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RESEARCH ARTICLE

Decreasing perceived optic flow rigidity increases postural sway

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Abstract Optic flow simulating self-motion through the environment can induce postural adjustments in observers. Some studies investigating this phenomenon have used optic flow patterns increasing in speed from center to periphery, whereas others used optic flow patterns with a constant speed. However, altering the speed gradient of an optic flow stimulus changes the perceived rigidity of such a stimulus. Optic flow stimuli that are perceived as rigid can be expected to provide a stronger sensation of self-motion than non-rigid optic flow, and this may well be reflected in the amount of postural sway. The current study, therefore, examined, by manipulating the speed gradient, to what extent the rigidity of an optic flow stimulus influences posture along the anterior–posterior axis. We used radial random dot expanding or contracting optic flow patterns with three different speed profiles (single-speed, linear speed gradient or quadratic speed gradient) that differentially induce the sensation of self-motion. Interestingly, most postural sway was observed for the non-rigid single-speed optic flow pattern, which contained the least self-motion information of the three profiles. Moreover, we found an anisotropy in that contracting optic flow produced more postural sway than expanding optic flow. In addition, the amount of postural sway increased with increasing stimulus speed, but for contracting optic flow only. Taken together, the results of the current study support the view that visual and sensorimotor systems appear to be tailored toward compensating for rigid optic flow stimulation.

Keywords Optic flow rigidity · Postural sway · Self-motion · Electromyography

Introduction

When we move through the environment, we experience so-called 'optic flow'. Optic flow provides information about our direction of movement (Warren and Hannon 1988) and the three-dimensional structure of the environment (Gibson 1979; Koenderink 1986). Visual input can contain different optic flow types (expansion–contraction, rotation, translation) and can conflict with other sensory (vestibular and proprioceptive) inputs (Peterka and Benolken 1995; Edwards et al. 2010). This has been demonstrated, for example, by the classic swinging room studies (Lishman and Lee 1973; Lee and Aronson 1974; Lee 1980; Bronstein 1986; Stoffregen 1986), in which optic flow was used to simulate self-motion. An observer was standing inside a room, while the movement of the room generated optic flow corresponding to forward or backward self-motion. Observers experienced the room movement as if they were actually moving through the room themselves and as a result they made compensatory movements in the same direction as the room's movement. This postural response is the result of visual information overriding the information coming from the proprioceptive and vestibular systems.

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In the swinging room studies, the entire room is moved, resulting in a stimulus containing *coherent* visual information inducing observer movement, as it would be visually perceived by the observer when moving through a room. In contrast, optic flow patterns projected on a flat projection screen can only simulate motion in front of the observer, which one might compare to just the motion of the front wall of a moving room. Such a stimulus is likely to generate a weaker sensation of self-motion than the moving room. Generally, moving through the environment creates optic flow patterns that contain a speed gradient, meaning that the optical speed at the center of the flow pattern is lower than at the periphery. De Bruyn and Orban (1990) removed the speed gradient of a radial expanding optic flow stimulus and investigated whether observers perceived the resulting stimulus as rigid or non-rigid. The fact that observers are well able to distinguish rigid motion (a change in position does not change the size and shape of the object) from non-rigid motion (a change in position is combined with a change in shape) had been shown before (Todd 1982). De Bruyn and Orban (1990) demonstrated that when the speed gradient of the optic flow pattern was removed, observers perceived the optic flow pattern as non-rigid, since the center appeared to move faster than the periphery. When the optic flow pattern contained a linear speed gradient (dots have a linear increase in speed toward the periphery, simulating a planar surface translating toward or away from the observer), the optic flow stimulus was perceived as rigid. De Bruyn and Orban (1990) concluded that the speed of an expanding optic flow stimulus has to be zero at the center and linearly increase in speed toward the periphery to be perceived as rigid.

Previous studies have shown that changing the characteristics of an optic flow stimulus by altering for instance the spatial frequency (Masson et al. 1995), motion direction (Lestienne et al. 1977) or the position in the visual field (Andersen and Dyre 1989) influences the amount of induced postural sway. Earlier studies investigating the effect of simulated self-motion by an optic flow stimulus also have shown that optic flow influences postural sway. However, these studies used optic flow stimuli with dissimilar speed gradients. Some studies used optic flow patterns with a speed gradient (rigid) (Lestienne et al. 1977; Gielen and van Asten 1990) while more recently a study used an optic flow pattern without a speed gradient (non-rigid) (Wei et al. 2010). Rigid optic flow has been shown to induce a stronger sensation of self-motion than non-rigid optic flow (Nakamura 2010), which might be reflected in a differential amount of postural sway when exposed to these different optic flow types. In the current study, we therefore question whether the perceived rigidity of an optic flow stimulus influences the amount of postural sway. In experiment 1, we will examine whether changing the rigidity of an optic flow stimulus, by manipulating the speed gradient, differentially affects the magnitude of induced postural sway. Our stimuli consist of randomly placed dots that simulate motion toward (expanding) or away (contracting) from the observer. We will use three different speed gradients: *single-speed* and a *linear* as well as a *quadratic* speed gradient. The single-speed optic flow stimulus does not contain a speed gradient and will therefore be perceived as non-rigid. The second optic flow stimulus contains a linear speed gradient, resulting in a rigid percept, and the third stimulus contains a quadratic speed gradient simulating observer movement through a circular tunnel. This third optic flow stimulus will also be perceived as rigid and is expected to induce the strongest sensation of self-motion of the three optic flow types. We hypothesize that the optic flow stimulus that generates the strongest sensation of self-motion will cause the most postural sway. Therefore, we expect that most postural sway will be induced by an optic flow stimulus containing a quadratic speed gradient. Apart from the speed gradient, we also vary the overall speed of the optic flow stimuli to determine whether an increase in optic flow speed results in an increase in postural sway. Previous studies have shown such a speed increase to result in an increase in postural sway, while postural sway amplitude decreases again at the highest stimulus velocities (Lestienne et al. 1977; Wei et al. 2010). Based on the results of these studies, we expect postural sway to increase with higher optic flow speeds until a saturation level is reached. In addition, we will determine whether this saturation level is influenced by the perceived rigidity of the optic flow stimulus.

In a second experiment, we examine whether any observed anisotropy in postural sway, caused by expanding versus contracting optic flow as has been reported by other studies (Lestienne et al. 1977; Palmisano et al. 2009; Wei et al. 2010) might be explained by anticipatory co-contraction of the lower leg muscles during expanding optic flow. It is conceivable that expanding optic flow patterns are encountered more often when moving through the environment than contracting optic flow patterns. This may result in anticipatory responses of the lower leg muscles when perceiving such an expanding optic flow pattern.

Experiment 1

We validated our stimuli in a small-scale experiment, in which observers indicated the perceived rigidity as well as the strength of the self-motion sensation induced by each optic flow type (see Table 1). We first replicated and extended the procedure of De Bruyn and Orban (1990) to examine the perceived rigidity of the three optic flow types (single-speed, linear speed gradient and quadratic speed

Table 1 For each condition, the percentage of trials and the corresponding standard error of the mean that an optic flow pattern was perceived as rigid (a) which is a replication and extension the experiment of De Bruyn and Orban (1990) or that optic flow with a linear (L) or quadratic (Q) speed gradient was perceived as more rigid (b) or inducing more self-motion (c) than single-speed (S) optic flow or an optic flow stimulus with a linear speed gradient

	Expanding (deg/s)		Contracting (deg/s)	
	6	24	6	24
Rigid (%) (a)				
S	5 (5)	5 (3)	8 (8)	0 (0)
L	83 (9)	67 (15)	87 (9)	67 (16)
Q	87 (10)	67 (15)	84 (13)	67 (16)
More rigid (%) (b)				
L versus S	96 (3)	99 (1)	100 (0)	100 (0)
Q versus S	99 (1)	96 (2)	93 (3)	100 (0)
Q versus L	54 (14)	54 (16)	48 (15)	57 (18)
More self-motion (%) (c)				
L versus S	94 (4)	100 (0)	78 (12)	78 (12)
Q versus S	95 (4)	99 (1)	83 (11)	80 (10)
Q versus L	74 (8)	84 (8)	78 (10)	67 (15)

Observers ($N = 8$, 2 observers only viewed expanding optic flow) had to indicate in a two-alternative-forced-choice task which of two subsequently presented optic flow patterns, containing a speed of 6 or 24 deg/s, appeared more rigid or induced more self-motion. All conditions were presented in pseudo-random order. There were 10 replications of all conditions per observer. Optic flow stimuli were identical to experiment 1. Presentation durations were comparable to one epoch (random noise + stimulus presentation) of experiment 1

gradient). Subsequently, we measured for each optic flow type whether it was perceived as *more* rigid or induced *more* self-motion than an optic flow pattern with a different speed gradient. We also examined whether there was a difference in the strength of self-motion induced by an expanding or contracting optic flow stimulus, using a quadratic speed gradient optic flow stimulus with a speed of 6 deg/s.

In the main experiment, we examined to what extent the perceived rigidity of an optic flow stimulus, by manipulating the speed gradient, influences the amount of postural sway along the anterior–posterior axis.

Methods

Observers

Fifteen observers (age range between 19 and 28 years) participated in the experiment. All had normal or corrected-to-normal visual acuity. Informed consent was obtained from all observers, and the experiment was approved by the local ethics committee and performed in accordance with the Declaration of Helsinki. Four observers were excluded from the analysis. Debriefing revealed that two observers tried to actively manipulate their postural sway, while two others became nauseous during the experiment and had to stop.[1]

Apparatus

Stimuli were generated on a MacPro and projected on a flat rear projection screen by a DepthQ HDs3D-1 projector (refresh rate 120 Hz, resolution 1,280 × 720). Postural sway of the observers was measured using a custom-made forceplate (ForceLink BV) with a sample rate of 1,000 Hz.

Stimuli

Radial optic flow stimuli were composed of randomly placed dots with an unlimited lifetime and a dot density of 0.17 dots/deg^2. Stimuli subtended 87° by 56° and were viewed from a distance of 116 cm. The center of the stimulus contained a black circle with a radius of 5°. Dot size increased with radius to provide an extra depth cue. It was smallest (0.21°) at the inner border of the stimulus and linearly increased with radius to a dot size of 0.30° at the outer border.

Speed gradient Optic flow stimuli contained one of three different speed gradients. Manipulating the speed gradient of an optic flow stimulus changes whether it is perceived as rigid or non-rigid (De Bruyn and Orban 1990). The first optic flow pattern we used had a constant angular retinal speed, resulting in a visual percept of which the center appeared to move faster than the periphery (see Online Resource 1) and is therefore perceived as non-rigid (see Table 1). We will refer to this optic flow type as the *single-speed* type. To obtain a constant angular retinal speed, the absolute speed of a dot (pixels/s) increased with eccentricity to compensate for larger visual angles at the periphery than at the center of the visual field (Fig. 1a).

The second optic flow stimulus contained a *linear speed gradient* and is perceived as rigid (De Bruyn and Orban 1990). The dot speed was proportional to the distance from the center, so the speed increased linearly from the inside border of the stimulus to the outside. The resulting visual percept was a planar surface consisting of random dots (see Online Resource 2), which simulated motion of a fronto-parallel plane toward or away from the observer (Fig. 1b). To prevent a 'collision' between the simulated plane and the observer, the formula that determined the movement of the fronto-parallel plane toward the observer caused the simulated fronto-parallel plane to exponentially slow down in the expanding conditions. This does not affect

[1] A separate set of 8 observers were used for stimulus validation (see Table 1).

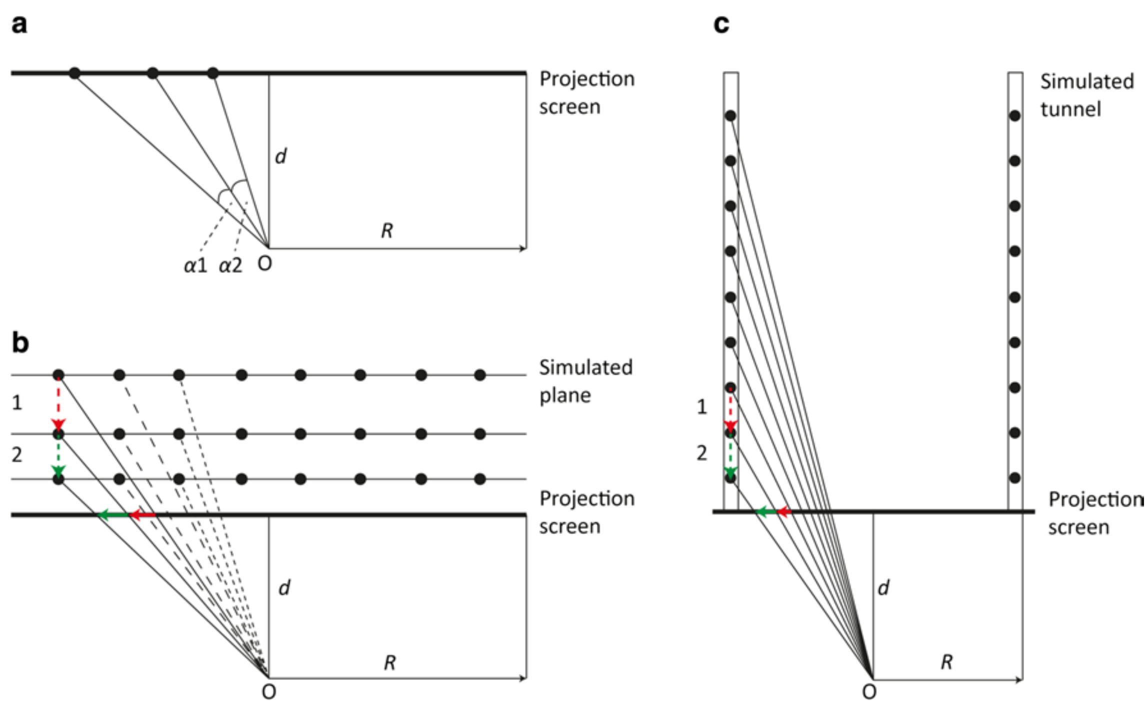

Fig. 1 Schematic *top view* of the speed gradients of the optic flow stimuli used in the experiment. The observer is at O. *d* Is the distance between the participant and the projection screen. *R* is the radius of the optic flow stimulus. **a** Optic flow containing a constant angular speed (single-speed). The absolute speed of a dot increases with eccentricity to maintain a constant angular displacement (α1, α2). **b** Optic flow with a linear speed gradient, simulating motion of a fronto-parallel plane toward the observer. The simulated motion of the plane (*dashed red* and *green arrow*) is exponentially slowed down toward the participant resulting in a smaller dot displacement (*solid red* and *green arrow*) on the projection screen in the first frame (*red*) than at the second frame (*green*). Dot displacements of two other dots are indicated with *dashed black lines*. **c** Optic flow with a quadratic speed gradient simulates observer movement through a circular tunnel. For each frame (1,2), the simulated motion of the dots composing the tunnel remains constant (*dashed red* and *green arrow*). On the projection screen, however, the dot displacement (*solid red* and *green arrow*) of a dot that is simulated to be close to the participant (*green*) is larger than a dot that is simulated to be further away from the participant (*red*). Dot displacements of other dots are indicated with *solid black lines* (color figure online)

the translational speed of the dots on the projection screen since as the simulated plane moves closer to the observer, small movements of the simulated plane are sufficient to generate high translational speeds on the projection screen. In contracting conditions, the movement velocity of the plane increased exponentially and simulated motion of the plane away from the observer.

The third optic flow pattern contained a *quadratic speed gradient*, is perceived as rigid (see Table 1) and simulates observer movement through a circular tunnel (see Online Resource 3). The visual percept of a circular tunnel is created by a quadratic acceleration of the dots from the inside to the outside of the stimulus (Fig. 1c).

Optic flow speed Four optic flow speeds were used in the experiment. Single-speed optic flow contained a constant angular speed of 6, 12, 24 or 48 deg/s.[2] For optic flow containing a speed gradient, the speed varies from center to periphery. The speed gradient curve of these optic flow stimuli is equal to the selected speeds only at a single eccentricity. To keep the eccentricity where the speed of the speed gradient curve (linear or quadratic speed gradient) was equivalent to 6, 12, 24 or 48 deg/s identical across speed conditions, we calculated the integral under the speed gradient curve (linear or quadratic) and divided it by two. The eccentricity corresponding to the outcome of this calculation (half the integral) was chosen to be identical for the selected speeds. Changing the input speed will shift the speed gradient curve up or down, but the curve itself does not change. A selected speed was therefore always at the same eccentricity of the optic flow stimulus containing a particular speed gradient (Fig. 2).

Procedure

Observers stood in a completely darkened room on a forceplate that was covered with foam. Debriefing revealed that the observers were unaware of standing on a forceplate.

[2] For stimulus validation, only two speeds (6 and 24 deg/s) were used.

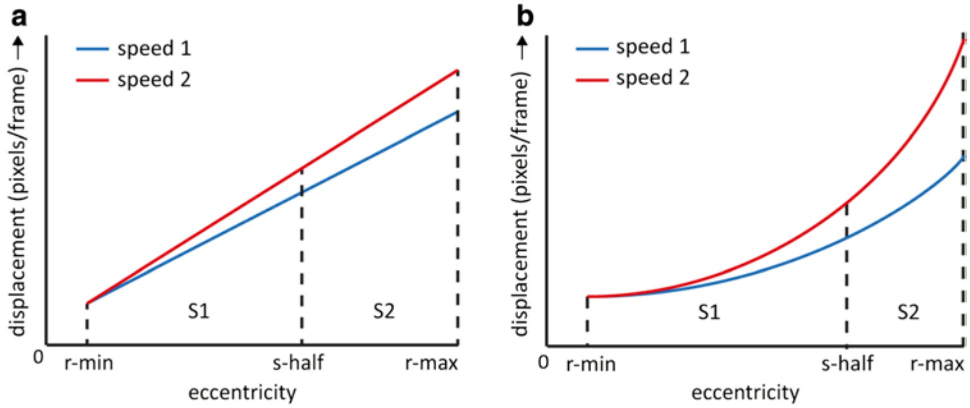

Fig. 2 Schematic illustration of the speed *curves* of a linear (**a**) and quadratic (**b**) speed gradient. The dot displacement in pixels/frame is plotted against the eccentricity of the optic flow stimulus. The integral was calculated between the minimal radius (*r*-min) and the maximal radius (*r*-max) of the flow stimulus. The eccentricity where the integral is half (*s*-half) of the total integral (S1 + S2) was determined. The dot speed belonging to the eccentricity *s*-half was chosen to be equal to one of the selected speeds (6, 12, 24 and 48 deg/s). Increasing the dot speed causes the *speed gradient curve* to shift but *s*-half remains at the same eccentricity

Observers were asked to stand with their feet approximately shoulder width apart, keep their weight equally distributed between their feet and hold their arms at their sides. Optic flow patterns were presented in a pseudo-random order for 4 s, and observers were instructed to fixate on the middle of the black circle at the center of the stimulus. In total, 24 optic flow conditions (3 flow types, 4 flow speeds and 2 directions) were used in the experiment. Optic flow stimuli were interleaved by dynamic visual noise patterns with a random duration between 3.4 and 4.2 s. Dynamic noise patterns were similar to the optic flow patterns, except that the dots were randomly replaced every frame. Noise patterns also contained a fixation dot with a diameter of 0.30° at the center of the screen. To prevent observers from being actively aware of their posture, they had to perform a memory task. The color of the fixation dot could randomly vary between red, green, yellow and blue. Observers were told to fixate on the fixation dot and count how often they had observed the fixation dot to be of a particular color during each block of 24 conditions. After finishing the block, observers reported the number to the experimenter in the room. Observers had to perform 20 blocks of about 205 s, and after every block, they could take a short break (~2 min) and after 4 blocks a longer break (~5 min). During longer breaks, observers were allowed to leave the room.

Analysis

After downsampling the data from the forceplate to 125 Hz, the center of pressure (COP) in the anterior–posterior direction was calculated. To remove measurement noise, COP data were filtered with a low-pass fourth-order Butterworth filter with a cutoff frequency of 10 Hz. To be able to calculate the COP deviation per trial, COP at stimulus onset served as baseline. For the total duration of the stimulus and the minimal duration of dynamic noise (4 + 3.4 s), COP deviation from baseline was determined. For each trial, we checked for outliers using the procedure of Wei et al. (2010); no trial had to be discarded from the analysis. For each observer, the COP deviation from baseline was averaged over 20 trials per condition. The area under the curve between 1 and 4 s after stimulus onset was subsequently calculated for each condition and was used as a measure of sway magnitude. We also calculated the area under the curve of the first second after stimulus onset (initial stimulus onset sway) and the first second of dynamic noise (initial noise onset sway). For the calculation of the initial noise onset sway, the COP at the onset of dynamic noise served as baseline.

Statistics To examine postural sway differences between conditions, separate repeated measures analyses of variance (ANOVAs) were performed on the area under the curve of all observers between 1 and 4 s after stimulus onset, the initial stimulus onset sway and the initial noise onset sway. A factorial design was used, involving the within-subject factors motion direction (2 levels: expansion and contraction), the speed gradient of the optic flow stimulus (3 levels: single-speed optic flow; optic flow with a linear speed gradient; and optic flow with a quadratic speed gradient) and optic flow velocity (4 levels: 6, 12, 24 and 48 deg/s). Partial eta squared (η_p^2) was used to report effect sizes for main and interaction effects. In case the assumption of sphericity was violated, the number of the degrees of freedom was adjusted using the Greenhouse–Geisser method. Pairwise comparisons with a Sidak correction were used to compare main effects and examine significant differences between conditions.

Results

Stimulus validation

The percentage of trials that a particular optic flow type (linear or quadratic speed gradient) was perceived as (more) rigid or inducing more self-motion than another optic flow type (single-speed or linear speed gradient) is shown in Table 1.

It is immediately apparent that for both motion directions, single-speed optic flow was perceived as less rigid than an optic flow pattern containing a linear ($t(7) > 17.58$, $p < 0.001$, for all comparisons) or quadratic speed gradient ($t(7) > 13.00$, $p < 0.001$, for all comparisons). The perceived rigidity of a linear and a quadratic stimulus was approximately equal ($t(7) > 0.14$, $p < 0.89$, for all comparisons), but the quadratic speed gradient optic flow stimulus induced a stronger sensation of self-motion ($t > 3.44$, $p < 0.030$, for all comparisons). Interestingly, in contrast to the results of Bubka et al. (2008), expanding optic flow (quadratic speed gradient) did not induce a weaker sensation of self-motion than contracting optic flow ($t(5) = -1.79$, $p = 0.13$).

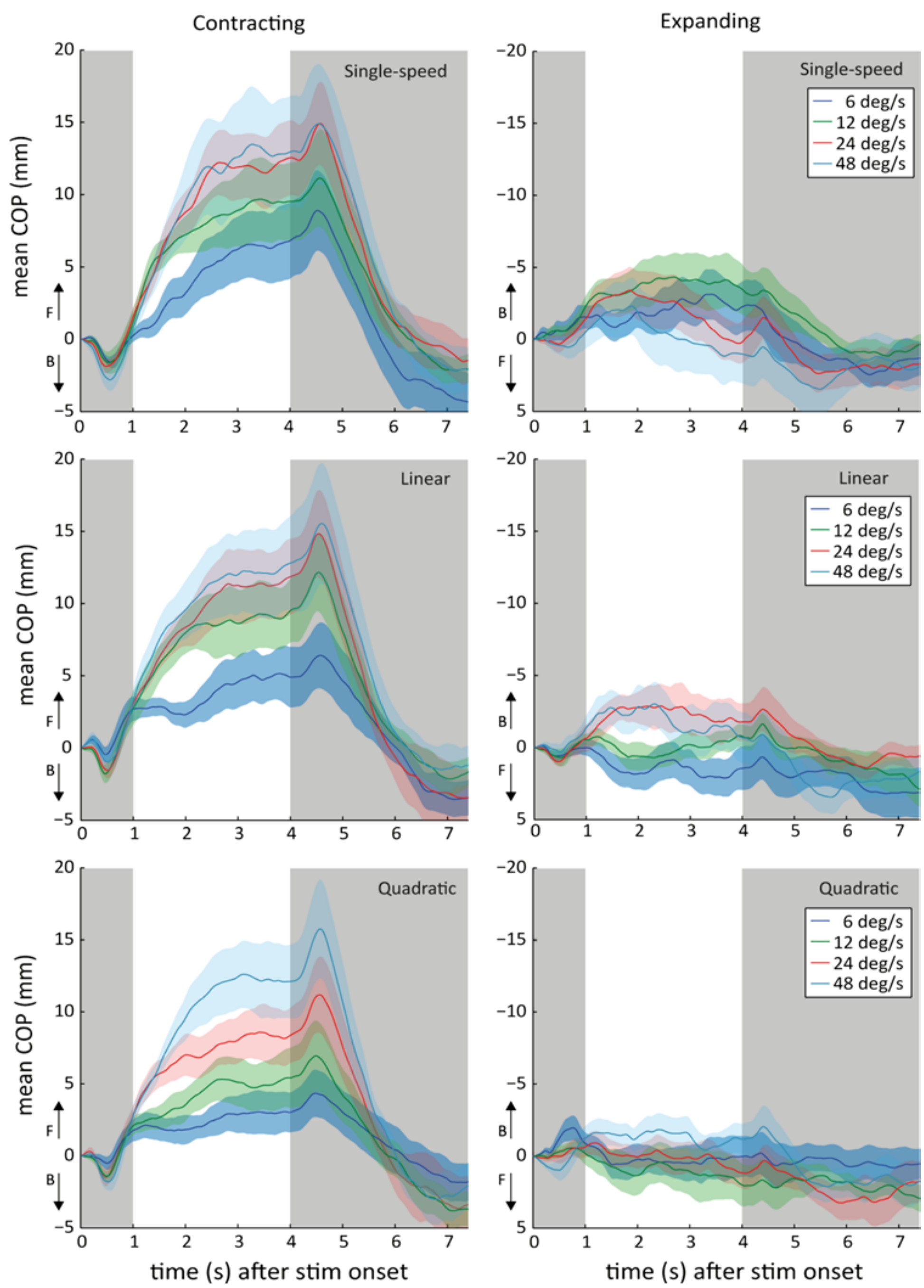

Fig. 3 Mean center of pressure (COP) trajectories averaged across all observers for different optic flow conditions and velocities (6, 12, 24 and 48 deg/s). The *colored regions* represent the standard error of the mean and the *bold lines* the mean across trials of one condition. Dynamic noise was presented 4 s after stimulus onset. Positive COP values represent forward (*F*) sway, whereas negative values correspond to backward (*B*) sway. COP trajectories in the gray regions represent the postural sway in the first second after stimulus onset and during dynamic noise presentation (color figure online)

In fact, on average in 69 % of the trials, expanding optic flow induced more self-motion than contracting optic flow.

In Fig. 3, the mean center of pressure (COP) deviation from baseline of all observers is plotted against the time after stimulus onset. COP trajectories for contracting optic flow stimuli are depicted in the left column, whereas COP trajectories for expanding optic flow stimuli are presented in the right column.

The integral of the COP deviation from baseline between 1 and 4 s after stimulus onset is shown in Fig. 4. We initially examined the observed postural sway for each of the three speed gradients (2) and the four optic flow speeds (3). Based on these results, we also analyzed the postural sway for each of the two optic flow directions (4).

Speed gradient of optic flow stimuli

Three different speed gradients were used in the experiment (single-speed, linear speed gradient and quadratic speed gradient). In Fig. 3, each row represents a different speed gradient. In general, decreasing the speed gradient (smaller absolute dot speed difference between center and periphery) of the optic flow stimulus causes more postural sway (mean integral at single-speed optic flow = 14.3, linear speed gradient = 12.0 and quadratic speed gradient = 8.4). This is also demonstrated by a significant main effect of the speed gradient of the optic flow stimulus on the amount of postural sway ($F(2,20) = 4.73$, $p < 0.045$, $\eta_p^2 = 0.32$). In addition, a significant interaction effect between the speed gradient and the speed of the optic flow stimulus was observed ($F(6,60) = 2.44$, $p < 0.005$, $\eta_p^2 = 0.28$). Further analyses of the results indicated that this interaction is likely to be caused by postural sway in the expanding conditions, since the interaction effect was only significant in this motion direction ($F(6,60) = 4.25$, $p < 0.005$, $\eta_p^2 = 0.30$). Considering contracting optic flow only, there is an effect of the speed gradient on the amount of postural sway ($F(2,20) = 4.95$, $p < 0.02$, $\eta_p^2 = 0.33$) and more sway is generated by an optic flow stimulus with a linear speed gradient than an optic flow stimulus containing a quadratic speed gradient ($p < 0.015$).

Directly after stimulus onset (0–0.5 s), the observed postural sway is mainly in the same direction as the simulated motion direction of the optic flow stimulus (i.e. backward sway at a contracting optic flow stimulus, see Fig. 3). At about one second after stimulus onset, the COP deviation has returned to baseline. The amount of postural sway in this period (0–1 s after stimulus onset) depends on the speed gradient and the motion direction of the optic flow stimulus, as is indicated by a significant interaction effect between these two factors ($F(2,20) = 5.95$, $p < 0.01$, $\eta_p^2 = 0.37$). More specifically, only for contracting optic flow, the speed gradient influences the amount of postural sway as is indicated by a significant main effect of the speed gradient on postural sway ($F(2,20) = 7.61$, $p < 0.005$, $\eta_p^2 = 0.43$), with more sway occurring at single-speed optic flow than at an optic flow stimulus containing a linear speed gradient ($p < 0.01$).

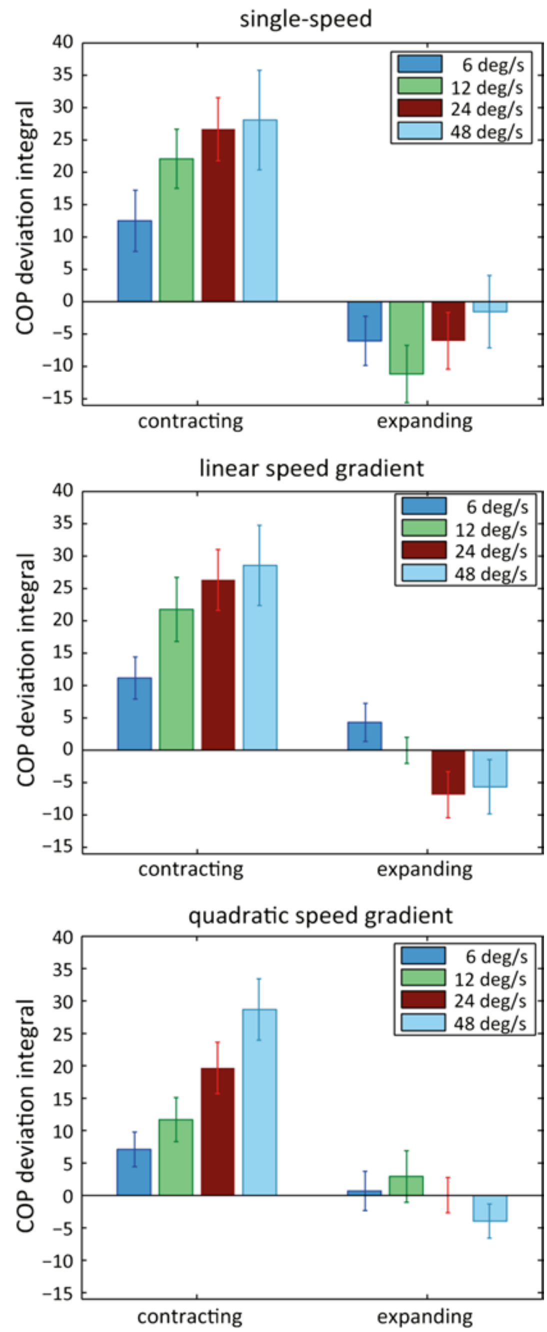

Fig. 4 COP deviation integral (area under the COP trajectories (Fig. 3) between 1 and 4 s after stimulus onset) for different speed gradients and optic flow speeds. A positive integral corresponds to forward postural sway, whereas a negative integral represent to backward sway. *Error bars* represent the standard error of the mean

Optic flow speed

We used four optic flow speeds in the experiment (6, 12, 24 and 48 deg/s). For the speed range we used, changing optic flow speed influenced the amount of postural sway (Figs. 3, 4) as is indicated by a significant main effect of optic flow speed on postural sway ($F(3, 30) = 6.97$, $p < 0.01$, $\eta_p^2 = 0.41$). Pairwise comparisons showed that this effect was mainly induced by a significant difference between an optic flow speed of 6 and 24 deg/s ($p < 0.03$). Separately analyzing postural sway induced by contracting and expanding optic flow stimuli revealed only for contracting optic flow stimuli a significant main effect of optic flow speed on postural sway ($F(3, 30) = 14.38$, $p < 0.001$, $\eta_p^2 = 0.59$). That is, for contracting optic flow stimuli, the amount of postural sway increases with increasing optic flow speed. Pairwise comparisons showed for contracting optic flow significant differences in postural sway between optic flow speeds of 6 and 12 deg/s ($p < 0.045$), 6 and 24 deg/s ($p < 0.005$) and 6 and 48 deg/s ($p < 0.01$). For contracting single-speed optic flow and optic flow with a linear speed gradient, COP deviation from baseline is almost equal for an optic flow speed of 24 and 48 deg/s (Fig. 3). The difference in postural sway between these two speeds is larger at a contracting optic flow stimulus with a quadratic speed gradient. Contrary to contracting optic flow, statistical effects between optic flow speed and the postural sway amplitude were absent for expanding optic flow. This direction-dependent effect of optic flow speed on postural sway may have caused the significant interaction effect between motion direction and optic flow speed ($F(3, 30) = 10.22$, $p < 0.001$, $\eta_p^2 = 0.51$).

Simulated motion direction

Two optic flow directions were presented in the experiment. Contracting optic flow stimuli induced more postural sway than expanding optic flow stimuli, as is demonstrated by a significant main effect of simulated motion direction on postural sway ($F(1,10) = 40.23$, $p < 0.001$, $\eta_p^2 = 0.80$). Presenting a contracting optic flow stimulus to observers initially resulted in a negative shift of the COP compared to baseline, indicating a backward movement of the observer (Fig. 3). After this initial movement, COP started to increase until it flattened toward the end of stimulus presentation, indicating that observers moved forward and maintained this position until the onset of dynamic noise at 4 s. For contracting optic flow, the first second of dynamic noise caused the COP to increase more than for expanding optic flow as is indicated by a significant main effect between direction and postural sway ($F(1,10) = 18.44$, $p < 0.005$, $\eta_p^2 = 0.65$). The increase in COP was followed by a decrease in COP below baseline. This indicates that during dynamic noise presentation, observers returned to the starting position but overcompensated for the disappearance of the optic flow stimulus. Overall, the expanding optic flow stimuli resulted in a COP trajectory (i.e. a backward movement) opposite to that observed for the contracting conditions.

Experiment 2

In the first experiment, we observed an anisotropy in postural sway between expanding and contracting optic flow. Since it is plausible that expanding optic flow is encountered more often in our natural environment, one might argue that observers may be more proficient in compensating for this type of stimulus. A possible mechanism to compensate might be anticipatory co-contraction of the lower leg muscles during expanding optic flow. In the second experiment, we examined whether the observed anisotropy could be explained by such a mechanism.

Methods

The methods of experiment 2 are identical to experiment 1 except for the specific differences mentioned below.

In a new set of 10 observers, lower leg muscle activity was measured during optic flow presentation while simultaneously measuring their postural sway. The optic flow pattern contained a constant angular speed (single-speed optic flow), and in total, 4 optic flow conditions were used: 2 speeds (12 or 24 deg/s) and 2 directions (contracting or expanding). Observers did not have to perform a memory task during the experiment.

Electromyography (EMG) was recorded from the antagonist right lower leg muscles *tibialis anterior (tib)* and *gastrocnemius (gast)*. The activity of these muscles was determined by calculating the root mean square (RMS) of the EMG signal (RMS–EMG) with a window length of 7.8 ms. The integral of the RMS–EMG signal of each muscle was calculated per condition. Then, the muscle activity contrast, which was used as an indication of the co-contraction magnitude, was calculated for each condition. It was determined by calculating the Michelson contrast between the RMS–EMG integral of the *gastrocnemius* and the *tibialis anterior*.

Results

In line with the results of experiment 1, contracting optic flow stimuli induced more postural sway than expanding optic flow (Fig. 5), as is demonstrated by a significant main effect of simulated motion direction on postural sway ($F(1,9) = 17.12$, $p < 0.005$, $\eta_p^2 = 0.66$).

Concerning the muscle activity (Fig. 6), the *gastrocnemius* was more active than the *tibialis anterior* in

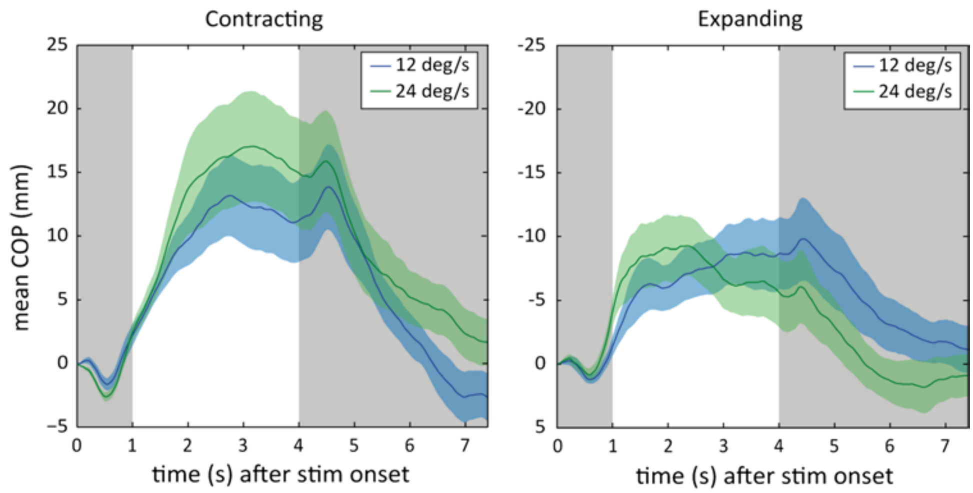

Fig. 5 Mean COP trajectories averaged across all observers for different optic flow directions and speeds (12, 24 deg/s). The *colored regions* represent the standard error of the mean and the *bold lines* the mean across trials. Dynamic noise was presented 4 s after stimulus onset. Positive COP values represent forward sway, whereas negative values correspond to backward sway. COP trajectories in the *gray regions* represent the postural sway in the first second after stimulus onset and during dynamic noise presentation (color figure online)

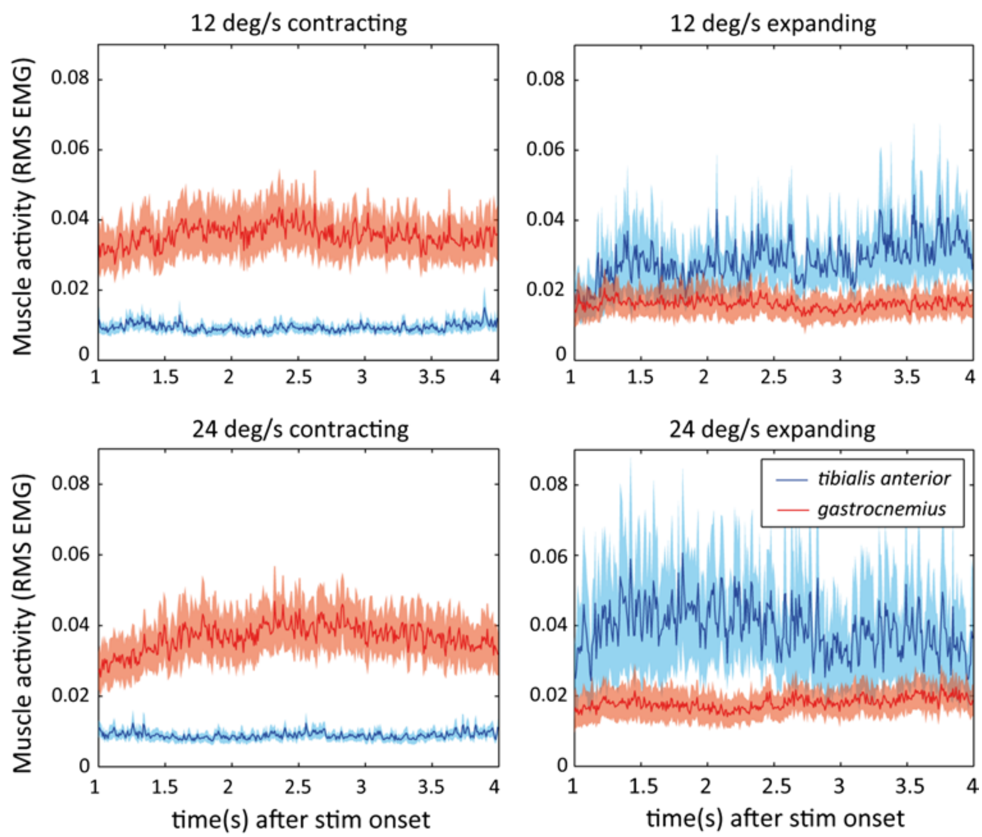

Fig. 6 Muscle activity (RMS EMG) of the *tibialis anterior* and the *gastrocnemius* between 1 and 4 s after stimulus onset averaged over all observers for different optic flow directions and speeds (12, 24 deg/s). The *colored regions* represent the standard error of the mean and the *bold lines* the mean across trials (color figure online)

contracting conditions ($t(19) = -6.78$, $p < 0.001$), whereas the recorded muscle activity of the *tibialis anterior* appeared higher in expanding conditions (as this difference approached significance $t(19) = 2.08$, $p = 0.051$).

In Fig. 7, the integral of the COP deviation from baseline between 1 and 4 s after stimulus onset is plotted against the muscle activity contrast. If more co-contraction of the right lower leg would occur at expanding optic flow, the muscle activity contrast should differ between expanding and contracting optic flow patterns. However, there is no significant influence of the motion direction of the optic flow stimulus on the muscle activity contrast ($t(1) = -7.76$, $p = 0.08$). Furthermore, there is also no significant effect of optic flow speed on the muscle activity contrast ($t(1) = -1.71$, $p = 0.34$).

Since no significant effect of optic flow direction on the muscle activity contrast was found, we questioned whether the lower leg muscles were activated earlier after stimulus

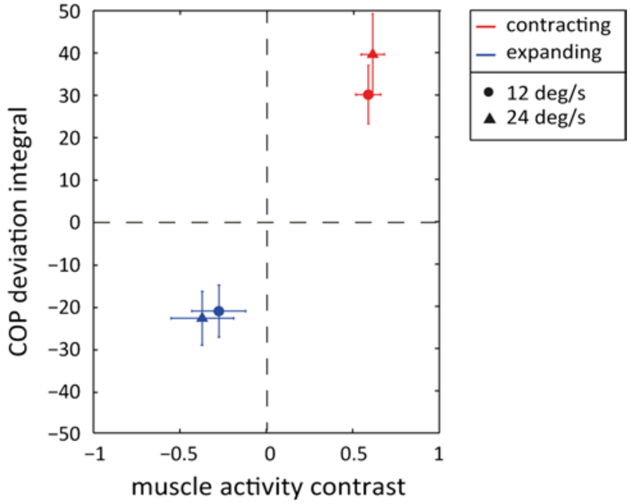

Fig. 7 COP deviation integral and corresponding muscle activity contrast (*gast-tib*/*gast* + *tib*) for different optic flow speeds and directions. A *positive* contrast indicates higher activity of the *gastrocnemius,* whereas a *negative* contrast indicates higher activity of the *tibialis anterior*. A *positive* COP deviation integral corresponds to forward postural sway, whereas a *negative* integral represents backward sway. *Error bars* represent the standard error of the mean

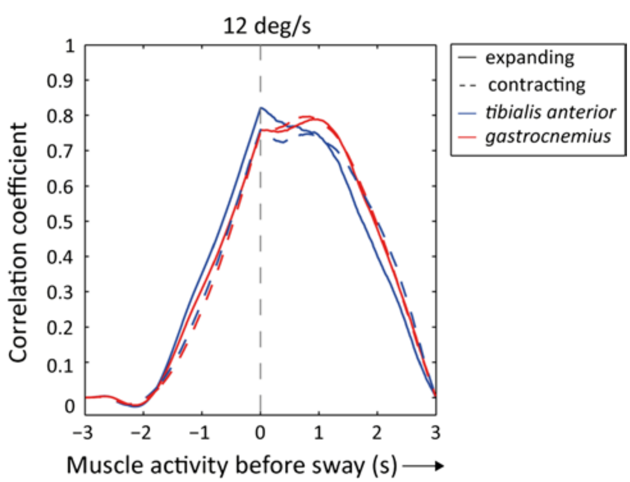

Fig. 8 Cross-correlation between postural sway and the corresponding muscle activity (between 1 and 4 s after stimulus onset) of the *tibialis anterior* or the *gastrocnemius* for an optic flow speed of 12 deg/s. A positive muscle activity before sway indicates that an increase in muscle activity precedes postural sway. Similar results were found for a speed of 24 deg/s

onset for expanding optic flow patterns than for contracting optic flow. If this were to be the case, then the observed anisotropy in postural sway might be caused by anticipatory activation of the lower leg muscles for the expanding optic flow conditions. A cross-correlation between the amount of postural sway and the recorded muscle activity (Fig. 8) showed that there is no difference in anticipatory activation of the lower leg muscles between expanding and contracting optic flow, since the duration that lower leg activity precedes postural sway does not differ between expanding and contracting conditions ($t(3) = -0.89$, $p = 0.44$).

General discussion

Speed gradient of optic flow stimuli

The main goal of this study was to investigate whether varying the speed gradient, and as such the perceived rigidity, of an optic flow stimulus affects postural sway. We expected that optic flow stimuli that are perceived as rigid would generate more postural sway, since it is likely that they are more common in the natural environment and provide a stronger sensation of self-motion than non-rigid optic flow stimuli (Nakamura 2010). The results presented in Table 1 show that a single-speed stimulus is perceived as less rigid and induces a weaker sensation of self-motion than an optic flow stimulus containing a linear or quadratic speed gradient. The perceived rigidity of a linear and a quadratic stimulus was approximately equal and would according to Nakamura (2010) induce a similar sensation of self-motion. However, the quadratic speed gradient optic flow stimulus induced a stronger sensation of self-motion. Therefore, the perceived rigidity does not in all conditions correlate with the strength of self-motion perception. This is in accordance with the findings of Palmisano et al. (2012) who demonstrated that more rigid optic flow stimuli do not under all viewing conditions produce a stronger sensation of self-motion.

Contrary to our expectation, the current results show that most postural sway is induced by the non-rigid optic flow pattern with dots moving at a single-speed and that postural sway decreases when the optic flow pattern contains a linear or quadratic speed gradient. One could argue that the dot speed at, for instance, the central part of the stimulus (e.g. 5°–10°) can explain the results, since the dot speed at the central region is the highest for single-speed optic flow and the lowest for a quadratic speed gradient. However, the average dot speed at this central (or arbitrary other) region is not (linearly) related to the observed postural sway.

For instance, a slow average dot speed at the center (e.g. contracting optic flow, 48 deg/s quadratic speed gradient or 24 deg/s linear speed gradient) generated more postural sway than a faster central average dot speed (e.g. the single speed 12 deg/s condition; see ellipse in Fig. 9). The same holds for the average dot speed at a larger central region (5°–20°, or about half of the total radius) and also the periphery (33°–43°) of the optic flow pattern. Hence, the average dot speed at a particular region of the stimulus does not explain why most postural sway is induced by a single-speed optic flow pattern.

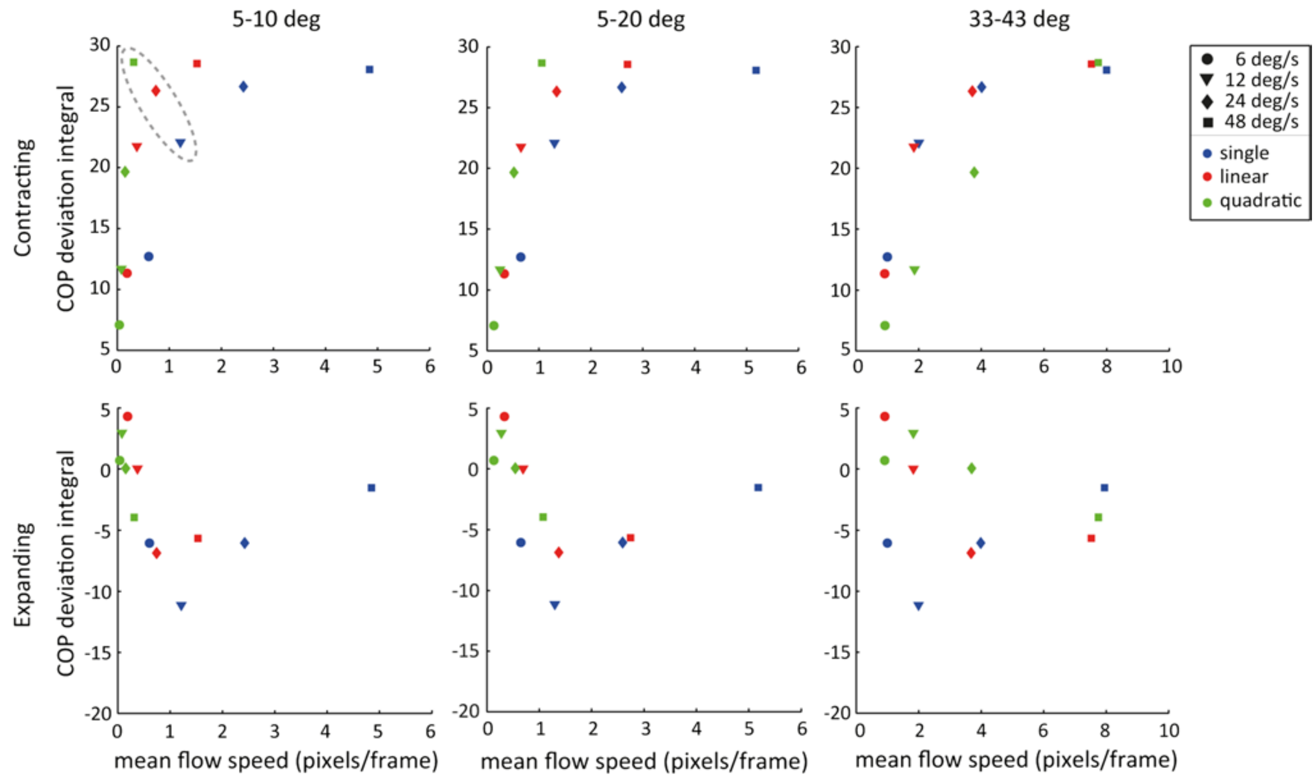

Fig. 9 COP deviation integral of contracting (*top*) and expanding (*bottom*) optic flow (area under the COP trajectories (Fig. 3) between 1 and 4 s after stimulus onset) plotted against the mean optic flow speed (pixels/frame) for different conditions and eccentricities (5°–10°, 5°–20°, 33°–43°). The speed gradient (single, linear and quadratic) of the optic flow stimuli is represented with colors and the speed with different symbols. The *ellipse* at the *top left panel* denotes the conditions that are discussed in the text (color figure online)

Considering the results from a more ecological perspective may provide an explanation. Single-speed optic flow patterns do not generate a three-dimensional rigid percept (De Bruyn and Orban 1990) and are rarely encountered when an observer moves through the environment. On the other hand, optic flow stimuli with a linear or quadratic speed gradient generate a stronger sensation of self-motion, are perceived as rigid and are probably more frequent in the natural environment. Visual information is known to be complemented by non-visual information from the sensorimotor systems (Peterka and Benolken 1995). Since less postural sway was observed for rigid optic flow stimuli inducing a strong sensation of self-motion, it seems plausible that interactions between the visual and sensorimotor systems are tailored toward compensating for these (rigid) optic flow stimuli. The less frequent single-speed optic flow may induce this compensatory mechanism to a lesser extent and increased postural sway will be the result. Though speculative, this is in line with explanations based on the exposure history of a stimulus, which have been used previously by Bubka et al. (2008) to explain why contracting optic flow patterns induce a stronger vection magnitude than expanding flow. Incoming sensory information is compared with that of the past, called exposure history (Held 1961). In the natural environment, sensory information will rarely differ from the individual's exposure history. If we assume that observers more often perceive optic flow patterns with a speed gradient than without a speed gradient, their exposure history is obviously stronger for these types of optic flow. As a result, exposure to an optic flow stimulus containing a speed gradient but without the corresponding non-visual input will cause a greater inconsistency with the exposure history than optic flow without a speed gradient. This detected inconsistency may induce a compensatory mechanism inhibiting postural sway and will be stronger for an optic flow pattern with a speed gradient. Encountering optic flow without a speed gradient will probably result in a weaker inconsistency with the exposure history and less compensation occurs. This leads to more postural sway when confronted with a single-speed optic flow pattern.

Optic flow speed

We varied the speed of the expanding and contracting optic flow patterns to investigate whether optic flow speed affected postural sway, as has been demonstrated by other studies (Lestienne et al. 1977; Wei et al. 2010). We expected postural sway magnitude to increase with higher optic flow speeds, until a saturation level. When contracting optic flow is considered, the amount of postural sway increased with increasing flow speed. For an optic flow pattern containing a single-speed or a linear speed gradient, this increase indeed appeared to saturate at the higher flow speeds used (24 and 48 deg/s). We did not observe a decrease in sway amplitude at our highest speeds, yet we cannot rule out the possibility that even higher optic flow speeds might have resulted in such a decrease, as demonstrated by earlier research (Lestienne et al. 1977; Wei et al. 2010). However, in these studies, the decrease already occurred at optic flow speeds of 24 deg/s, while at our study, no decline occurred even at 48 deg/s. Future studies will have to elucidate this saturation and decline further. Although we do find a clear effect of optic flow speed on postural sway for contracting optic flow, for expanding flow, the sway amplitude appears to be much less dependent on optic flow speed. This is in agreement with Wei et al. (2010). For expanding optic flow stimuli, they only observed an effect of optic flow speed on postural sway when comparing the 40 deg/s condition with the 80 deg/s condition. We cannot compare the result of our two highest speeds with their result, since we have not used such a high optic flow speed in our experiment.

Optic flow direction

Our results show that contracting radial optic flow patterns generated more postural sway than expanding patterns, irrespective of the speed gradient in the optic flow stimulus. This asymmetry has been reported in several other studies as well (Lestienne et al. 1977; Palmisano et al. 2009; Wei et al. 2010). An explanation for this asymmetry in postural sway might be that observers are more sensitive in the detection of contracting optic flow patterns, since findings of previous studies have shown that observers have a lower detection threshold for contracting than for expanding optic flow patterns (Edwards and Badcock 1993; Edwards and Ibbotson 2007; Shirai et al. 2009). A higher sensitivity for contracting optic flow seems to contradict the findings of Schiff et al. (1962) who discovered that monkeys show more avoidance responses to a looming (expanding) stimulus than to a contracting stimulus. However, the stimulus used by Schiff et al. (1962) increased in size to simulate expanding motion while in the current study the stimulus size did not change. Besides a difference in sensitivity, the induced sensation of self-motion might account for some of the observed anisotropy in postural sway. Results of our stimulus validation experiment showed that in 69 % of the trials, an expanding optic flow pattern containing a quadratic speed gradient induced more self-motion than a contracting pattern. This is in line with the above reasoning that stimuli generating a stronger sensation of self-motion induce a compensatory mechanism, that is, inhibit postural sway to a larger extent than stimuli that produce a weaker sensation of self-motion.

Another explanation for the observed anisotropy in postural sway that has been advocated is that it is caused by the biomechanics of the foot (Lestienne et al. 1977; Palmisano et al. 2009). Our feet project forward and the anatomical asymmetry of the foot causes most of the base of support to be anterior of the center of rotation (Eklund and Lofstedt 1970). As a result, humans can sway forward at a greater angle without losing balance compared to backward sway. This might explain why the amplitude of forward sway, produced by contracting optic flow, was larger than the amplitude of backward sway. In order to scrutinize this explanation, we calculated for each motion direction (expansion/contraction) the percentage of observed sway compared to the maximum sway without losing balance. After this normalization procedure, postural sway during contracting optic flow was still larger than during expanding flow stimuli. As a consequence, this result indicates that the anatomical asymmetry of the foot does not (fully) account for the observed anisotropy in postural sway.

Our results show that the anisotropy in postural sway between expanding and contracting optic flow is also not caused by anticipatory co-contraction of the lower leg muscles during expanding optic flow. Although we did not observe co-contraction during expanding or contracting optic flow, the observed anisotropy might still be reflected in the muscle activity of other body parts. If observers predominantly make anticipatory upper body movements, the COP differentiates from baseline but no co-contraction occurs in the muscles of the lower leg. Although this may explain our current results, the resolve will have to wait for future research. The observed anisotropy in postural sway can also be explained using the earlier mentioned exposure history, since it is plausible that expanding optic flow is encountered more often in the natural environment than contracting optic flow. A contracting optic flow stimulus will therefore cause a weaker inconsistency with the exposure history and generate more postural sway than an expanding optic flow pattern.

In conclusion, this study shows that the speed gradient and therefore the perceived rigidity of an optic flow pattern influences the magnitude of postural sway. In contrast to our expectation that most postural sway would be induced by optic flow patterns that are perceived as rigid and provide the strongest sensation of self-motion, most postural sway was generated by a non-rigid single-speed optic flow stimulus inducing the weakest sensation of self-motion. In addition we demonstrated that the observed anisotropy in postural sway (for contracting vs. expanding patterns) is not caused by anticipatory co-contraction of lower leg muscles, since the muscle activity contrast does not differ significantly between expanding and contracting optic flow. All in all, the current study supports the view that visual and sensorimotor systems appear to be tailored toward compensating for rigid optic flow stimulation providing the strongest sensation of self-motion.

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