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## RESEARCH ARTICLE

# Influence of vestibular and visual stimulation on split-belt walking

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**Abstract** We investigated the influence of vestibular (caloric ear irrigation) and visual (optokinetic) stimulation on slow and fast split-belt walking. The velocity of one belt was fixed (1.5 or 5.0–6.0 km/h) and subjects ( $N = 8$  for vestibular and  $N = 6$  for visual experiments) were asked to adjust the velocity of the other belt to a level at which they perceived the velocity of both the belts as equal. Throughout all experiments, subjects bimanually held on to the space-fixed handles along the treadmill, which provided haptic information on body orientation. While the optokinetic stimulus (displayed on face-mounted virtual reality goggles) had no effect on belt velocity adjustments compared to control trials, cold-water ear irrigation during slow (but not fast) walking effectively influenced belt velocity adjustments in seven of eight subjects. Only two of these subjects decreased the velocity of the ipsilateral belt, consistent with the ipsilateral turning toward the irrigated ear in the Fukuda stepping test. The other five subjects, however, increased the velocity of the ipsilateral belt. A straight-ahead sense mechanism can explain both decreased and increased velocity adjustments. Subjects decrease or increase ipsilateral belt velocity depending on whether the vestibular stimulus is interpreted as an indicator of the straight-ahead direction (decreased velocity) or as an error signal relative to the straight-ahead direction provided by the haptic input from the space-fixed handles along the treadmill (increased velocity). The missing effect during fast walking corroborates the findings by others that

the influence of vestibular tone asymmetry on locomotion decreases at higher gait velocities.

**Keywords** Caloric ear irrigation · Optokinetic nystagmus · Gait control · Haptic perception

## Introduction

Vestibular tone influences the direction of gait. Typically, subjects with an acute unilateral decrease of vestibular tone, such as in vestibular neuritis, deviate toward the side of the deficit while walking (Peitersen 1974). Similarly, while stepping in place with the eyes closed, these patients tend to rotate about the earth-vertical axis toward the ear with the lower vestibular tone (Fukuda 1959).

In a dog and subsequently in human subjects, Brandt and co-workers observed that the influence of vestibular tone imbalance on gait direction depends on gait velocity; subjects deviated less during running than walking (Brandt et al. 1999; Jahn et al. 2000). The authors speculated that, with rising step frequency, automatic spinal cord mechanisms associated with locomotion (Dietz et al. 1994a) increasingly suppress influences from the vestibular system. Later, this hypothesis was extended to non-vestibular influences on locomotion, such as the sense of optic flow (Jahn et al. 2001), ocular motor efference copy during spontaneous nystagmus (Jahn et al. 2002), and proprioceptive input (Dietz et al. 2001).

Hypothetically, the effect of vestibular tone imbalance and optic flow asymmetries on locomotion can be mediated by two alternative neural mechanisms. The first mechanism, which we will call direct spinal mechanism, would influence the spinal cord centers that encode the velocity of the two legs. The second mechanism, which we will call

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straight-ahead sense mechanism, uses vestibular and other sensory inputs to compute an internal representation of the straight-head direction. A mismatch of the perceived direction of locomotion and the internal straight-ahead direction would lead to a difference in velocity between the two legs such that the body turns toward the direction of the internal straight-ahead direction.

Conceivably, both hypothetical mechanisms may be inhibited by the velocity of locomotion. Thus, decreasing gait deviation with increasing gait velocity would not be a feature that allows distinguishing between the two hypotheses. To discriminate between the direct spinal mechanism and the straight-ahead sense mechanism, we applied vestibular (caloric) and visual (optokinetic) stimuli to healthy human subjects, while they were walking on a split-belt treadmill. Subjects held on to the sidebars parallel to the belts at pelvic height, which prohibited a turning of the body and also provided haptic information on the actual straight-ahead direction. The velocity of the belt for one leg was fixed, while the velocity of the belt for the other leg had to be adjusted by the subject.

With this paradigm, the direct spinal mechanism hypothesis predicts that, in every case, the velocity of the leg on the side, to which the subject would deviate when freely walking, would be lower than the velocity of the other leg. The straight-ahead sense mechanism hypothesis, however, predicts that, depending on whether the vestibular or visual signal is perceived as a “true” straight-ahead signal or an error signal, the ipsilateral or contralateral leg becomes slower.

## Methods

### Subjects

Twelve healthy subjects (24–35 years old; 4 female) gave their informed consent to participate in this study. The experimental protocol was approved by the local ethics committee (canton of Zurich), and adhered to the Declaration of Helsinki for research involving human subjects. All subjects were free from disease and none of them were taking any medication at the time of the experiments.

### Experimental setup

The subjects walked on a split-belt treadmill with the two belts moving at different velocities (Dietz et al. 1994b; Prokop et al. 1995), with both hands holding on to handles that were oriented parallel to the belts at pelvic height. The body was secured in a parachute harness to prevent injuries in case of falls. During experiments, the velocity of one

belt was fixed and subjects had to adjust the velocity of the other belt by turning on a potentiometer knob placed between thumb and index finger of the ipsilateral hand. The instruction was always to adjust the velocity of the variable belt to a value that was perceived as equal to the velocity of the other belt. Subjects were asked to keep their head in the neutral position as during normal walking, i.e. pointing straight ahead and not turning left or right. This was controlled visually by the experimenter. Between adjustments, the experimenter decreased the velocity of the variable belt to a random value between zero and the velocity of the other belt. We opted for adjustments starting from lower initial values only because, in pilot experiments, we found larger variabilities when adjustments from lower and from higher initial values were intermingled. The strain of vestibular stimulation (see below) did not allow performing both increasing and decreasing adjustments.

The velocity of each belt was measured from an analog output (sampling frequency 100 Hz). The adjusted velocity was determined when the subject had ceased turning the knob and verbally confirmed that he had finished the adjustment. The verbal confirmation had to take place within 15 s after the beginning of the adjustment or else the trial was repeated. This time limit ensured that adjustments occurred during primary nystagmus.

### Experimental paradigms

Subjects participated in two sets of experiments: (1) split-belt walking during vestibular stimulation and (2) split-belt walking during visual stimulation. Eight subjects were exposed to the vestibular paradigms and six subjects to the visual paradigms. Two subjects were involved in both sets of experiments.

In the first set of experiments (vestibular stimulation), blindfolded subjects were exposed to cold-water irrigation of the right ear. On the treadmill, ten velocity adjustments of the right belt were performed for control (after three initial practice trials). Thereafter, the right ear was irrigated with cold water (20°C) during 30 s with the head retroflexed by at least 45°. The effectiveness of the caloric stimulation was verified using the subjects' verbal confirmation of induced vertigo and the appearance of nystagmus on uncalibrated binocular direct-current electro-oculography (EOG). Then they were asked to hold their head upright again and to complete another trial by adjusting the velocity of the right belt while walking. Adjustments were assessed at two different velocities of the left belt: 1.5 km/h (=0.42 m/s, “slow walking”) and 6.0 km/h (=1.67 m/s, “fast walking”). As a control, i.e. separately from experiments on the split-belt treadmill, the effectiveness of the caloric stimulus was assessed by letting subjects step in

place (Fukuda 1959) after cold-water irrigation of the right ear. All subjects turned 90° to the right within 40 s.

In the second set of experiments (visual stimulation), subjects were exposed to a horizontal optokinetic stimulus consisting of black and white vertical stripes (width 3.75°) moving from left to right with 22.5°/s. The resulting temporal frequency of the stripe pattern was 3 Hz. This optokinetic stimulus was applied with a face-mounted binocular virtual reality display (Eye-Trek FMD-200 manufactured by Olympus Corporation, Japan), which consists of two liquid crystal panels (LCD) displaying 180,000 pixels each. The viewing angles are 30° horizontal and 23° vertical. The stripe pattern was generated on a personal computer and sent to the RGB input of the virtual reality display with a frame rate of 60 Hz and 800 × 600 pixel resolution. Each stripe was 100 pixels wide. Care was taken to select a velocity of the optokinetic stimulus with only discrete pixel shifts. The images displayed on the two LCDs were identical. On the treadmill, four blocks with ten adjustments each had to be performed (after three initial practice trials at the beginning of every block): (1) white display, left belt at 1.5 km/h (=0.42 m/s, “slow walking”), right belt to be adjusted; (2) rightward optokinetic stimulus, left belt at 1.5 km/h, right belt to be adjusted; (3) white display, right belt at 1.5 km/h, left belt to be adjusted; (4) rightward optokinetic stimulus, right belt at 1.5 km/h, left belt to be adjusted. The four blocks were then repeated, but the velocity of the non-modifiable belt was 5.0 km/h (=1.39 m/s, “fast walking”). Compared to the experiments with caloric stimulation, the “fast walking” velocity was slightly reduced (by 1/6) to minimize the movements of the face-mounted visual display induced by excessive body and head movements around the upper limit of possible walking velocity. The effectiveness of the optokinetic stimulus was assessed by the Fukuda stepping-test. Subjects turned 90° to the right within 30 s.

#### Statistical methods

Differences between values assessed in the presence of vestibular or visual stimuli and values from the respective control experiments were evaluated by paired *t* tests. Averages were considered to be different at a significance level of  $P < 0.05$ .

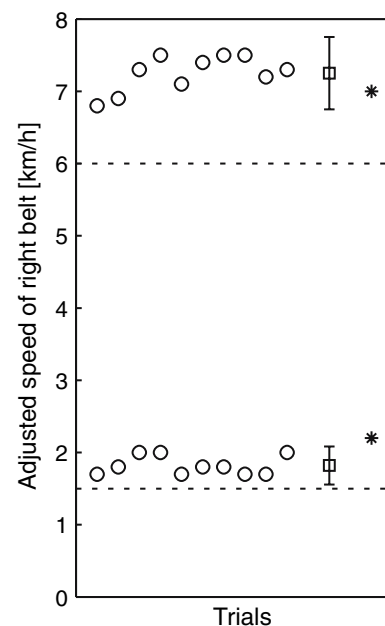
#### Computer simulation

To construct a computer model that was able to qualitatively reproduce our data, we used Simulink 6.2 (The MathWorks, Inc., Natick, MA).

## Results

### Vestibular experiments

On the treadmill, subjects performed ten adjustments of the right belt for control before the right ear was irrigated with cold water and subjects were asked to complete another adjustment. At two different velocities of the left belt (“slow walking” = 1.5 km/h; “fast walking” = 6.0 km/h), Fig. 1 shows a typical example with experimental blocks of ten control adjustments (open circles) and a subsequent adjustment after cold-water irrigation of the right ear (asterisk). Typically, but not in every subject, the ideal velocity is overestimated when initial velocities before adjustments are below the ideal value, as was the case in our experiments (Jensen et al. 1998). If the right belt was adjusted as suggested by the Fukuda stepping-test, trials after cold-water ear irrigation would result in a velocity reduction, reflecting a rightward rotation of the body during walking on normal ground. In this example, however, the adjusted velocity after caloric stimulation was more than two standard deviations (SD; error bar) above the mean of the control trials (open square) during slow walking. On the other hand, no substantial effect of caloric stimulation was found during fast walking.



**Fig. 1** Adjusted velocities of the right belt in a typical subject before and after caloric stimulation. Two experimental blocks with fixed velocities (*dashed lines* 1.5 and 6.0 km/h) of the left belt. Before adjustment by the subject, the velocity of the right belt was randomly set to a value below the fixed velocity of the left belt. *Open circles* control trials. *Asterisks* trials after cold-water irrigation of the right ear. *Squares* averages of control trials. *Error bars*  $\pm 2SD$

**Fig. 2** Adjusted velocities (**a**, **b**) and relative changes of adjusted velocities (**c**, **d**) of the right belt in all tested subjects ( $N = 8$ ) before and after cold-water irrigation of the right ear. **a** Slow walking (left belt: 1.5 km/h). Asterisks trial after cold-water irrigation of the right ear. Squares average of control trials. Error bars  $\pm 2SD$ . Dashed lines fixed velocities of the left belt. Values below the dashed line would lead to a curvature of gait to the right, if subjects were able to walk freely on the ground. **b** Fast walking (left belt 6.0 km/h). Symbols as in **a**, but scale of the ordinate is twice as large. **c** Relative changes of adjusted velocities from **a**. Units: standard deviations. Dashed lines  $\pm 2SD$  from zero baseline. **d** Relative changes of adjusted velocities from **b**

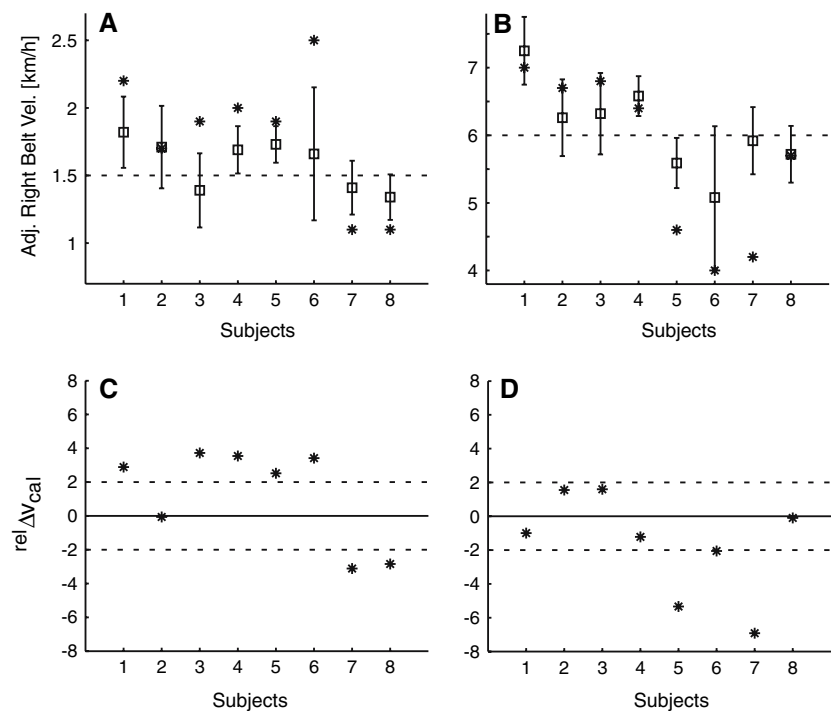


Figure 2 summarizes the results in all eight subjects for the cold-water irrigation of the right ear. During slow walking (Fig. 2a), five subjects adjusted the velocity of the right belt more than 2SD above the average of the control trials. In one subject, however, adjusted velocity was within the range of  $\pm 2SD$  and in two subjects below. Interestingly, these two subjects underestimated the ideal velocity of the right belt during control trials. In seven of the eight subjects, caloric stimulation led to a change of adjusted velocity in the same direction as the average bias during baseline testing. This caloric induced direction-specific increase of adjusted belt velocity, however, was not significantly different from zero ( $t$  test  $P > 0.05$ ).

During fast walking (Fig. 2b), cold-water irrigation of the right ear led to adjusted velocities that were all below the upper limit of 2SD above average. In five subjects, the velocities were inside the range of average  $\pm 2SD$ , while in the other three subjects the values were below the range of average  $\pm 2SD$ . The caloric induced increase in the direction of the average bias during baseline testing, present in five of the eight subjects, was not significant ( $t$  test  $P > 0.05$ ).

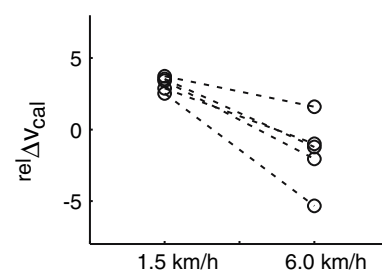
To compare the data between the slow and fast walking conditions, the relative change of adjusted velocity after caloric stimulation ( ${}^{\text{rel}}\Delta v_{\text{cal}}$ ) was computed:

$${}^{\text{rel}}\Delta v_{\text{cal}} = (v_{\text{cal}} - \bar{v})/SD_v$$

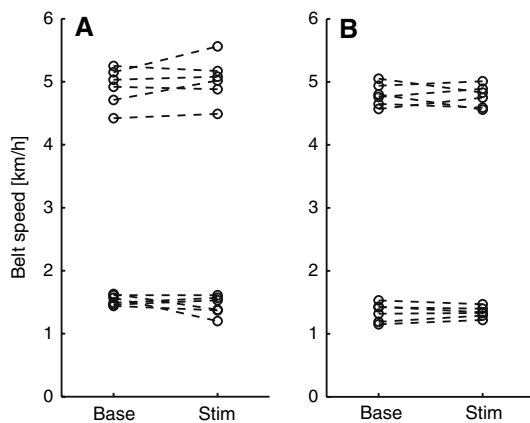
whereby  $v_{\text{cal}}$  represents the adjusted velocity during caloric stimulation,  $\bar{v}$  the average value of the control trials

( $N = 10$ ), and  $SD_v$  the corresponding standard deviation. On average,  ${}^{\text{rel}}\Delta v_{\text{cal}}$  was 1.26 ( $\pm 2.9$  SD) during slow walking (Fig. 2c) and  $-1.69$  ( $\pm 3.06SD$ ) during fast walking (Fig. 2d). The difference between the two averages was not significant in the paired  $t$  test ( $P > 0.05$ ).

The missing significance of the difference between slow and fast walking might be due to different cognitive strategies that subjects used to interpret the vestibular signal (see Discussion). We therefore analyzed the subgroup of five subjects who adjusted the velocity of the right belt higher than 2SD above the control average during slow walking. Figure 3 compares  ${}^{\text{rel}}\Delta v_{\text{cal}}$  during slow and fast walking in these five subjects. On average,  ${}^{\text{rel}}\Delta v_{\text{cal}}$  was 3.22 ( $\pm 0.50SD$ ) during slow walking and  $-1.60$  ( $\pm 2.50SD$ ) during fast walking. The difference between the two



**Fig. 3** Relative changes of adjusted velocities of the right belt after cold-water irrigation of the right ear. Dashed lines connect intra-individual data obtained during slow and fast walking. Only subjects are shown in whom the adjusted velocity was more than 2SD above the control average during slow walking ( $N = 5$ )



**Fig. 4** Adjusted belt velocities in all tested subjects ( $N = 6$ ) with and without optokinetic stimulation. *Open circles* averages of ten trials. *Base*: trials with *white* display. *Stim*: trials with optokinetic stimulation to the right. Intra-individual data points are connected by *dashed lines*. **a** Adjustments of right belt, velocities of left belt at 1.5 or 5.0 km/h, respectively. **b** Adjustments of left belt, velocities of right belt at 1.5 or 5.0 km/h, respectively

averages was highly significant (paired  $t$  test  $P = 0.007$ ). Values during fast walking in these subjects were not significantly different from zero ( $t$  test  $P > 0.05$ ).

#### Visual experiments

On the treadmill, subjects were exposed to a horizontal optokinetic stimulus moving to the right. The velocity of either the right or left belt was fixed at 1.5 or 5 km/h, while the velocity of the other belt had to be adjusted. Figure 4 shows the effect of the optokinetic stimulus on the velocity adjustment of the right belt (Fig. 4a) and the left belt (Fig. 4b) in comparison to the control experiments with a white display. Averages computed from ten trials in each subject (open circles) were not significantly different ( $P > 0.05$ ) between conditions without (*Base*) and with (*Stim*) the optokinetic stimulus, during both slow and fast walking.

Vestibular and visual experiments differed in subjects who performed only one adjustment during caloric stimulation, while ten adjustments were performed during optokinetic stimulation. This difference was mandatory, as caloric irrigation puts much more strain on subjects than an optokinetic stimulus. To exclude the possibility that habituation could have influenced the outcome of the optokinetic experiment, as data were averaged over ten trials, we also compared the initial adjustment during optokinetic stimulation with the control data. All initial adjustment values during optokinetic stimulation were within the range of the average  $\pm 2SD$  obtained in the control trials.

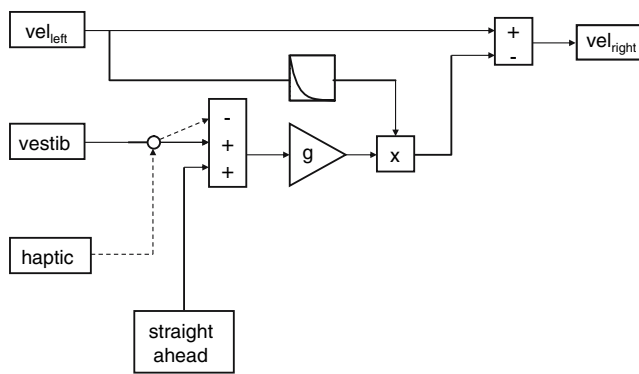
#### Discussion

We investigated the influence of vestibular (caloric) or visual (optokinetic) stimulation on locomotion during slow and fast walking on a split-belt treadmill. The task was to adjust the velocity of one belt to the constant velocity of the other belt, so that the velocities of both the legs were perceived as equal. Importantly, throughout all experiments, subjects bimanually held on to space-fixed handles, which provided haptic information on the orientation of the body relative to the treadmill.

The rightward optokinetic stimulus did not cause any significant changes in the adjusted slow or fast belt velocities, although, while stepping in place (Fukuda stepping test), subjects rotated to the right. Especially at higher velocities, an adequate visual effect was possibly prevented by the limited size of the visual field and by the concurrent movements of the mask. Caloric stimulation, however, led to clear effects during slow walking in seven of eight subjects. If the effect of caloric stimulation on the treadmill had been the same as during the subsequent stepping in place, a decreased adjustment of ipsilateral belt velocity, consistent with ipsilateral turning, was expected. This was the case in only two subjects, who already tended to underestimate the ipsilateral belt velocity during the control trials. Whether this finding is coincidental, cannot be answered with the available data. In the other five subjects, the velocity of the belt ipsilateral to the side of cold-water ear irrigation was adjusted higher than the preset velocity of the other belt.

Our results can not be explained by a direct spinal mechanism (see “[Introduction](#)”), because this hypothesis predicts that all subjects would react with decreased velocity adjustments of the belt ipsilateral to cold-water ear irrigation. A straight-ahead sense mechanism, however, can explain both decreased and increased velocity adjustments of the belt ipsilateral to cold-water ear irrigation. Depending on whether the vestibular stimulus is interpreted as an indicator of the straight-ahead direction or an error signal relative to the straight-ahead direction provided by the haptic input from the space-fixed handles, adjusted ipsilateral belt velocity is decreased or increased, respectively.

Figure 5 schematically describes this hypothesis by a simple model. If the vestibular input influences the sense of straight-ahead and haptic input from the handles is neglected, the straight-ahead direction will be perceived somewhat to the right of the heading direction, i.e. to the side of the ear irrigated with cold water. Therefore the velocity of the right belt will be adjusted to a lower level than the fixed velocity of the left belt. Correspondingly, on normal ground the body would rotate to the right. The results from two of the eight subjects were compatible with this strategy (solid line arrow at switch). If, however, the



**Fig. 5** Model explaining the differential velocity adjustment of the right belt in the presence of cold-water irrigation of the right ear depending on whether the haptic input from the handles is used to indicate the straight-ahead direction. In parentheses: values used in the Simulink™ implementation of the model. Inputs are the fixed velocity of the left belt (1.5 or 6.0 km/h), the vestibular tone asymmetry represented by slow-phase eye velocity (e.g.  $10^\circ/s$ ), the haptic input from the handles (on or off), and straight ahead ( $0^\circ$ ). Output is the adjusted velocity of the right belt. A look-up table element is used to implement the decreasing influence of vestibular signals with increasing gait velocity ( $\exp(-u \times 0.2)$ ). The vestibular velocity signal is converted into a position signal by a leaky integrator before being added to (without haptic input; *solid line arrow* after switch) or subtracted from (with haptic input; *dashed line arrow* after the switch) straight ahead relative to the body. The gain element ( $g = 0.02$ ) scales the deviation of straight ahead

haptic input from the handles is used as an indicator of the straight-ahead direction, the vestibular signal is interpreted as deviation of the body from straight-ahead, which subjects compensate by increasing the velocity of the right belt. On normal ground, this would rotate the body to the left. Five of eight subjects used this second strategy (dashed line arrow at switch).

The findings by others that vestibular influences on locomotion decrease with higher locomotion velocity (Brandt et al. 1999; Jahn et al. 2000), is also implemented in the model (lookup-table element with a decaying curve). In fact, our results confirmed this inverse relation between gait velocity and vestibular influences on balance during locomotion: adjusted belt velocities were significantly less influenced by caloric stimulation during fast walking than during slow walking. We propose, however, that gait velocity influences the impact of the straight-ahead sense rather than directly the impact of the vestibular input. Therefore, in the model, the gait velocity signal enters the model after vestibular and haptic inputs interacted.

It has been shown that the sense of straight-ahead and, similarly, the localization of imaginary targets can be manipulated by vestibular input (Karnath et al. 1994; Schmal et al. 2000). Haptic stimuli, on the other hand, are able to supplement or counteract vestibular influences on postural balance (Holden et al. 1994; Jeka and Lackner

1994; Bortolami et al. 2003). The results of our experiments support the hypothesis that the sense of straight ahead, rather than the direct vestibular input, influences the adjustment of belt velocity during split-belt walking. We would like to suggest that this hypothetical straight-ahead sense mechanism can be extended to gait deviations during normal walking in the presence of a vestibular tone asymmetry. Furthermore, we expect that stronger optokinetic stimuli occupying a larger range of the visual field with compensation of head movements would have a similar effect as a vestibular tone asymmetry, as vestibular and optokinetic signals already converge at the level of the vestibular nuclei (Waespe and Henn 1977).

Our results could also be explained by another mechanism, which we shall call perception-of-turning mechanism. According to this mechanism, the majority of subjects would match belt velocities to the perception of turning. Decreased vestibular tone on the side of the cold-water irrigation evokes the perception of being rotated to the contralateral side. Because the subjects cognitively know from the sensory input of the space-fixed handles that their body is not turning, they would increase the ipsilateral belt velocity to match gait to the perception of turning. The minority of subjects, on the other hand, would try to compensate for the perceived turning and decrease the velocity of the ipsilateral belt.

Based on the data, we cannot exclude the perception-of-turning mechanism. However, since the subjects' task was to adjust the velocity of the variable belt to a value that was perceived as equal to the velocity of the other belt, an adjustment of gait to the perception of turning would constitute a clear violation of the experimental instruction. Therefore we consider the straight-ahead sense mechanism as the more likely mechanism controlling split-belt walking at low velocity.

Finally, the influence of haptic input on split-belt walking in the presence of tonic vestibular asymmetry resembles that of vision on eye drift. While patients with an acute unilateral peripheral vestibular lesion have unimpeded spontaneous nystagmus when their eyes are closed, vision (=eyes open) counteracts the low frequency vestibulo-ocular reflex by means of the smooth pursuit system. This in turn suppresses spontaneous nystagmus and stabilizes the visual surround. Thus, only when the haptic or visual influences are absent, does the low frequency vestibular system assert itself.

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## References

- Bortolami SB, DiZio P, Rabin E, Lackner JR (2003) Analysis of human postural responses to recoverable falls. *Exp Brain Res* 151:387–404
- Brandt T, Strupp M, Benson J (1999) You are better off running than walking with acute vestibulopathy. *Lancet* 354:746
- Dietz V, Colombo G, Jensen L (1994a) Locomotor activity in spinal man. *Lancet* 344:1260–1263
- Dietz V, Zijlstra W, Duysens J (1994b) Human neuronal interlimb coordination during split-belt locomotion. *Exp Brain Res* 101:513–520
- Dietz V, Baaken B, Colombo G (2001) Proprioceptive input overrides vestibulo-spinal drive during human locomotion. *Neuroreport* 12:2743–2746
- Fukuda T (1959) The stepping test: two phases of the labyrinthine reflex. *Acta Otolaryngol* 50:95–108
- Holden M, Ventura J, Lackner JR (1994) Stabilization of posture by precision contact of the index finger. *J Vestib Res* 4:285–301
- Jahn K, Strupp M, Schneider E, Dieterich M, Brandt T (2000) Differential effects of vestibular stimulation on walking and running. *Neuroreport* 11:1745–1748
- Jahn K, Strupp M, Schneider E, Dieterich M, Brandt T (2001) Visually induced gait deviations during different locomotion speeds. *Exp Brain Res* 141:370–374
- Jahn K, Strupp M, Krafczyk S, Schuler O, Glasauer S, Brandt T (2002) Suppression of eye movements improves balance. *Brain* 125:2005–2011
- Jeka JJ, Lackner JR (1994) Fingertip contact influences human postural control. *Exp Brain Res* 100:495–502
- Jensen L, Prokop T, Dietz V (1998) Adaptational effects during human split-belt walking: influence of afferent input. *Exp Brain Res* 118:126–130
- Karnath HO, Sievering D, Fetter M (1994) The interactive contribution of neck muscle proprioception and vestibular stimulation to subjective “straight ahead” orientation in man. *Exp Brain Res* 101:140–146
- Peitersen E (1974) Measurement of vestibulo-spinal responses in man. In: Kornhuber HH (ed) *Vestibular system, part 2: psychophysics, applied aspects and general interpretations*. Springer, Berlin pp 267–280
- Prokop T, Berger W, Zijlstra W, Dietz V (1995) Adaptational and learning processes during human split-belt locomotion: interaction between central mechanisms and afferent input. *Exp Brain Res* 106:449–456
- Schmal F, Kunz R, Stoll W (2000) The localization of an imaginary target under the influence of caloric vestibular stimulation in healthy adults. *Eur Arch Otorhinolaryngol* 257:473–479
- Waespe W, Henn V (1977) Neuronal activity in the vestibular nuclei of the alert monkey during vestibular and optokinetic stimulation. *Exp Brain Res* 27:523–538