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Postural Control Adaptation During Galvanic Vestibular and Vibratory Proprioceptive Stimulation

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Abstract—The objective for this study was to investigate whether the adaptation of postural control was similar during galvanic vestibular stimulation and during vibratory proprioceptive stimulation of the calf muscles. Healthy subjects were tested during erect stance with eyes open or closed. An analysis method designed to consider the adaptive adjustments was used to evaluate the motion dynamics and the evoked changes of posture and stimulation response.

Galvanic vestibular stimulation induced primarily lateral body movements and vibratory proprioceptive stimulation induced anteroposterior movements. The lateral body sway generated by the galvanic stimulation was proportionally smaller and contained more high-frequency movements (>0.1 Hz) than the anteroposterior body sway induced by the vibratory stimulation. The adaptive adjustments of the body sway to the stimulation had similar time course and magnitude during galvanic and vibratory stimulation. The perturbations induced by stimulation were gradually reduced within the same time range (15–20 s) and both kinds of stimulation induced a body leaning whose direction was dependent on stimulus. The similarities in the adjustment patterns suggest that postural control operates in the same way independent of the receptor systems affected by the disturbance and irrespective of whether the motion responses were induced in a lateral or anteroposterior direction.

Index Terms—Postural control, proprioception, vestibular.

I. INTRODUCTION

THE maintenance of equilibrium in upright posture is a dynamic process including components such as the detection of movement as well as control of coordinate muscle responses. The balance control process can be viewed as a dynamic feedback control system. The input signals to the control system originate in the afferent sensory input from the visual, vestibular, and somatosensory receptors, which report changes in position and velocity of the body [1], [2], whereas the output responses are shown in the body motions used to maintain balance. If a repeated disturbance of postural control is intense enough, an adaptive process is usually initiated to improve the control performance [3]–[5]. Acquisition of a motor skill is typically a gradual process requiring many repetitions over a period of time [6] and several reports have shown that the body movements induced during repeated exposure to postural disturbances are gradually reduced [7]–[9]. The adaptive adjustments to the individual perturbations are also combined with "strategic" adjustments of body posture such as leaning forward [3], [4], [7]. Repeated exposure to a postural disturbance can generate functional and structural adaptation in the neuromuscular system. However, many of these changes seem to be restricted to the specific situation encountered [10].

Postural disturbances can be induced in various ways. Some methods use physical movements by inducing for example translation or inclination of the supporting surface [11]. Other methods aim to isolate the stimulus effect to a single sensory input, i.e., visual stimulation by altering or moving the visual surrounds [11], [12], vestibular stimulation by galvanic transmastoidal currents [13], [14], or proprioceptive stimulation by vibration of muscles or muscle tendons [15]. However, the movements induced by stimulation of a single sensory input will be detected by other sensory receptors, and the sensory mismatch could be reduced by reweighting the sensory information to more reliable sensory inputs [8], [16]. The suppression of mismatching disturbances from sensory lesions by reweighting the sensory information is most likely an important part of the adaptation and rehabilitation process. Considering this aspect of postural control adaptation, it might be a disadvantage to use physical movements as stimuli when studying adaptation. The imposed movements and strength of the stimulation will be the same throughout the tests, so the postural disturbances cannot be suppressed by using alternative information sources, only counteracted by choosing other postures or movement strategies.

We chose to use galvanic vestibular stimulation and vibratory proprioceptive stimulation in this study. Galvanic vestibular stimulation changes the firing rate of the vestibular nerve [17], [18]. A bipolar bilateral transmastoidal galvanic stimulation induces a lateral body deviation toward the anode if a subject stands with the head facing forward [19]. Vibration applied to a muscle or a muscle tendon increases the firing of the muscle spindles, thus signaling that the muscle is being stretched [20]. The stimulated muscle responds to this with a reflexive contraction (tonic vibratory reflex) [15]. Calf muscle stimulation induces body sway in anterior-posterior direction [21]. Repeated exposure to vibratory proprioceptive stimulation generally leads to an adaptive process that gradually decreases the vibration-induced body sway [22], [23]. The adaptive adjustments in postural control during the posturography tests are

quantified by a recently developed method, which describe the adaptive changes of posture as well as the response adjustments to the individual stimulation pulses [22], [24]. This information about the adaptive changes is used to estimate a time-invariant feedback control model that mathematically describes the body motion characteristics and the relationship between the induced disturbances and the counteractive motion responses.

The aim of this study was quantify the motion dynamics and compare the evoked adaptive adjustment of posture and stimulation response of postural control during vestibular stimulation and vibratory proprioceptive stimulation. Similar adaptive responses, independent of the receptor system affected by the disturbance, would indicate a generalized adaptive process.

II. MATERIAL AND METHODS

A. Subjects

Posturographic tests were performed on 22 test subjects. A prerequisite for participation in the study was that the subjects had not participated in any other kind of posturographic experiments during the preceding six months. The test group was divided into two subgroups, in order to obtain the novel adaptive response to the balance disturbances and to minimize the effect of adaptation to repeated posturographic tests and to the posturographic test situation itself. Each subgroup was only given one kind of stimulation, either to galvanic or vibratory stimulation, and each test subject was submitted to this stimulation two times, ones with eyes open and ones with eyes closed. Galvanic vestibular stimulation was performed on 12 test subjects (six men and six women, mean age 41 years; range 23–56 years). Vibratory proprioceptive stimulation was performed on 10 healthy subjects (six men and four women, mean age 37.5 years; range 29–56 years). The subjects had no history of vertigo, central nervous system (CNS) disease, or injury of the lower extremities. At the time of the investigation, no subject was on any form of medication or had consumed alcoholic beverages for at least 24 h. Written, informed consent was obtained from all subjects prior to testing. The experiments were performed in accordance with the Helsinki declaration of 1975 and approved by the local ethics committee.

B. Equipment

The galvanic vestibular stimulation was applied as bipolar and binaural transmastoidal square pulses of 1-mA amplitude with shifting polarity. The pulses were delivered pseudorandomly by a custom-made constant current generator through two electrodes, made of carbon rubber and 3.5 × 4.5 cm in size (Sentry TENS, Sentry Medical Products, Irvine, CA). The electrodes were placed on each of the mastoids and held in place by contact gel and headphones.

Vibratory stimulation was applied simultaneously to the belly of the gastrocnemius muscles of both legs. The vibratory stimulus was generated by a revolving DC-motor (Escap, Geneva, Switzerland) equipped with a 3.5-g weight placed 1.0 mm eccentric at one end. The DC-motor was embedded in a plastic cylinder of 6 cm in length and 1 cm in diameter. One vibrator was placed on each leg and held in place by elastic straps around the leg. The vibratory amplitude was 1.0 mm and the frequency

85 Hz. Forces and torques actuated by the feet were recorded with six degrees of freedom (DOFs) by a custom-made force platform developed at the Department of Solid Mechanics, Lund Institute of Technology. Data were sampled at 10 Hz by a computer equipped with an analog-to-digital converter and a customized program controlled sampling and stimulation.

C. Procedure

The test subjects in the two subgroups exposed either to galvanic or vibratory stimulation, were identically instructed throughout the trials. The subjects were told to stand without shoes on the force platform and to stand in an erect and relaxed posture, with arms crossed over the chest and feet at an angle of about 30° open to the front and the heals approximately 3 cm apart. The subjects were instructed to focus on a marking on the wall placed 1.5 m straight ahead of them, or instructed to stand with their eyes closed. Before the galvanic/vibratory stimulation started, spontaneous sway was recorded for 30 s. The stimulations were executed according to a computer controlled pseudorandom binary sequence (PRBS) schedule [25] for 205 s, either by turning on the galvanic current and randomly shifting the current polarity, or by turning on/off the vibratory stimulation. The PRBS schedule was composed of stimulation shift periods with random duration between 0.8 s and 6.4 s, which yielded an effective bandwidth of the test stimulus in the region of 0.1–2.5 Hz. The same PRBS schedule was used in all galvanic/vibratory tests. Each test lasted 235 s including the quiet stance preceding the stimulation. The experiments were conducted first with eyes closed and then with eyes open. The subjects stepped down from the force platform and relaxed for three minutes between the tests. The subjects wore headphones relaying music during the tests in order to suppress auditory feedback from the stimulation and surroundings.

D. Analysis

The measured lateral torque during galvanic stimulation and anteroposterior torque during vibratory stimulation was analyzed with a method that considered the adaptation of postural control. The adaptation analysis method, where multiple time-variant dynamical and biological changes are quantified by iteratively estimated nonlinear functions, is described in detail elsewhere [22], [24]. The modeling technique used aims to describe the adaptation of posture as well as the adjustments of stimulation responses during the first 100 s of exposure to stimulation. This information was used to estimate a time-invariant feedback control model that mathematically describes the relationship between the stimulation and measured body sway responses [22]. The three components of feedback control, postural and stimulus adaptation are separated in an identification procedure with five steps.

Step 1) *Preliminary feedback model:* A third-order autoregressive moving average with external input (ARMAX) model [25], [26] (A, B, and C polynomials are of third order) was used to estimate a preliminary feedback model between (input) stimulation and (output) measured torque responses.

Step 2) *Preliminary posture adaptation model:* The feedback model contribution in Step 1) was removed from original measured torque data and the slow changes of the remaining output data were described by the "Posture adaptation" function [see function (1)].

Step 3) *Stimulus adaptation model:* The slow changes described by the "Posture adaptation" function in Step 2) were removed from the original measured torque. The remaining data were rectified and used for an estimation of the changes in stimulation-response relationship as described by the "Stimulus adaptation" function [see function (1)].

Step 4) *Feedback model:* Based on the results from steps 2 and 3, the (input) stimulation and (output) torque responses were thereafter compensated for adaptation and used in an estimation of a feedback model describing the steady-state relationship. The input signal amplitude was altered by superimposing the changes found in the stimulus-response according to the "Stimulus adaptation" function. The output signal was modified by removing the changes described by the "Posture adaptation" function. The feedback model was evaluated with increasing model orders until its performance fulfilled the χ^2-criteria of white noise properties. The optimum time delay between input and output was found by using the Akaike final prediction error [25], [26].

Step 5) *Posture adaptation model:* The feedback model contribution in Step 4) was removed from original measured data and the slow changes of posture were finally determined by a renewal estimation of the "Posture adaptation" function [see function (1)].

The results from the adaptation analysis method can be divided into three categories.

- Adaptation of body leaning and induced body sway by the repeated stimulation.
- Motion dynamics and motion complexity.
- Stimulus-induced body sway and spontaneous body sway.

E. Adaptation of Body Leaning and Induced Body Sway by the Repeated Stimulation

Two exponential functions were used to describe the adaptive changes in response amplitudes and slow changes in posture. The "Stimulus adaptation" function describes the adaptive changes in body sway amplitude induced by the repeated stimulation over time and the "Posture adaptation" describes the slow adaptive change of posture, such as adopting new body leaning. The adaptation function consists of a sum of two exponential terms and is formulated as

$$Y = A_1 e^{-t/\tau_1} + A_2 e^{-t/\tau_2} + C \qquad (1)$$

where τ_1, τ_2 denotes the time constants (in seconds) and the exponential term with the shortest time constant subscripted "1" and the other "2" A_1, A_2 denotes amplitude [in torque (Nm)], C a constant term (in Nm), and Y the measured adjustment
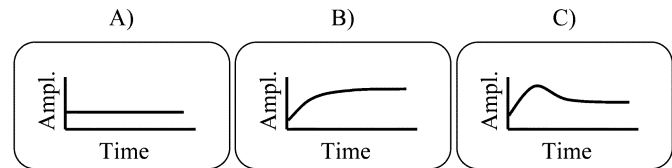

Fig. 1. Schematic examples of adjustment patterns classified by (A) a constant value, (B) one time constant, and (C) two time constants.

pattern (in Nm). The obtained parameters were evaluated and terms with negligible or time-invariant influence were removed before the statistical evaluation. The number of negligible or time-invariant terms was used to classify whether the adjustment pattern had properties that were best described with a constant value, one time constant or two time constants (Fig. 1). An exponential term was considered time-invariant if the time constant was longer than 100 s or shorter than 0.1 s (one sample interval). A term was also considered of negligible influence if the magnitude was more than 100 times lower in gain than the other exponential term presupposed that the other exponential term had a time constant within the acceptable time range (>0.1 s–<100 s). If both exponential terms, according to the two criteria's above, were considered time-invariant or had negligible influence the adjustment pattern was classified to be best described with a constant value. If one exponential term was excluded according to the criteria's the pattern was classified to be best described with one time constant and subsequently if none of the terms were excluded according to the criteria's the pattern was classified to be best described with two time constants.

F. Motion Dynamics and Motion Complexity

The relationship between the stimulation and the recorded body sway responses was described with an ARMAX feedback model, see identification procedure Step 4) [22]. This model evaluated the dynamical properties of the movements induced by the stimulation and estimated the latency between the individual stimulation pulses and recorded motion responses. The model also evaluated the dynamical complexity of the body sway induced by the stimulation, in terms of the degree of parameters needed to describe the relationship between stimulation and motion responses.

The dynamics of the estimated ARMAX feedback model were analyzed in terms of three normalized dynamical parameters: swiftness, stiffness; and damping, which was obtained by normalization of the parameters from a third-order ARMAX model [27]. If the estimated feedback model was of higher model order, model-order reduction [25] was used to obtain a third-order ARMAX model before the normalization procedure. The dynamical parameters correspond to the parameters of a proportional, integrative, and derivative control used in automatic control theory [25], [26]. Swiftness corresponds to the integrative control and a high swiftness value means that the adjustments to a disturbance are rapid and that the subject quickly returns to the chosen equilibrium body position after a perturbation. Stiffness describes the reaction to a deviation from the assumed equilibrium position and a high stiffness value means that the subject reacts strongly to a small deviation of body position. Damping describes the control action dependent

TABLE I

MEDIAN AND 25%–75% QUARTILE VALUES (25%, 75%) FOR THE ABSOLUTE AMPLITUDE [Nm] AND TIME CONSTANT [s] VALUES ACROSS SUBJECTS OBTAINED FROM THE "POSTURE ADAPTATION" AND "STIMULUS ADAPTATION" FUNCTIONS. THE ADJUSTMENT PATTERN VALUE SHOWS THE PERCENTAGE OF AMPLITUDE ALTERATIONS DESCRIBED BY 2: TWO TIME CONSTANTS, 1: ONE TIME CONSTANT, AND 0: A CONSTANT VALUE WITHIN THE GROUP (SEE, ALSO, FIG. 1)

Posture adaptation		Amplitude A_1	Time const. τ_1	Amplitude A_2	Time const. τ_2	Adj. pattern (2,1,0)
Galvanic	Closed	25.4 (13.4, 39.4)	3.0 (1.6, 3.8)	28.3 (9.8, 46.7)	13.9 (10.1, 21.4)	(50, 42, 8)
	Open	10.2 (5.7, 51.0)	17.0 (2.8, 22.1)	22.5 (11.7, 68.9)	22.9 (9.3, 44.3)	(58, 34, 8)
Vibration	Closed	18.2 (14.6, 33.3)	3.4 (2.3, 4.4)	30.1 (15.9, 37.2)	58.8 (36.9, 65.1)	(30, 60, 10)
	Open	29.9 (5.5, 79.2)	14.4 (5.7, 29.7)	65.1 (31.4, 90.6)	31.4 (18.5, 44.6)	(60, 20, 20)

Stimulus adaptation		Amplitude A_1	Time const. τ_1	Amplitude A_2	Time const. τ_2	Adj. pattern (2,1,0)
Galvanic	Closed	5.4 (4.2, 19.4)	18.4 (4.9, 32.5)	6.0 (3.3, 22.6)	19.9 (13.0, 33.0)	(50, 50, 0)
	Open	4.6 (1.9, 8.1)	1.5 (0.7, 2.5)	4.0 (0.7, 43.3)	32.8 (14.0, 43.4)	(50, 50, 0)
Vibration	Closed	22.9 (10.0, 33.3)	6.4 (2.2, 28.6)	19.1 (11.5, 28.3)	16.8 (10.0, 24.9)	(80, 20, 0)
	Open	9.1 (5.0, 43.6)	6.1 (2.4, 11.5)	54.5 (17.8, 88.5)	9.2 (8.5, 23.9)	(40, 40, 20)

on the velocity of the body sway and a high damping value means fewer oscillations of lower velocity around the chosen equilibrium position after a perturbation.

The complexity of the body movements induced by the stimulation are reflected in the degree of A, B, and C polynomials in the feedback model. A feedback model with few parameters is sufficient to describe the movements if the body strictly moves like a single-link pendulum during the analyzed period. However, it is necessary to increase the degree of model parameters if the body movements contain multisegmental motions in hip and knees or if the movement characteristics are changed by adaptation during the test period.

G. Stimulation-Induced Body Sway and Spontaneous Body Sway

The body sway content was evaluated by three variance ratio values [22], [24]. The stimulation-induced sway value shows the proportion of total measured torque $y(t)$ that can be explained by the analysis method as responses to the stimulation and as adaptive changes. The quotient defining the amount of stimulus-induced sway V_{si} (2) is calculated from the variance of measured torque $y(t)$ and variance of the model error $y_e(t)$, i.e., the remaining part of the body sway that cannot be explained by the model in terms of posture motion $y_p(t)$ and stimulus-response motion $y_{feed}(t)$

$$y_e(t) = y(t) - y_{feed}(t) - y_p(t)$$
$$V_{si} = \frac{\text{var}(y(t)) - \text{var}(y_e(t))}{\text{var}(y(t))}. \qquad (2)$$

The spontaneous body sway is the remaining part of the body sway, which is not related to the stimulation or to adaptive adjustments. The spontaneous high-frequency motion value shows the proportional size of the spontaneous body sway due to high-frequency motions above 0.1 Hz. Somewhat arbitrarily, we chose to consider motions above 0.1 Hz as high-frequency motions and motions below 0.1 Hz as low-frequency motions. A reason for this frequency choice is that the cutoff frequencies of the vestibular and visual sensory systems are around 0.1

Hz [28], [29]. The quotient defining the spontaneous high-frequency motion value V_{fe} (3) is calculated from the variance of the model error $y_e(t)$ and variance of the high-frequency part of the error above 0.1 Hz. The high-frequency data $y_{fe}(t)$ is extracted by using a fifth order low-pass filter with a cutoff frequency of 0.1 Hz. The filter uses a Butterworth finite impulse response design [30] and the filtration is performed twice, once forward and thereafter reversed to achieve a zero-phase distortion

$$V_{fe} = \frac{\text{var}(y_{fe}(t))}{\text{var}(y_e(t))}. \qquad (3)$$

The residual rate value V_r (4) describes the prediction performance of the estimated model from the variance of measured torque $y(t)$ and the variance of the feedback model residual $\varepsilon(t)$. A higher residual rate value indicates that a larger part of the recorded body sway is not induced by the individual stimulation pulses, thus that a larger part of the body sway is either spontaneous sway or adaptive adjustments. The presence of any information remaining in the residuals is a clue that the model might be insufficiently complex or otherwise inappropriate

$$V_r = \frac{\text{var}(\varepsilon(t))}{\text{var}(y(t))}. \qquad (4)$$

H. Statistical Analysis

The comparisons between the galvanic and vibration tests, separately for eyes closed and eyes open, were done with the Mann–Whitney nonparametric test. The comparisons between tests performed with eyes closed and eyes open, separately for galvanic and vibratory stimulation, was done with the Wilcoxon nonparametric test. Nonparametric tests were used since the values were not normally distributed even after logarithmic transformation [31]. Normality of distribution was tested with the Shapiro-Wilk test. In all tests $p < 0.05$ was considered to be statistically significant [31]. Only the exponential term denoted with index 1 in Table I, of the two exponential terms in the "Posture adaptation" and "Stimulus adaptation" function was statistically evaluated since the exponential term denoted
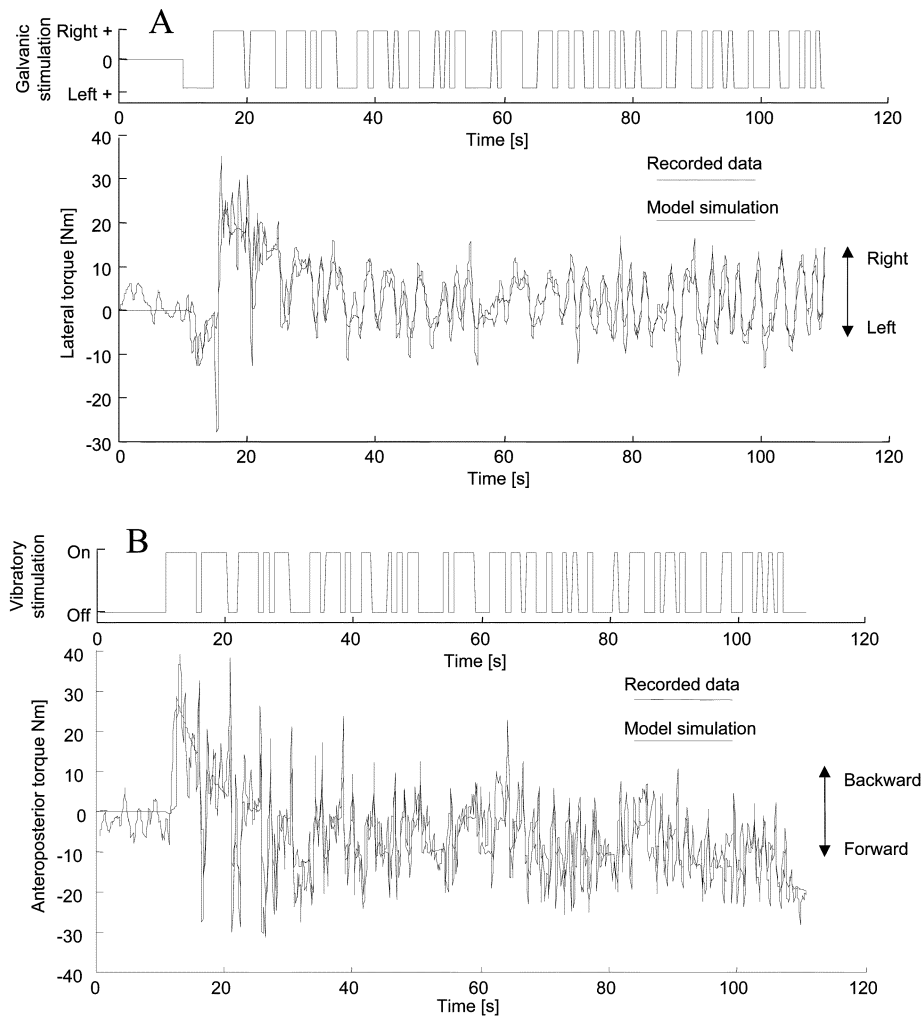
Fig. 2. Model simulation values and measured torque in the lateral (A) and anteroposterior (B) direction from two subjects exposed to galvanic (A) and vibratory (B) stimulation with eyes closed. During both galvanic vestibular and vibratory proprioceptive stimulation there were clear adaptive adjustments over time in terms of reduced sway responses to the stimulation and gradual changes in center of pressure position. Note the similarities between body sway induced by the galvanic and vibratory stimulation and the high accordance between the model simulation values from the adaptation analysis method (red) and recorded body sway (green).

with index 2, was considered time-invariant or of negligible influence in approximately 40% of the cases according to our exclusion criteria.

III. RESULTS

The galvanic vestibular stimulation initially causes the subjects to change the average center of pressure position toward the right [Fig. 2(a)]. The vibratory proprioceptive stimulation initially changes the subject's center of pressure backward [Fig. 2(b)]. The body posture is then gradually adjusted during the first 30–40 s of stimulation to the position chosen before the stimulation started (galvanic) or a posture where the subject leans somewhat more forward than the initial position (vibration). The amplitude of the individual stimulation-induced sway responses is apparently reduced during the first 30–40 s.

A. Adaptation of Body Leaning and Induced Body Sway by the Repeated Stimulation

The total number of evaluated posturographic tests was 44; 20 tests from vibratory stimulation and 24 tests from galvanic stim-

ulation. The parameter values obtained from the "Posture adaptation" and "Stimulus adaptation" functions shows that there were considerable adaptive adjustments of the posture and to the stimulus during most of the tests, both during galvanic and vibratory stimulation (Table I). Adjustment patterns 1 and 2 represent a time-variant amplitude alteration (Table I, right column). The responsiveness to stimulus was changed in 42 of 44 (95%) posturographic tests and the posture was altered during 39 of 44 (89%) of the tests. The median parameter values are within the same range both during galvanic and vibratory stimulation, but the values also indicate a considerable interindividual variation of the adaptation time constants, amplitudes and of the adjustment pattern. There were no significant differences in amplitudes and time constant parameters in the "Posture adaptation" and "Stimulus adaptation" functions between any of the test conditions.

B. Motion Dynamics and Motion Complexity

The dynamical parameter values show that the subjects responded more rapidly (swiftness) to the galvanic stimulation with eyes open than with vibratory stimulation (Fig. 3). How-
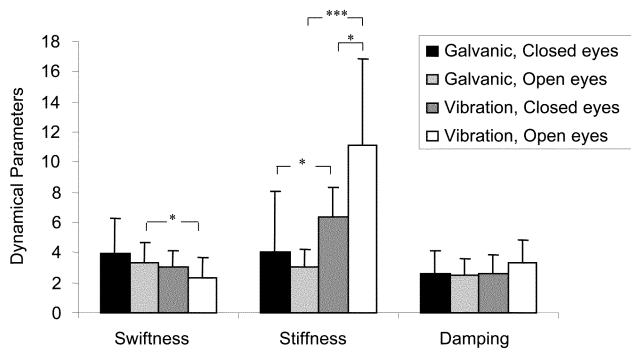
Fig. 3. The dynamic parameters swiftness, stiffness and damping were significantly different between test with galvanic and vibratory stimulation and between open and closed eyes test (mean and standard deviation values, $* = p < 0.05, ** = p < 0.01$, and $*** = p < 0.001$). The subjects responded more rapidly (swiftness) to the galvanic stimulation than with vibratory stimulation with eyes open but the responses induced by the body deviations (stiffness) were not as strong during galvanic stimulation compared with vibratory stimulation both during tests with eyes open and closed.

Fig. 5. The variance ratios were significantly different between test with galvanic and vibratory stimulation and between open and closed eyes test (mean and standard deviation values $* = p < 0.05, ** = p < 0.01$, and $*** = p < 0.001$). The body sway induced by the stimulation was proportionally lower during galvanic stimulation with eyes closed whereas the spontaneous high-frequency motions were proportionally larger during galvanic stimulation compared to during vibratory stimulation. The residual rate values suggest that proportionally more of body sway was directly related to the stimuli during vibratory stimulation compared with galvanic stimulation with eyes open.

C. Stimulation-Induced Body Sway and Spontaneous Body Sway

The stimulation-induced body sway was proportionally lower during galvanic stimulation compared with vibratory stimulation with eyes closed (Fig. 5). The stimulus-induced sway was also proportionally lower with eyes closed compared with eyes open during galvanic stimulation. Moreover, the spontaneous high-frequency motions were proportionally larger during galvanic stimulation than during vibratory stimulation. The spontaneous high-frequency motions were proportionally lower with eyes open during both kinds of stimulations. The higher residual rate values with eyes closed suggest that the body sway to a larger extent were directly related to the individual vibration pulses in the stimulation with eyes open compared with eyes closed. The residual rate values also suggest that proportionally more of body sway was directly related to the individual vibration pulses during vibratory proprioceptive stimulation compared with galvanic vestibular stimulation with eyes open.
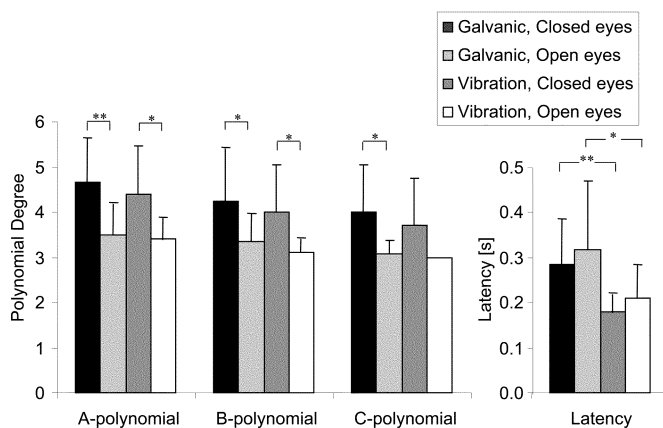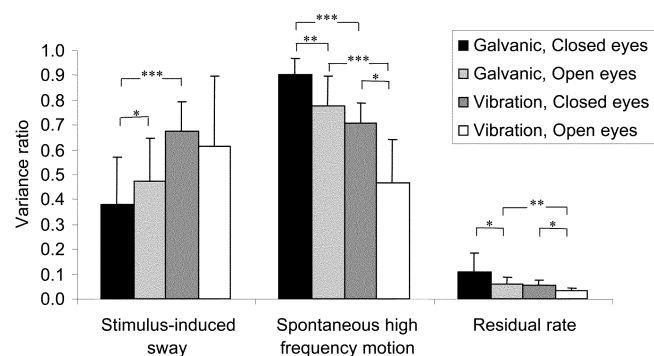

Fig. 4. Motion complexity as reflected by the degree of A, B, and C-polynomials needed to describe the stimulus-motion response relationship, and estimated latency between stimulation and motion responses (mean and standard deviation values, $* = p < 0.05$, and $** = p < 0.01$). The motion complexity values were higher during tests with eyes closed and the response latency was significantly longer during galvanic vestibular stimulation. The findings suggest that the movement characteristics were more complex during tests with eyes closed compared to tests with eyes open.

IV. DISCUSSION

Adaptation and habituation are common in many biological systems and effects of adaptation in the human biological system can for example be observed in the motor control [32], [33] and in the CNS [34]. We have previously reported that postural control adaptation during repeated balance perturbations seems to contain at least two separate adaptive processes [22], [35]. One adaptation process can be seen in the progressive reduction of body sway in response to stimuli, the other in the change of posture or body leaning over time. These two adaptive developments can be manipulated separately and act at different time scales [24], [36], [37]. Thus, the adaptive adjustments of postural control have properties that suggested contributions from multiple partly independent adaptive procedures. Our approach to analyze postural control responses that are affected by adaptation, is to separate the body sway into three categories: adaptation to the stimulation, adaptation

ever, the responses induced by the body deviations (stiffness) were not as strong during galvanic stimulation compared with vibratory stimulation both with eyes open and closed. The stiffness value was also clearly lower with eyes closed compared with eyes open during vibratory stimulation.

The most prominent difference between galvanic and vibratory stimulation was the longer response latency during galvanic stimulation (Fig. 4). The complexity of the body movements induced by the stimulation was similar with galvanic and vibratory stimulation and the motion complexity was reduced in a similar way by visual input during both kinds of stimulation. Thus, the findings suggest that the movement characteristics were more complex during tests with eyes closed compared to tests with eyes open.

of posture and a feedback model that describes the dynamics of the body motions [24]. This method for adaptation analysis is a novel way to analyze biological and biomechanical systems with multiple adaptive processes, which have individual characteristics and time courses. The high accordance between the model simulation values from the adaptation analysis method and recorded body sway from tests with galvanic vestibular and vibratory proprioceptive stimulation, suggests that the used principal for adaptation analysis might be a valid method during various postural control conditions (see Fig. 2). Parallel adaptive processes related to specific components in the chemical or biological environment might be common in many biological systems [38], [39]. Thus, the procedures employed in this study to describe postural adaptation could rather easily be applied to other kinds of adaptive processes in various biological and biomechanical systems.

The findings in this study suggests that postural control adapts the body posture and stimulation responses in a similar way to a repetitive vestibular or proprioceptive stimulation, irrespective of whether the body sway was induced in lateral or anteroposterior direction. The adaptation affected posture leaning in 89% of the posturographic tests and changed over time the individual perturbation responses induced by the galvanic and vibratory stimulation in 95% of the posturographic tests. Similar findings have previously been observed during somewhat different test conditions with continuous and transient postural perturbations [4], [35], [40], [41]. The similarity and close interaction between vestibular and leg proprioceptive inputs when maintaining upright stance has also been demonstrated by Hlavacka *et al.* [42]. Upon combined vestibular and proprioceptive stimulation, the obtained results essentially reflected a summation of the individual vestibular and proprioceptive effects. The similar adaptive response with common pattern and duration, which is independent of the receptor system affected by the disturbance, suggests that the adaptation of postural control is an integrated process in the CNS. The motor activity for balance control involves neuronal activation at many levels, including spinal cord, brainstem and cerebellum, basal ganglia and thalamus, and cerebral cortex [43]. Thus, adaptation of postural control to a proprioceptive or vestibular disturbance is likely to partly involve the same structures in the CNS [6], [42].

The individual variation in adaptation time course and magnitude reflects an interindividual variation in the adaptation pattern. Thus, some subjects rapidly selected a new posture and suppressed the effects of stimulation whereas others adjusted their responses to stimulation over a longer period (see Table I). These results confirm previous findings that there exist a large variety of dynamic postures, rather than one particular configuration, which assures stability [44], [45]. This individuality in the adaptation pattern might have various origins. Since ankle joint stiffness depends on the momentum carried by the joint [46], there is a possibility to adjust the level of ankle stiffness by adjusting the postural alignment, i.e., by leaning more or less forward. The choice of body leaning could be based upon a trade-off between accuracy of maintained body position and the requirement set by limited muscle load or expenditure of metabolic energy [47]. Another possibility could be individual

variation in the ability to determine and maintain an accurate posture during the initial exposures to the perturbations, i.e., to determine that vibratory stimulation induces a leaning backward and that galvanic stimulation induces a leaning toward the anode. Moreover, the subject's point of view toward the test situation itself, i.e., whether a postural stimulation actually could seriously threaten their balance, and the subject's level of attention and attitude may also affect the responses [40], [48]. Ishizaki *et al.* demonstrated that subjects instructed to stand as stable as possible swayed significantly less compared to subjects instructed to stand relaxed [49]. Moreover, previous experience of the test situation and perceived level of postural threat during the test situation have a profound influence on the chosen body leaning and postural control [23], [40], [50]. This may impose a conflict of interest in terms of study design and statistical evaluation. It is usually more compelling to compare the responses from the same participant during the various test circumstances. However, our previous findings during similar test circumstances have shown that there is a profound effect on the novel adaptive responses when a test subject is repeatedly exposed to similar posturographic tests [23], [24]. Our study design was therefore implemented to minimize the effect of adaptation to repeated posturographic tests, exposing each test subject to a minimum of tests, in order to obtain the novel adaptive response to the balance disturbances. The test subjects' physical body constitution seemed to be of minor importance for the adjustment pattern during the present test conditions. A statistical evaluation of the adaptation parameters showed no correlation to the subjects weight or length.

Although the adaptive adjustments were similar during vibration and galvanic stimulation, the two kinds of stimulation induced different sensations of dysequilibrium and induced differently directed movements [19], [20]. These differences were reflected by the dynamical characteristics of body sway as described by the feedback model parameters. The response latencies were significantly longer during galvanic vestibular stimulation but the stimulation responses contained more rapid motions. The galvanic stimulation induced proportionally less body sway compared to the vibratory proprioceptive stimulation with eyes closed; nevertheless, the total body sway contained proportionally more high-frequency motion (>0.1 Hz) during galvanic vestibular stimulation. One explanation for these dynamical differences might be that biomechanical constraints alter and reduce the posture motions in the lateral direction. For example, the mobility in the spinal column, hip and knee joints are more restricted in the lateral direction than in the anteroposterior direction. The movements in the respective direction are also partly activated by different muscle groups [43]. Another possible reason is that galvanic stimulation with symmetrical polar shifts induces symmetrical bi-directional responses in opposite directions over time, whereas vibration induces responses only in one direction, which might be easier to withstand with an intentional forward or backward leaning. Considering these biomechanical differences, bilateral monopolar galvanic stimulation might be preferred as this vestibular stimulation primarily induces anteroposterior movements. However, the monopolar stimulation increases or decreases simultaneously the firing frequency in the vestibular

nerves on both sides, which neutralize the effects on the canal efferents. Therefore, the observed effects from bilateral monopolar stimulation might primarily contain responses evoked by pure otolith stimulation [51]. Thus, the vestibular effects induced by bilateral monopolar galvanic stimulation might be considered to be unphysiological, whereas the effects of bilateral bipolar stimulation is similar to the vestibular signals attained during normal head movements or to the asymmetrical vestibular responses obtained during common vestibular lesions such as vestibular neuritis.

The lower stimulus-induced sway values and higher residual rate values during galvanic stimulation suggests that binaural galvanic stimulation with a 1-mA current induces less disturbance to postural control than vibratory proprioceptive stimulation of 1.0-mm amplitude and 85-Hz frequency toward the calf muscles does. The observed latency difference of about 100 ms between the responses induced by galvanic and vibratory stimulation is supported by EMG studies [52], [53]. Tendon vibration of flexor carpi radialis evoked significant EMG responses after about 38 ms [53], whereas galvanic vestibular stimulation induced EMG responses appropriate to produce body sway after about 115 ms [52], [53]. A more precise analysis of the response latency between the two kinds of stimulus based on system identification analysis of posturography was not achievable in this study due to that the sampling rate and identification procedures were selected to promote analysis of the body sway within the frequency range which contained most power, i.e., the low-frequency body sway below 5 Hz.

Vision provides important feedback information about the body sway and complements information supplied by the other receptor systems [29], [54], [55]. The importance of vision was confirmed by the findings that the body sway during tests with eyes closed contained more high-frequency motions (>0.1 Hz) and the dynamics in the motion responses had higher complexity (Fig. 4). With eyes open larger parts of the body sway were directly caused by the individual stimulus perturbations (Fig. 5, residual rate) and contained less spontaneous high-frequency body sway (Fig. 5). Most of the findings suggest that visual information has a similar effect on the stimulation responses both during galvanic and vibratory stimulation. However, the proportional amount of stimulus-induced body sway was significantly larger with eyes open compared to eyes closed during galvanic stimulation, whereas the value was unaffected by vision during vibratory stimulation. Moreover, the responses induced by the body deviations (Fig. 3, stiffness) was significantly larger with eyes open compared to eyes closed during vibratory stimulation, whereas the stiffness value was unaffected by vision during galvanic stimulation.

Coordinated control of the body segments is a complex aspect of human postural control, owing to the multiple DOFs of the controlled system. Several interacting subsystems are involved in the dynamics of human posture and locomotion, including the skeletal, neuromuscular and sensory systems. Buchanan *et al.* have shown that both sensory and biomechanical constraints limit postural coordination patterns as a function of translation frequency of the supporting surface [56]. The test subjects were able to maintain inverted pendulum motions during the low-frequency translations but altered to multisegmental movements when visual information was available during high-frequency translations. Moreover, Day *et al.* have shown that the lateral motions in response to galvanic vestibular stimulation could not always be approximated with inverted pendulum motions [57]. The head tilted more than the trunk and the trunk tilted more than the pelvis, during the continuous galvanic stimulation, producing a leaning and bending of the body toward the anodal ear. However, our measurements of the body motions using an ultrasound movement analyzing system (Zebris™ CMS-HS Measuring System for 3D-Motion Analysis), suggests that the test subjects maintain inverted pendulum motions throughout posturographic tests when perturbed by a randomized vibratory and galvanic stimulation of the same kind as was used in this study (P. A. Fransson, unpublished observations). Moreover, the analysis method used in this study is designed to consider the effects of altered complexity of the ground reaction forces induced by either inverted pendulum or multisegmental body sway.

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