

Influence of expectation on postural disturbance evoked by proprioceptive stimulation

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Received: 30 March 2007 / Accepted: 20 July 2007 / Published online: 17 August 2007
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Abstract Recent experiments have shown that the vestibular channel of balance control differs fundamentally from the visual channel. Whereas the response to a visual perturbation can be suppressed if the subject has awareness that an upcoming disturbance is likely to be caused by an external agent rather than by self-motion, a similar assumption cannot be made concerning the vestibular system. The present experiment investigated whether postural responses evoked by a proprioceptive perturbation (vibration of the Achilles' tendon at 90 Hz for 2.2 s) are either automatic and immune to expectation (similarly to vestibular responses) or cognitively penetrable (similarly to visual responses). Subjects ($n = 12$) stood on a force platform while stimuli were delivered either by the subject himself (self-triggered condition) or by the experimenter. For the latter condition, the stimulus was delivered either without warning (unpredictable condition) or at a fixed interval (500 ms) following an auditory cue (precue condition). Results showed that the backward CoP displacement induced by vibration was delayed by approximately 500 ms in the expected and self-triggered conditions compared to the unexpected condition. However, once initiated, the velocity of the backward displacement was higher in the self-triggered condition as compared

to the unexpected condition. After a period of 2.2 s of vibration, the amplitude of this backward CoP displacement was similar in the three experimental conditions. Therefore, although expectation appears to delay the upcoming of the main backward body sway, it does not appear to be able to weight the impact of the proprioceptive stimulation. This suggested that afferents provided by the different sensory channels involved in postural control are not similarly susceptible to high level processes such as expectation.

Keywords Expectation · Vibration · Posture · Sensory weight

Introduction

Tendon vibration technique is commonly used to investigate the influence of proprioception and particularly muscle spindles in postural control. Roll and Roll (1988) showed that vibration of any muscle involved in postural adjustments, from the ankle to the eyes, gives rise to compensatory postural responses. The direction of such compensatory motor responses is related to the function of the target muscle. For instance, vibration applied to either the soleus, the sterno–cleido–mastoidus or the inferior recti (extraocular muscle) induces almost analogous postural effects (Roll and Roll 1988, p. 160).

The similarity of the postural responses with different vibration locations suggests that the evoked response is not simply the results of a local tonic vibration reflex. More likely, it reflects a common central processing that takes into account the afferents of all the body segments from the feet to the head which serves to the elaboration of a coherent body reference (Roll and Roll 1988). Additional arguments

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which attest of the complex and high level processes involved in such responses stem from the fact that these responses are readily modifiable by many different factors. These factors include the support surface or stability (Ivanenko et al. 1999, 2000; Hatzitaki et al. 2004), availability of other sensory cues (Smetanin et al. 2002; Adamcova and Hlavacka 2007), adaptation to perturbation (Fransson 2000; Nashner et al. 1982; Roll et al. 1998) or the nature of the task in which subjects are engaged (Lackner et al. 2000). Arguments in favor of high level sensory re-weighting can also be found in central pathologies such as Parkinson disease (PD). Indeed, Valkovic et al. (2005, 2006) showed that in advanced stage PD patients, vibration of either the neck (2005) or the soleus muscles (2006), as well as any other sudden change of sensory condition (for visual and vestibular stimulation see Bronstein et al. 1990; Pastor et al. 1993, respectively), has a significant impact on the scaling of postural response which are of larger amplitude than in either early stage PD patients or controls.

The purpose of the present experiment was to question whether cognitive factors such as expectation of the forthcoming proprioceptive disturbance could similarly exert an influence on such postural responses. Concerning the visual channel, Guerraz et al. (2001b) and more recently Freitas Junior and Barela (2004) showed that under certain circumstances we are able to suppress the inappropriate balance response. Indeed, an unpredictable displacement of the visual environment, which creates a visual flow similar to that experienced during self motion, evokes compensatory postural responses (Lee and Lishman 1975; Lestienne et al. 1977; Bronstein 1986; Guerraz et al. 2000, 2001a, c). However, when subjects controlled the direction and timing of the visual scene with a joystick, or were instructed by a precue of the forthcoming disturbance, the response was strongly reduced (Guerraz et al. 2001b). Thus, when subjects had the explicit prior knowledge that an upcoming sensory perturbation is likely to be caused by an external agent rather than by a real, unplanned body movement, response suppression occurred (Guerraz et al. 2001b; Freitas Junior and Barela 2004). Similarly, a virtual reality visual stimulus has been shown to have a weaker postural effect than a real world scene (Mergner et al. 2005). Although there can be different reasons why visual stimulation with virtual reality has weaker effect than a real world scene, Mergner et al. 2005 attributed this weaker effect to a cognitive mechanism by which subjects weight the impact of the visual stimulus based on an estimate of its reality character (Mergner et al. 2005; Blumle et al. 2006).

Although these data suggest that cognitive processes can modulate the influence of visual information on balance control, this does not appear to be a general principle. Indeed, Guerraz and Day (2005) have shown that the vestibular channel differs fundamentally from the visual one

for balance control. Expectation of a vestibular perturbation, either through a voluntary action that initiates it (self-triggered condition) or through a prior knowledge of the event and timing cues (predictable condition), had no consistent effect on the evoked whole-body response. Suppression did not occur even though subjects knew when the stimulus would happen, that it was artificial, and that it had the potential to make them sway sideways. Therefore, the present experiment investigated whether expectation of a proprioceptive perturbation, either through a voluntary action that initiates it (self trigger condition) or through prior knowledge of the event and timing cues (precue condition) would affect the evoked postural response.

Methods

Subjects

Twelve (age range: 20–25 years; mean 22.1, 8 females and 4 males) healthy subjects consented to participate in the experiment according to guidelines of the local ethics committee and to the declaration of Helsinki. No subjects had known history of vestibular, orthopedic or neuromuscular disorders.

Vibration stimulation

A 2.2 s vibration was applied to the Achilles tendons of both legs by means of inertial vibrators (VB 100 Dynatronic) with a frequency of 90 Hz.

Postural recordings

Subjects stood barefoot on a force plate (type AMTI OR-6), which registered ground reaction forces in the three dimensions. From these data, the position of the center of foot pressure (CoP) was calculated. Since vibration of the Achilles tendon induces body sway mainly along the antero-posterior axis, CoP parameters were evaluated for that axis only. The data were collected with a sampling frequency of 100 Hz.

Procedure

Subjects were instructed to stand still and relaxed with the head facing forwards, the hands at their side and their feet 10 cm apart. A lightweight push-button box was held in the right hand throughout the experiment. The experiment involved three vibration conditions: (1) “unpredictable” condition in which vibration was triggered by the experimenter at a random time. Prior to each trial, subjects were naive as to whether or not, and when they would be stimulated.

(2) “Precuing” condition in which subjects were informed by a tone delivered 500 ms before the vibration that they were going to be stimulated. The volume of the tone was set at a comfort hearing level. (3) “Self-triggered” condition in which subjects were instructed during the trial that they should trigger the vibration themselves using the push-button within 1–2 s after the verbal instruction. Subjects were aware that the stimulus was delivered as soon as they pressed the button. The three vibration conditions were combined with two visual conditions, either darkness or with visual cues. Visual conditions were manipulated in order to test the effect of predictability when subjects can rely either on one or two undisturbed sensory channels (vestibular and visual) while they were stimulated by vibration. In the visual cues condition, the visual scene was a 2D square (25 cm × 25 cm), consisting of 28 luminescent dots. The scene was placed at 150 cm in front of the subjects at eye level in an otherwise blacked-out room. The purpose of using a small visual display was to ensure that it would reduce the vibration evoked response compared to darkness but without suppressing it as reported by previous authors when destabilization was evoked either by proprioceptive (Smetanin et al. 2002) or vestibular stimulation (Guerraz and Day 2005; Day and Guerraz 2007). Six trials were performed for each of the six experimental conditions (3 vibration × 2 vision conditions). In addition, 24 control trials without any stimulation were also included, 12 in darkness and 12 with visual cues. The overall 60 trials were divided in two blocks with an equal number of trials per experimental condition. Subjects had a rest period of 10 min between the two blocks. In each block, trials were presented in a pseudo-random order with each trial lasting for 11 s. Prior to data recording, subjects practiced few trials for each vibration condition. This allowed them to familiarize with the stimulus and procedure.

Data analysis

For each subject, each condition and each block, position signals were averaged. The time of stimulus onset was used to synchronize the different trials. From the individual average CoP under each condition, several parameters were computed. The postural response to vibration of the Achilles’ tendon is characterized by an early component consisting of a small forward shift of the CoP (Polonyova and Hlavacka 2001; Adamcova and Hlavacka 2007; Smetanin et al. 2002; Valkovic et al. 2006). The time during which the COP was above the baseline level (mean position of the COP over the 2 s before stimulus onset) was used to measure the duration of this forward displacement. The main displacement in the direction of the vibrated muscle was analyzed by: (1) the amplitude of the backward response. This was calculated as the difference between the baseline

level and the one achieved after 2.2 s of vibration [over 10 data points (100 ms) at the end of stimulation]. (2) The velocity of the backward displacement, which was measured from the slope of the backward response. For each subject and in each condition, the slope was based on least-squares linear regression fitted over a period covering n data points from the onset of the backward displacement till the vibration stimulation offset.

The different dependent variables were submitted to separate analyses of variance (ANOVA) with repeated measures on the three factors (3 vibration conditions [unpredictable, precue and self-triggered] × 2 visual conditions [darkness and vision] × 2 blocks of trials [first and second blocks]). Newman–Keuls method was used for post hoc comparisons whenever necessary. A 0.05 P level of significance was set for all the forthcoming statistical analyses.

Results

The postural response to Achilles tendons vibration was similar to that described in the literature (Polonyova and Hlavacka 2001; Adamcova and Hlavacka 2007; Smetanin et al. 2002). The mean time course of the responses is shown in Fig. 1. It illustrates, for the three vibration conditions with (Fig. 1a) or without visual cues (Fig. 1b), the average antero-posterior CoP position. As can be seen in Fig. 1, CoP displacement evoked by lower leg vibration started in all experimental conditions with an early small forward shift of the CoP followed by the late main displacement in the opposite direction, i.e., in the direction of the vibrated muscle. As reported previously by Polonyova and Hlavacka (2001), another small increase in the backward direction could be observed at stimulus offset followed by a rapid return of the COP towards its initial position.

Early forward shift of the COP according to the vibration condition

As seen in Fig. 1, whatever the experimental condition, an early forward shift of the CoP occurred with a similar latency of ~110 ms. However, this forward displacement of the CoP was only transient in the unexpected condition, but was sustained in the expected and self-triggered conditions (see Table 1a). Analysis of the total duration of the forward shift (see Fig. 2a), indicated a significant effect of vibration condition [$F(2,22) = 3.7$, $P < 0.05$]. Newman Keuls analyses revealed that the duration of this forward shift was longer in the self-triggered than in the precue condition, this later being longer than in the unexpected condition ($P < 0.05$). There was no significant effect of visual cues [$F(1,11) = 0.04$, $P > 0.05$] on this early forward CoP

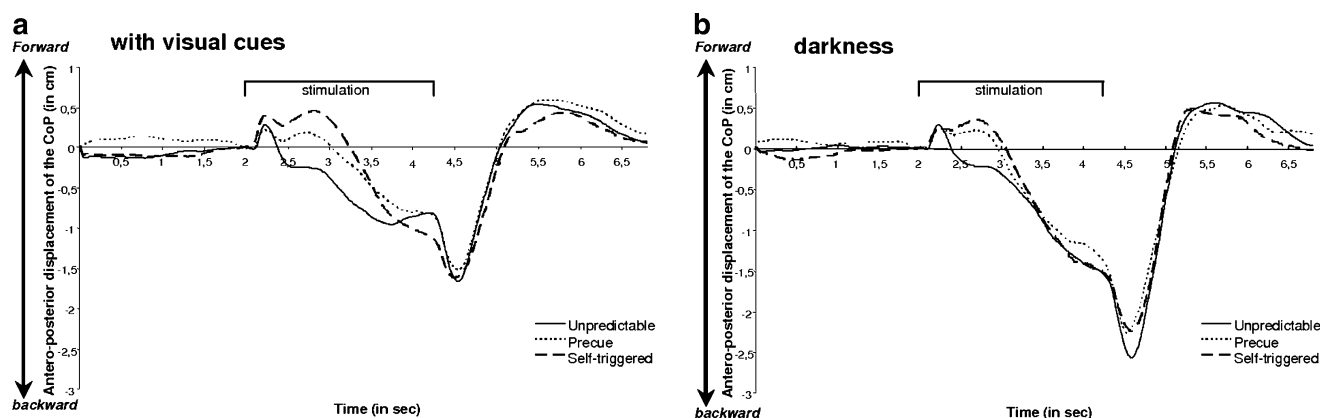


Fig. 1 Mean antero-posterior displacement of the CoP for the different vibration conditions and visual conditions. Onset and offset of vibration were, respectively, at 2 and 4.2 s. A negative result signifies a backward displacement

Table 1 Mean and standard errors (in brackets) of the duration of the forward responses in seconds (a), amplitude in cm (b) and velocity in cm/s (c) of the backward responses for each modality of the vibration (unpredictable–precue–self-triggered), visual (visual cues–darkness) and block (block 1–block 2) factors

	Block 1		Block 2	
	Visual cues	Darkness	Visual cues	Darkness
a. Duration of the forward response (s)				
Unpredictable	0.600 (0.139)	0.535 (0.099)	0.514 (0.100)	0.796 (0.127)
Precue	0.872 (0.141)	0.698 (0.109)	0.975 (0.198)	0.968 (0.134)
Self-triggered	1.121 (0.099)	0.857 (0.116)	1.184 (0.119)	1.288 (0.143)
b. Amplitude of the backward response (cm)				
Unpredictable	0.922 (0.263)	1.5753 (0.215)	0.739 (0.220)	1.396 (0.322)
Precue	1.299 (0.236)	1.521 (0.166)	0.435 (0.284)	1.265 (0.280)
Self-triggered	1.523 (0.280)	2.012 (0.427)	0.776 (0.384)	0.981 (0.286)
c. Velocity of the backward response (cm/s)				
Unpredictable	1.104 (0.318)	1.523 (0.213)	0.658 (0.181)	1.378 (0.377)
Precue	1.405 (0.212)	1.427 (0.157)	0.680 (0.190)	1.624 (0.215)
Self-triggered	2.111 (0.317)	2.015 (0.260)	1.477 (0.238)	1.710 (0.276)

displacement but a significant main effect of block [$F(1,11) = 5.10$ $P < 0.05$]. The forward shift of the COP lasted longer in the second block than in the first one (see Table 1).

Backward shift of the COP according to the vibration conditions

As can be seen in Figs. 1 and 2b and in Table 1b, the use of visual cues had a significant main effect on the amplitude of the backward CoP displacement [$F(1,11) = 11.4$, $P < 0.01$]. The amplitude of the response was reduced by approximately 57% when visual cues were available in comparison to complete darkness. ANOVA also revealed that the factor vision did not interact with the vibration conditions ($P = 0.51$). Similarly, block analysis revealed that the amplitude of the backward displacement was larger during the first than during the second block [$F(1,11) = 17.2$, $P < 0.01$]. This decrease of the postural response to tendon

vibration reflected the well described phenomenon of adaptation (see Fransson et al. 2000, 2004). Interestingly, despite variable delays of initiation of the backward displacement (see above), the amplitude of the backward CoP displacement was similar in the three vibration conditions at stimulation offset [$F(2,22) = 0.58$ $P = 0.57$] in both visual conditions. This absence of difference after 2.2 s of vibration can be understood when considering the dynamic of CoP displacements in response to vibration (Fig. 2c). Indeed, slope analysis (velocity of the backward displacement) indicated that once the backward CoP displacement was initiated, its velocity was higher in the self-triggered than in the precue condition (see Fig. 2c; Table 1c), this later being higher than in the unexpected condition [$F(2,22) = 10.81$, $P < 0.001$]. Post-hoc comparisons revealed that only the self-triggered condition differed from the other two conditions ($P < 0.01$). The ANOVA also revealed a significant reduction of velocity when visual cues were available compared to darkness [$F(1,11) = 43$ $P < 0.01$],

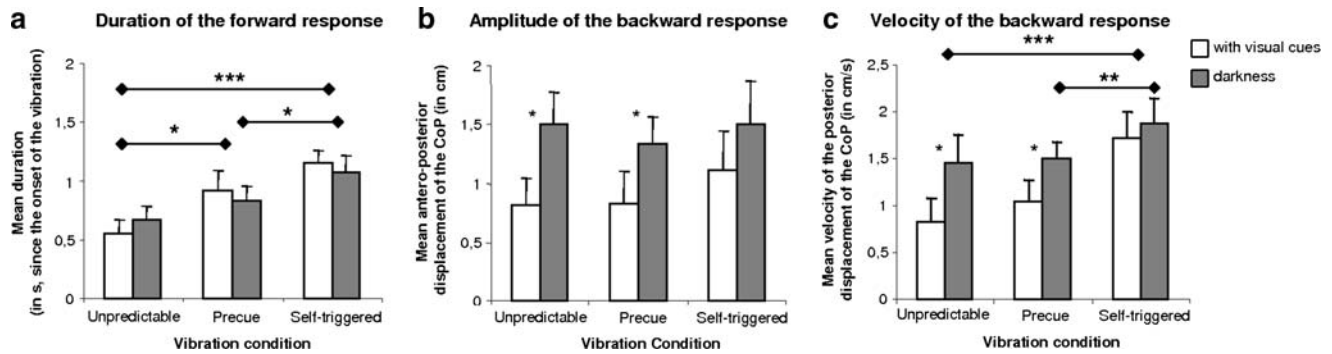


Fig. 2 Mean results and standard *errors bars* for the different parameters analyzed depending on the different vibration conditions and visual conditions. **a** Mean duration of the forward displacement of the CoP (early component of the response). **b** Mean amplitude of the back-

ward displacement of the CoP at the end of the stimulation (time: 4.2 s). **c** Mean velocity of the displacement of the CoP between the forward peak and the end of the stimulation

without any significant interaction with the block or vibration factors ($P > 0.05$).

Discussion

Despite their apparent automaticity, the postural responses evoked by either visual, vestibular or proprioceptive stimulation share the characteristic of being readily modifiable by many different factors, such as the support properties, the standing posture, the availability of other sensory cues, the adaptation to perturbation or even the nature of the task. However, these sensory channels appear to differ from each other relative to cognitive influences. Indeed, whereas the response to a visual perturbation is largely reduced if not suppressed when the subject is aware that an upcoming disturbance is likely to be caused by an external agent rather than by self motion (Guerraz et al. 2001b; Freitas Junior 2004), the same does not appear to be true for both the vestibular (Guerraz and Day 2005) and proprioceptive channels as presently evidenced.

In the present experiment, we investigated whether expectation of a proprioceptive perturbation (Achilles' tendon vibration), either through a voluntary action that initiates it (self triggered condition) or through prior knowledge of the event and timing cues (predictable condition) affects the evoked postural response. Results showed that whatever the vibration and visual condition, a short latency (~110 ms) forward CoP displacement, followed by a main backward CoP displacement was evoked by Achilles's tendon vibration. Results also showed that the amplitude of the main backward displacement was similar in the three vibration conditions. However, a difference appeared in the time course and dynamic of these events. Indeed, whereas in the unexpected condition, the short latency forward response was immediately followed by the main backward CoP displacement, it appeared that the later was delayed by

approximately 500 ms in both the self-triggered and expected conditions. In contrast, once initiated, the velocity of the backward displacement was even higher in the self-triggered than in the other two conditions. Therefore, although expectation appeared to delay the appearance of the main backward body sway, cognitive mechanisms did not appear to be able to weight the impact of the proprioceptive stimulation as evidenced by the amplitude and kinematics of the main backward responses.

Guerraz and Day (2005) proposed that the reason for the different sensitivity of the visual and vestibular channels to cognitive inputs arises from the natural ability of the two channels to signal self-motion. Both the vestibular and visual systems can potentially monitor self-motion but with one important difference. The vestibular system detects unambiguously the acceleration of the head in space and therefore always signals self-motion. The visual channel is different in that visual flow carries information regarding both self-motion and object-motion. A displacement of either the body or the visual scene can yield similar patterns of retinal motion stimuli. Thus, the origin of the visual flow information remains ambiguous. This could explain why a process has evolved that is able to suppress the postural response to a visual perturbation if the perturbation is deemed likely to result from object-motion or eye-motion (see also White et al. 1980), rather than self-motion. In contrast, there is no equivalent requirement for the vestibular channel and therefore no necessity for such a cognitive control: the vestibular information is unambiguous in that it systematically reflects head displacement.

Proprioceptive information about the angle of the leg with respect to the foot can also be potentially ambiguous. Indeed, modification of the ankle angle can occur either because the subject is leaning forward or backward on a stable support surface or because the foot is more plantar or dorsi flexed during a displacement of the support surface. However, in response to a displacement of the support

surface or to forward-backward displacements of the body, the central nervous system (CNS) is compelled to act on the input in order to maintain equilibrium (Nashner 1976; Horak et al. 1989; Maki and Whitelaw 1993). This is fundamentally different with vision for which the ambiguity is whether the input arises from body motion, which the CNS needs to act on, or from environmental motion, which it does not. Therefore, as for the vestibular channel, there is no requirement for a high level process (cognitive control) that would be able to suppress the balance response when the proprioceptive perturbation is deemed likely to result from an external unnatural stimulation.

Of interest, experiments in which proprioception was stimulated by a sudden displacement of the support surface have provided results that are in line with the present ones. Such displacements of the support surface on which subjects stand evoke fast muscle responses with a latency between the simple segmental reflex and volitional latencies (Horak et al. 1989). These early, automatic muscle responses, driven in part by somatosensory inputs (but also by vestibular afferents), represent a first line of defense to keep the body upright and are functionally important. Similarly to vibration evoked postural responses, these postural responses to a sudden support displacement also seem relatively immune to cognitive modulations. Indeed, precuing subjects with partial or complete information about the forthcoming disturbance of the support surface has either no effect (Diener et al. 1991) or only small effects (Maki and Whitelaw 1993; McChesney et al. 1996) on these automatic responses.

In the above-mentioned experiments, postural perturbation was the consequence of external destabilizing conditions (displacement of the support surface, vibration of the Achilles' tendon, etc.). Another source of potential body destabilization stems from the action of the subject himself. For instance, the action of unloading a heavy object or rising the arm or the leg have the effect of displacing the centre of mass which could eventually induce a disequilibrium. However, in those circumstances, prior to the onset of a rapid arm movement for instance, a specific pattern of acceleration of the trunk is generally observed (Bouisset and Zattara 1987; Nougier et al. 1999). The self-triggered postural perturbation is then compensated for by anticipatory postural adjustments (APAs) (Dufosse et al. 1985; Lacquaniti and Maioli 1989). Interestingly, in those tasks which can have the consequence of acting on different sensory channels (usually the vestibular or proprioceptive channels), the generation of efficient APAs requires a direct relationship between the motor action and the expected perturbation (Aruin and Latash 1995; Aruin et al. 2003). In other words, expectation or the explicit knowledge (high cognitive level) of the forthcoming destabilizing situation is not sufficient to trigger robust and well adapted APAs,

which is consistent with the results of the present experiment and with that of Guerraz and Day (2005) concerning the vestibular channel. However, in some circumstances, APAs could be generated without any direct action by the subject (Massion 1992). For example, APAs associated with a load catching can be observed when information about the upcoming object is conveyed by the visual channel. When the eyes are closed and subjects receive an auditory cue on the release of the object, the APAs are either absent or not consistent (Lacquaniti and Maioli 1989).

Current research has demonstrated that postural control is less automatic than previously thought (Shumway-Cook et al. 1997; Vuillerme et al. 2000; Ehrenfried et al. 2003) and can therefore be affected by high level processes (Guerraz et al. 2001b; Hunter and Hoffman 2001). The interest of the present research is that the inputs provided by the different sensory channels are not equally susceptible to the influence of high level processes (cognitive processes) such as expectation.

Acknowledgments We thank Vincent Nougier for his guidance and help in the achievement of this work, Remy Cuisinier for expert technical assistance and BL Day for personnel communication. We also thank the reviewers for their valuable comments.

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