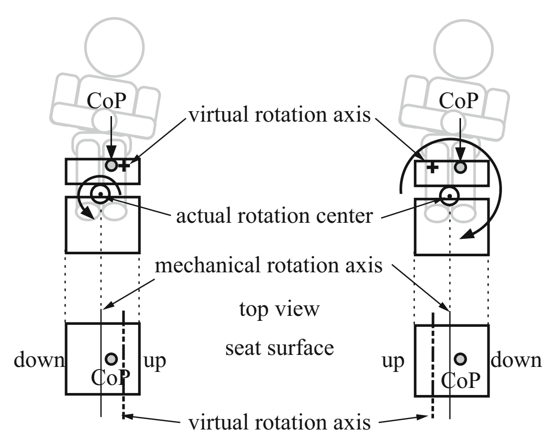


Fig. 3 Virtual rotation axis

Thus, the seat surface rotates to the right when the CoP is to the right of the virtual rotation axis, even though it is actually to the left of the mechanical rotation axis, as shown on the left of Fig. 3.

In this task, we ask participants to maintain their balance while keeping the seat surface horizontal. Then, the participants have to control their CoP to exactly above the virtual rotation axis. Furthermore, if the virtual rotation axis repeatedly shifts to the one side, e.g., to the RIGHT, the participants will slant their upper body to the right in synchronization with the virtual rotation axis. This is exact situation for which we aimed. We call this disturbance the RIGHT disturbance.

In the actual experiments, both kinds of disturbance were applied in the same 8-s period. The stool at first slides 0.2 m to the right in 4 s and then goes back in 4 s. Simultaneously, in the RIGHT disturbance condition, the virtual rotation axis moves 0.025 m to the right from the initial position of 0.005 m left from the stool center and then goes back to the initial position. This 8-s movement is treated as one learning trial.

Before the experiments, we instructed participants to maintain their balance in the seated posture while keeping the seat surface horizontal. To help participants achieve this, we demonstrated the tilt of the seat, as well as the current position of the virtual rotation, axis with computer graphics on the HMD, as illustrated in Fig. 2a. The tilt angle of the horizontal bar denotes the actual tilted angle of the seat surface, and the circle indicates the position of the virtual rotation axis. Usually, the bar was yellow, but would turn red if the tilt angle exceeded 8°. We also told participants to keep the color of the bar yellow.

2.4 Perceptual tests

As an index of balance perception, we focused on the subjective upright posture. It is not an exact upright in the physical sense, but a posture at which a participant feels they are now upright.

To detect this posture, we asked participants to use a laterally tilted posture with various angles. Figure 2b illustrates our method. During the perceptual tests, on the HMD, we showed a vertical red bar moving left and right in synchronization with participants' upper body, as detected by the motion capture system. When the bar controlled by participants' upper body comes to the center of the display, it turns yellow. We ask participants whether they feel they are inclining to the left or right at this moment. Note that the angle of a participant's posture can be controlled with the initial position of the horizontal bar. The more to the right it the bar is displayed on the HMD, the more to the left their posture inclines. The initial position of the horizontal bar changes following the PEST (Taylor and Creelman 1967).

Before displaying the bar for the next test, the seat surface slides left and right, keeping it horizontal to reset the participant's posture. In one set of perceptual tests, six PEST runs were performed at different initial values. In the experimental setting, one pixel on the HMD equaled 1/4 mm in the actual experimental space.

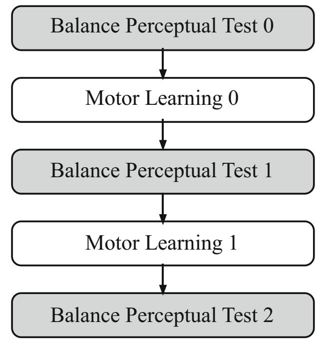


Fig. 4 Experimental procedure including 2 motor learning phases and 3 perceptual test phases

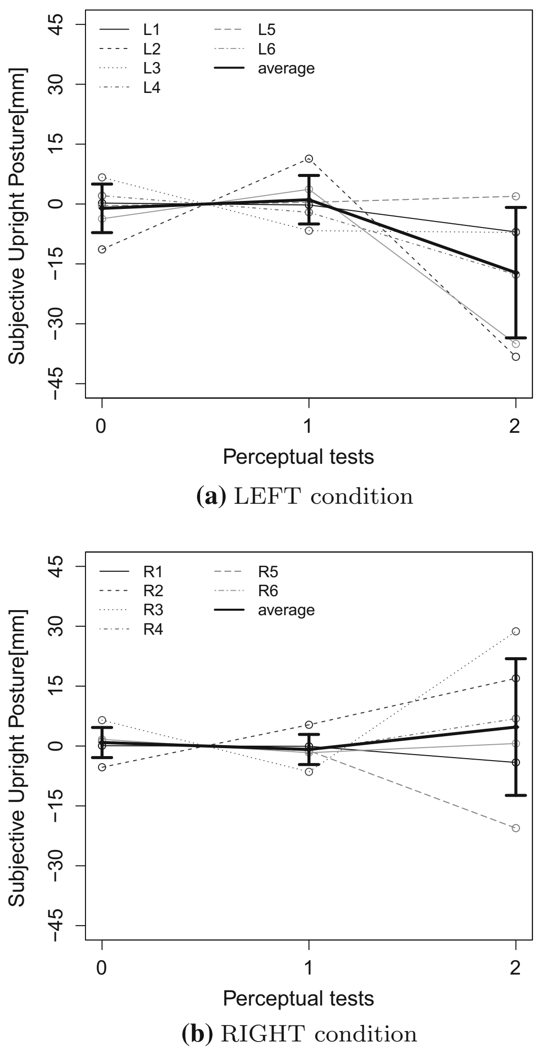
2.5 Experiment and results

After the experimental protocol was approved by the ethics committee of the School of Medicine at Gifu University (26–55), 12 participants between 20 and 24 years old were recruited; six were for the left disturbance condition, and six were for the right disturbance condition.

In the motor learning excluding the rotation disturbance (Motor Learning 0) in Fig. 4, 100 trials were conducted to establish a baseline, before 100 real motor learning trials were performed in Motor Learning 1. Before and after the motor learning, the perceptual tests were conducted, as shown in Fig. 4. In total, three set of perceptual tests were included for one experiment.

The psychometric function representing the relation between the upright body position and the ratio the participant answered "right" at this position was constructed from the answers of several tens perceptual tests for each set. Then, the subjective upright posture was estimated as the position that took the 0.5 ratio of the answer "right." The change in the subjective upright posture is summarized in Fig. 5a, b denotes the results of the left and right disturbance conditions, respectively. The positive vertical value represents the deviation of subjective upright posture to the participant's right direction, and 0, 1, and 2 denote the order of the perceptual test sets. The thin lines are the results for each participants, the thick lines are the average of the six participants, and the bars denote standard errors. To remove the bias of each participants, the data were realigned so as to zero the average of the perceptual test 0 and 1.

A two-way ANOVA found a significant difference $p = 0.0312$ among six averaged values (2 disturbance conditions $\times$ 3 sets of perceptual tests). Tukey's test indicated that two



(a) LEFT condition

(b) RIGHT condition

Fig. 5 Perceptual changes

averaged values of the last sets showed a significant difference between the left and right conditions ($p = 0.0125$).

3 Mathematical description of balance perception change

3.1 Purpose: hypothesis to prove

The result in Fig. 5 implies that:

- the sole symmetrical slide disturbance does not change balancing perception;
- the combination of the slide and asymmetrical rotational disturbances causes the changes in balancing perception; and
- the direction of the perceptual change was reversed between the left and right disturbance conditions.

Although another experimenter reported different results regarding the direction of the perceptual changes possibly due to the differences in the control experiment (Ito et al. 2014) (see also “Appendix D”), we aim to explain how the perceptual changes occurs by proposing a hypothesis of this adaptive process in Fig. 5. Namely, our attempt is to reproduce Fig. 5 by the dynamical system based on our hypothesis.

Figure 5 shows that the direction of the disturbance and the perceptual changes are the same; when the participants incline to the right during motor learning, the subjective upright posture moves to the right. The right shift of the virtual rotation axis forces the participants to incline to the right; thus, participants intend to incline to the right to stay upright. Thus, “the participants (humans) gradually come to recognize the posture they need to take to maintain their balance as being upright.” This is our hypothesis for the changes in balance perception. “Appendix D” also mentions where the above hypothesis connecting the balance perception and the inclined posture comes from.

In the following sections, we define a control law and an adaptive rule the participants is supposed to adopt. Then, to focus on the above point, we set the following assumptions:

- A1. The motions are restricted within the frontal plane.
- A2. The participants can be modeled as a two-link system with the base: the base corresponds to the lower part of the body (pelvis and legs), the first link corresponds to the torso, and the second link corresponds to the head, shoulders, and arms.
- A3. The shape of the model is symmetrical in the lateral direction, and the center line of the stool and base are aligned.
- A4. The base does not rotate or slip on the seat.
- A5. The participants can detect the sway angle and angular velocity of both links, as well as the CoP position under the base link. Furthermore, the current position of the virtual rotation axis is also known.
- A6. Arbitrary torque can be outputted at the first and second joints.
- A7. No delays exist in sensing and actuation.

The fourth assumption in the above is modeled here, considering the virtual joint around which the base link never rotates relative to the stool. A mechanical model is illustrated in Fig. 6, and its motion equation is described in “Appendix.” The notations are illustrated in Fig. 7.

Here, the deviation of the virtual rotation axis, x_{v}, as well as the CoP, P_{CoP}, on the seat surface is defined as the rightward distance from the common center line of the base link and stool. Namely, the situation $P_{\mathrm{CoP}} = 0$ is the most stable in the no disturbance condition, because the CoP stays at the center of the base link as well as the stool.

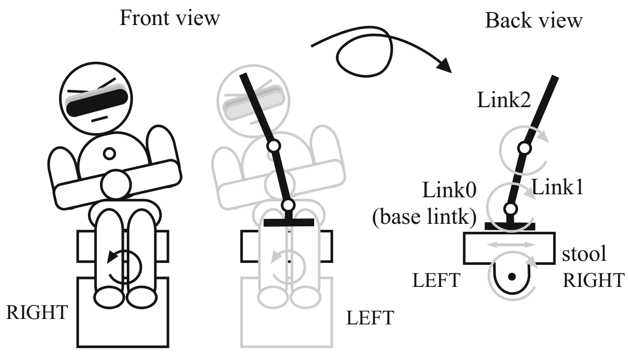


Fig. 6 A link model

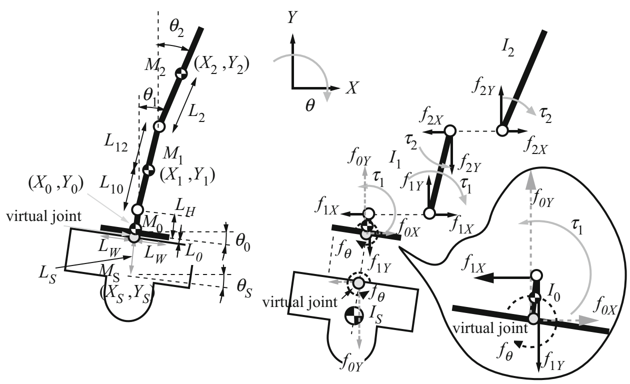


Fig. 7 Notation of the link parameters

3.2 Balance control

One of the instructions to the participants was to maintain balance while keeping the stool surface horizontal. It requires the CoP to follow the motion of the virtual rotation axis. We have already proposed a method for the CoP control to maintain the balance (Ito and Kawasaki 2005). This method is applied to τ_1.

$$\tau_1 = -K_{d1}\dot{\theta}_1 + K_{p1}(\theta_{d1} - \theta_1) + K_{CoP}\int (x_v - P_{CoP})dt \tag{1}$$

where x_v is the position of the virtual rotation axis and θ_{d1} is a nominal desired angle of θ_1 that should be zero (upright) in no disturbance condition. For τ_2, a simple PD control is adopted to maintain posture.

$$\tau_2 = -K_{d2}\dot{\theta}_2 + K_{p2}(\theta_{d2} - \theta_2) \tag{2}$$

Here θ_{d2} is a desired angle of θ_2 and also should be zero for the upright posture. As a result, the whole body consisting of two links inclines to the disturbance direction, in synchronization with the virtual rotation axis.

3.3 Perceptual changes

Our hypothesis in Sect. 3.1 implicitly indicates that participants sense of being upright is affected by the posture they need to maintain balance. We determined the rule of perceptual changes in the balancing task based on this concept.

The posture participants need to take can be represented as the desired joint angle if the balance is maintained based on the position controller achieving the suitable posture against disturbed conditions. From this viewpoint, we later attempt to update the subjective upright posture ϕ based on the desired angle of the control law (1). Regarding (2), we defined it to keep the upper body straight, implying that the whole sway is almost determined by the desired angle of (1). So, only the desired angle of (1) we regard as the position controller is focused.

We can redefine the control law (1) as a position control:

$$\tau_1 = -K_{d1}\dot{\theta}_1 + K_{p1}(\Theta_d - \theta_1) \tag{3}$$

$$\Theta_d = \theta_{d1} + K_{CoP}/K_{p1}\int (x_v - P_{CoP})dt \tag{4}$$

These equations mean that the desired posture Θ_d gradually changes with the disturbance (i.e., the motion of the virtual rotation axis).

In the normal situation without the disturbance, Θ_d should correspond to the upright position also in its physical meaning. Then, we inferred that Θ_d has a psychological connection to the sense of the upright direction, and that the posture participants need to have to maintain balance is tended to easily regarded as upright, or, in all modesty, this posture affects the subjective upright posture ϕ so that the upright sense approaches to Θ_d.

Based on this idea, we define the perceptual changes as follows:

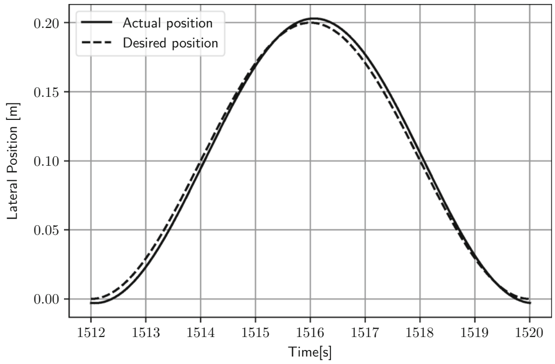
$$\dot{\phi} = k_\phi(\mathrm{LPF}(\Theta_d) - \phi) \tag{5}$$

Here, LPF means a low-pass filter operation. This dynamics describes the change of the perception that follows the slow dynamics of the desired angle of the body inclination.

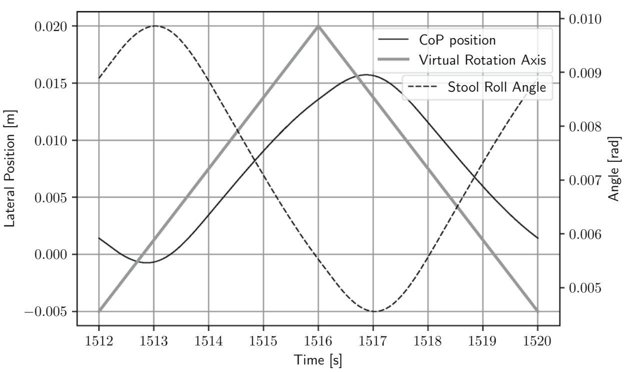
4 Simulations

4.1 Conditions

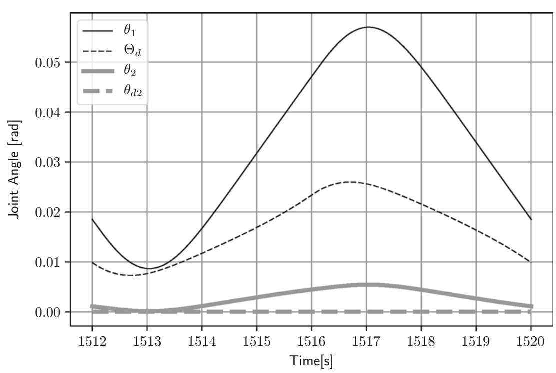
In the same way as the human measurements in Sect. 2, 100 trials were simulated in the sole slide disturbance before 100 trials under the condition containing also the rotational disturbance, the asymmetrical shift of the virtual rotation axis. A total of 10 trials were simulated for both the LEFT and RIGHT disturbance conditions. The motion of the stool for



(a) stool horizontal position



(b) CoP position and stool roll angle



(c) joint angles of the human model

Fig. 8 Simulation result of the link model during one trial (190th RIGHT condition)

disturbance was also set to the same as the human measurements, as described in Sect. 2.3.

The parameters were set as follows: $M_S = 20$, $M_0 = 20$, $M_1 = 15$, $M_2 = 20$, $I_S = 0.5$, $I_0 = 0.1$, $I_1 = 0.1$, $I_2 = 0.1$, $L_{0S} = 0.1$, $L_{01} = 0.1$, $L_{10} = 0.15$, $L_{12} = 0.15$, $L_2 = 0.2$, The gains were $K_{\mathrm{d1}} = 50$, $K_{\mathrm{p1}} = 250$, $K_{\mathrm{CoP}} = 300$, $K_{\mathrm{d2}} = 50$, $K_{\mathrm{p2}} = 500$ and $K_\phi = 0.005$. The first-order system with the time constant 10 was used for the LPF in (5). The simulations began with the upright posture. The fourth-order Runge–Kutta method was applied to numerical integration with the step size $\Delta T = 0.001$ s.

4.2 Results

To examine the behavior of the link model, the stool horizontal movement, stool roll rotation, and joint angles of the human model are depicted in Fig. 8a–c, respectively. These data were from the 190th trial in the RIGHT disturbance condition.

Additionally, the time course of the parameter indicating the subjective upright posture, ϕ, was depicted over all 200 trials in both the LEFT and RIGHT conditions, as shown in Fig. 9.

4.3 Discussion

The slide disturbance was applied as intended, since the stool followed its desired trajectory in Fig. 8a. The rotation disturbance was also applied with the shift of the virtual rotation axis (gray line) in Fig. 8b. Moreover, when the CoP position (black line) came to the right of (greater than) the virtual rotation axis, the stool angle (dashed line) was accelerating to the right (starting to turn clockwise). Accordingly, the same experimental conditions was provided in the simulations.

Under two disturbances, the human model maintained balance without falling over: Fig. 8c shows that θ_1 periodically varied rightward between approximately 0.01 rad and 0.06 rad (about 3°), to adapt to the periodic disturbance, while θ_2 was kept around 0 rad, with a 0.005 rad deviation at most, indicating the straight body posture was also maintained. Furthermore, as shown in Fig. 8b, the CoP position tended to follow the virtual rotation axis. Although the deviation range of CoP decreased, and the response delay was approximately 1s, these were also observed in the human measurements (Ito et al. 2014). Consequently, control law (1) and (2) produced the motion we intended: maintaining the balance while keeping the seat surface horizontal, with tracking the CoP to the virtual rotation axis by making the use of the upper body inclination.

Our hypothesis assumed that the desired angle Θ_{d} changed from the initial value 0 rad, depending on the averaged (low-pass-filtered) posture during trials. Namely, we consider the motor learning changes this desired posture with respect to the environmental conditions. Our hypothesis in this paper also supposed that this posture affects perception (i.e., the subjective upright posture) ϕ, changes toward the Θ_{d} according to (5). Figure 9 represents this change; the first 100 trials show no changes in ϕ, while the changes toward Θ_{d} appeared in the last 100 trials. These are the same as the results of the human measurements shown in Fig. 5.

The result of the human measurements shown in Fig. 5 implies that the deviation of the subjective upright posture is 17.19 mm in the LEFT condition, 4.74 mm in the RIGHT condition and thus about 11.0 mm in average. On the other hand, Fig. 9 indicates that the change of the sub-

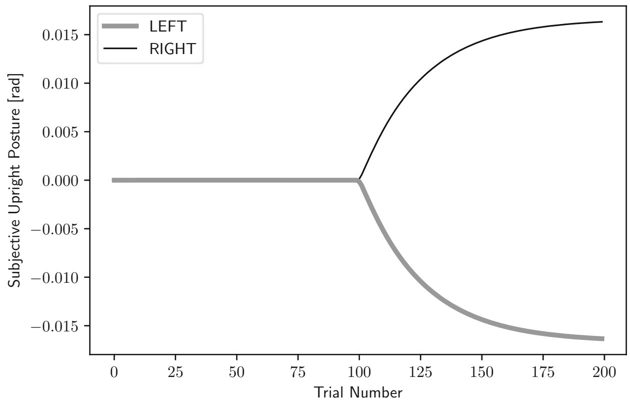


Fig. 9 Simulated perceptual changes

jective upright posture is about 0.016 rad after 100 trials under the disturbed condition. If the mark is assumed to be attached 0.5 m above the base joint, the marker deviation becomes $(0.5) \times 0.016 = 0.008$ m, which is the same order as the human results. Thus, these simulations have quantitatively replayed human behaviors; therefore, our hypothesis, "humans gradually come to consider the posture they need to take to maintain their balance as upright," is acceptable as a possible mechanism of human balance control and perception.

The validation of our hypothesis will require some analyses of the relationship in changes between participants' torso posture after adaption and the subjective upright posture: we expect a good correlation between them, and ideally, the variation of the subjective upright posture should be predicted from the participants' posture. Unfortunately, we have not obtained such evidences yet, probably because the balancing task is difficult for many participants to complete the motor learning. However, our another experiment provides a tendency that indicates the importance of the balancing posture during the motor learning to explain the perceptual changes (Kumagai et al. 2017), and our model here comes from the consideration based on them (see also "Appendix D"). Thus, our model might be a predictive one that can explain the human behaviors. Anyway, we need more human data to confirm our hypothesis and our theoretical model.

5 Conclusion

Inspired by the adaptation in somatosensory perception accompanying motor learning of arm reaching movements, human balance control and perception was examined in this paper. In our previous paper, human balance perception evaluated by the subjective upright posture was measured before and after the balancing task in the seated posture. As a result, changes in the subjective upright posture were detected after balance learning.

Based on the human experimental results, this paper aimed to explain this perceptual change in a balancing task utilizing a theoretical model. Then, a hypothesis was posited: "humans gradually come to recognize the posture they need to take to maintain their balance as being upright." Along with this hypothesis, we defined adaptive dynamics for a parameter indicating the subjective upright posture to approach the averaged posture in the period of balance control. For balance control, the CoP feedback we proposed in the previous paper was adopted, because the task requires regulation of the CoP position to avoiding the risk of falling.

Applying the balance control as well as the updated rule in the subjective upright posture to the two-link model with the base link, computer simulations reproduced the balance perceptual changes quantitatively. This implies that our theoretical model represents one of the possible mechanisms in human balance control and perception. One of the improvement point in our model is to taking the time loss or delay in the sensing and actuation into account. It is well known that the time loss has a large effect on the stability from the control point of view, but the human can manage it and continue to keep the balance. Future research should develop a robotic realization of this adaptive phenomenon considering the time loss.

Declarations

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

Appendices

A Motion equation

The Newton–Euler method provides the following motion equations for the mechanical model in Fig. 7.

$$M_S \ddot{X}_S = F_X - f_{0X} \tag{6}$$

$$M_S \ddot{Y}_S = f_Y - f_{0Y} - M_S g \tag{7}$$

$$I_S \ddot{\theta}_S = \tau_S - f_\theta - f_{0X} L_S \cos\theta_S + f_{0Y} L_S \sin\theta_S \tag{8}$$

$$M_0 \ddot{X}_0 = f_{0X} - f_{1X} \tag{9}$$

$$M_0 \ddot{Y}_0 = f_{0Y} - f_{1Y} - M_0 g \tag{10}$$

$$I_0 \ddot{\theta}_0 = f_\theta - \tau_1 - f_{0X} L_{0S} \cos\theta_0 + f_{0Y} L_{0S} \sin\theta_0 \tag{11}$$

$$- f_{1X} L_{0H} \cos\theta_0 + f_{1Y} L_{0H} \sin\theta_0 \tag{12}$$

$$M_1 \ddot{X}_1 = f_{1X} - f_{2X} \tag{13}$$

$$M_1 \ddot{Y}_1 = f_{1Y} - f_{2Y} - M_1 g \tag{14}$$

$$I_1\ddot{\theta}_1 = \tau_1 - \tau_2 - f_{1X}L_{10}\cos\theta_1 + f_{1Y}L_{10}\sin\theta_1 - f_{2X}L_{12}\cos\theta_1 + f_{2Y}L_{12}\sin\theta_1 \quad (15)$$

$$M_2\ddot{X}_2 = f_{2X} \quad (16)$$

$$M_2\ddot{Y}_2 = f_{2Y} - M_2 g \quad (17)$$

$$I_2\ddot{\theta}_2 = \tau_2 - f_{2X}L_2\cos\theta_2 + f_{2Y}L_2\sin\theta_2 \quad (18)$$

where F_x and τ_S are the control input of the stool defining the experimental conditions, as shown in Sect. B, and τ_1 and tau_2 are the control input given as (1) and (2), respectively.

Additionally, f_Y, f_θ, f_{0X}, f_{0Y}, f_{1X}, f_{1Y}, f_{2X} and f_{2Y} are the internal forces to constrain the links, which are calculated based on the following constraints, respectively. The stool motion is horizontal:

$$Y_S = \text{(constant)} \quad (19)$$

The base link does not relatively move on the stool, implying there are no rotations around the virtual joint,

$$\theta_s = \theta_0 \quad (20)$$

and that the position of the virtual joint (X_J, Y_J), calculated from the seat position (X_S, Y_S) and the base link (X_0, Y_0) takes the same values in the no slipping condition:

$$X_J = X_S + L_S\sin\theta_S = X_0 - L_{0S}\sin\theta_0 \quad (21)$$

$$Y_J = Y_S + L_S\cos\theta_S = Y_0 - L_{0S}\cos\theta_0 \quad (22)$$

Additionally, two joint positions are the same, even if they are calculated from both connected links.

$$X_0 + L_{01}\sin\theta_0 = X_1 - L_{10}\sin\theta_1 \quad (23)$$

$$Y_0 + L_{01}\cos\theta_0 = Y_1 - L_{10}\cos\theta_1 \quad (24)$$

$$X_1 + L_{12}\sin\theta_1 = X_2 - L_2\sin\theta_2 \quad (25)$$

$$Y_1 + L_{12}\cos\theta_1 = Y_2 - L_2\cos\theta_2. \quad (26)$$

B Stool motion

The simulations were conducted in the same disturbance condition as the human experiments in Sect. 2.

To simulate 8 s, 0.2 m slide of the stool, F_0 was defined as follows:

$$F_X = -K_{\mathrm{dx}}\dot{X}_S + K_{\mathrm{px}}(X_{\mathrm{ds}} - X_S) \quad (27)$$

where K_{ds} and K_{ps} are the feedback gains and X_{ds} is a desired position given by

$$X_{\mathrm{ds}} = \rho * A\left(1 - \cos\left(\frac{2\pi}{T_c}t\right)\right) \quad (28)$$

Here, $A = 0.1$ m, $T_c = 8$ s, $\rho = +1$ in the RIGHT condition, whereas $\rho = -1$ in the LEFT condition.

However, the rotation disturbance is defined as follows:

$$\tau_S = -K_{\mathrm{ds}}\dot{\theta}_S + K_{\mathrm{ps}}(\theta_{\mathrm{ds}} - \theta_S) \quad (29)$$

where K_{ds} and K_{ps} are the feedback gains, usually set large values for stabilization, and θ_{ds} corresponds to a desired position given by

$$\dot{\theta}_{\mathrm{ds}} = K_\theta(x_{\mathrm{CoP}} - x_{\mathrm{v}}) \quad (30)$$

Here, K_θ is a parameter controlling the speed of the seat surface rotation, usually set a comparatively small value to avoid rapid rotations for the safety, x_{v} is a position of the virtual rotation axis that varies following the next equation in every 8 s

$$x_{\mathrm{v}} = \rho\left(-\frac{0.025}{4.0}|t_{\mathrm{p}} - 4.0| + 0.02\right) \quad (31)$$

where t_{p} $(0 \leq t_{\mathrm{p}} < 8)$ is the time in each trial. These equations destabilize the seat surface rotation. Actually, if the CoP is controlled to just above the virtual rotation axis, i.e., $x_{\mathrm{CoP}} = x_{\mathrm{v}}$, the seat surface is stabilized at θ_{ds} since θ_{ds} never changes. However, if the CoP position is located to the right of the virtual rotation axis, i.e., $x_{\mathrm{CoP}} > x_v$, then the seat will rotate to the right since θ_{d0} increases. Note that we set a constant desired angle $\theta_{\mathrm{ds}} = 0$, in case of no rotational disturbance.

In the simulation, the feedback gains are set as $K_{\mathrm{dx}} = 100$, $K_{\mathrm{px}} = 1500$, $K_{\mathrm{ds}} = 100$, $K_{\mathrm{ps}} = 3000$, and $K_\theta = 0.1$, Those are selected so that the link model can always keep the stability as well as the change of the perceptual upright posture ϕ becomes the same order as that of the human measurement result in Fig. 5, i.e., around 0.01 m.

C CoP position

At the CoP, the total moment from the ground reaction force becomes the CoP position. Thus, P_{CoP} is provided as follows:

$$P_{\mathrm{CoP}} = -f_\theta / F_G^\perp \quad (32)$$

where

$$f_\theta = \tau_1 - M_0 g L_{0S}\sin\theta_0 + f_{1X}(L_{0S} + L_{01})\cos\theta_0 - f_{1Y}(L_{0S} + L_{01})\sin\theta_0 \quad (33)$$

$$\begin{aligned} F_G^{\perp} &= f_{0X} \sin\theta_0 + f_{0Y} \cos\theta_0 \\ &= f_{1X} \sin\theta_0 + (M_0 g + f_{1Y}) \cos\theta_0 \end{aligned} \tag{34}$$

D Results in our previous study

The last section briefly summarizes the results of our previous studies (mainly Kumagai et al. 2017) to explain how we came to consider there will be some relationship between subjective upright posture and the upper body posture during the motor learning phase.

This paper firstly reported several kinds of human experimental results with the same motor learning in Sect. 2.3, where only the control experiment was different. Most noticeable one is that the perceptual upright posture shifted to the opposite direction to the disturbance for the control experiments during which the participants just sit still on the stable stool. Because this result conflicted the ones based on this paper, we considered there would be some reasons behind these results: one candidate was the effect of the control experiment, and the other was the performance of the motor learning. To begin with the former, we conducted with the modified control experiment with stable stool, e.g., displaying the rolling spiral on the HMD or adding lateral shift of the stool with inward rotation to fix the spatial head position. Unfortunately, we did not obtain the result as we predicted. Further studies were required.

Next, we investigated the latter, the posture during the motor learning phase: the averaged roll angle of the seat, the relative phase of the CoP with respect to the virtual rotation axis, and the averaged horizontal deviation of the torso during 100 trials were analyzed for available ten participants. Because the task might be difficult for many subjects, the results were not uniform and thus different in participants. However, it seemed to be categorized to a few patterns.

To remove the data including insufficient learning effect, the phase shift of CoP was evaluated. If the participants learned a new experimental condition given as the periodic rotational disturbance created by the virtual rotation axis, the phase delay from the motion of the virtual rotation axis should decrease with the trials. Thus, three data where the relative phase of the CoP was getting larger were removed.

The rest seven data were able to be divided to two groups based on the trunk (torso) deviation except one data: In the first group of five participants, the trunk deviation was large in comparison with the average of ten participants, and its direction was the same as the disturbance (shift direction of the virtual rotation axis), while the trunk deviation was small and opposite in the second group of two participants.

This categorization brought us the following idea: the participants in the first group must take the posture in Fig. 10a to make the trunk deviation large, and then the subjective

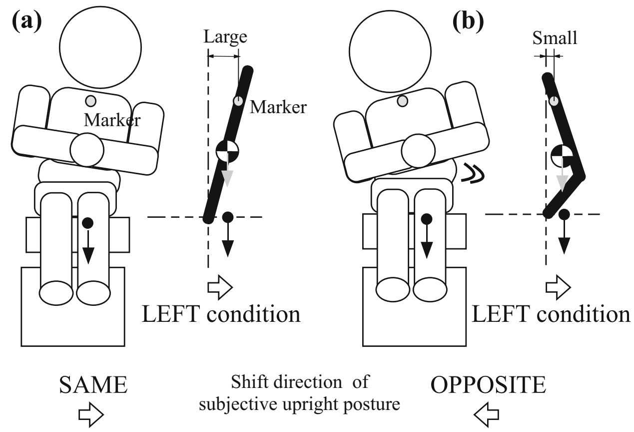


Fig. 10 Main result of our previous study

upright posture shifted to the same direction as the disturbance. So does it as for the second group based on Fig. 10b. In other words, we can expect that the subjective upright posture gradually changes toward the side to which the trunk leans during the motor learning, and our hypothesis in Sect. 2.1 was deduced. This paper attempted to theoretically explain the behavior of the first group and propose it as one of the possible models of human balance control. Note that, however, we have not obtained the evidence of this hypothesis yet.

References

Barbeau H (2003) Locomotor training in neurorehabilitation: emerging rehabilitation concepts. Neurorehabilit Neural Rep 17(1):3–11

Ito S, Kawasaki H (2005) Regularity in an environment produces an internal torque pattern for biped balance control. Biol Cybern 92(4):241–251

Ito S, Ishikawa Y, Minoru S (2014) Experiments on perceptual change accompanying motor learning in seated balance. Trans SICE 50(12):852–860 in Japanese

Kawato M (1996) Computational theory of brain. Sangyo Tosho **(in Japanese)**

Kumagai S, Ito S, Matsushita K, Sasaki M (2015) The balance perception changes by motor learning with active trunk movements. In: Proceedings of 2015 IEEE/SICE international symposium on system integration (SII2015) pp 936–941

Kumagai S, Morita R, Ito S (2017) Analysis and evaluation of equilibrium motor learning in seated state and its relation to accompanying perceptual changes in subjective upright posture. Trans Soc Instrum Control Eng 53(12):654–662 in Japanese

Luyat M, Gentaz E, Corte TR, Guerraz M (2001) Reference frames and haptic perception of orientation: body and head tilt effects on the oblique effect. Percept Psychophys 63(3):541–554

MacKay-Lyons M (2002) Central pattern generation of locomotion: a review of the evidence. Phys Ther 82(1):69–83

Mittelstaedt H (1983) A new solution to the problem of the subjective vertical. Naturwissenschaften 70(6):272–281

Oña ED, Cano-de la Cuerda R, Sánchez-Herrera P, Balaguer C, Jardón A (2018) A review of robotics in neurorehabilitation: towards an automated process for upper limb. J Healthc Eng 2018:9758939

Ostry DJ, Darainy M, Mattar AA, Wong J, Gribble PL (2010) Somatosensory plasticity and motor learning. J Neurosci 30(15):5384–5393
Ramadan A, Cholewicki J, Radcliffe CJ, Popovich JM Jr, Reeves NP, Choi J (2017) Reliability of assessing postural control during seated balancing using a physical human–robot interaction. J Biomech 64:198–205
Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. J Neurosci 14(5):3208–3224
Taylor M, Creelman CD (1967) Pest: efficient estimates on probability functions. J Acoust Soc Am 41(4A):782–787
Wedtgrube A, Bockisch C, Tarnutzer A (2020) Effects of prolonged roll-tilt on the subjective visual and haptic vertical in healthy human subjects. J Vestib Res 30(1):1–16

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.