

Visual directional anisotropy does not mirror the directional anisotropy apparent in postural sway

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Abstract. Presenting a large optic flow pattern to observers is likely to cause postural sway. However, directional anisotropies have been reported, in that contracting optic flow induces more postural sway than expanding optic flow. Recently, we showed that the biomechanics of the lower leg cannot account for this anisotropy (Holten, Donker, Verstraten, & van der Smagt, 2013, *Experimental Brain Research*, **228**, 117–129). The question we address in the current study is whether differences in visual processing of optic flow directions, in particular the perceptual strength of these directions, mirrors the anisotropy apparent in postural sway. That is, can contracting optic flow be considered to be a perceptually stronger visual stimulus than expanding optic flow? In the current study we use a breaking continuous flash suppression paradigm where we assume that perceptually stronger visual stimuli will break the flash suppression earlier, making the suppressed optic flow stimulus visible sooner. Surprisingly, our results show the opposite, in that expanding optic flow is detected earlier than contracting optic flow.

Keywords: vision, optic flow, continuous flash suppression, postural sway

1 Introduction

Visual stimuli simulating self-motion through the environment can induce postural adjustments in observers. Many studies have shown that contracting optic flow patterns produce more postural sway than expanding optic flow stimuli (eg Holten, Donker, Verstraten, & van der Smagt, 2013; Lestienne, Soechting, & Berthoz, 1977; Palmisano, Pinniger, Ash, & Steele, 2009; Wei, Stevenson, & Kording, 2010). We have previously demonstrated that this anisotropy is not caused by biomechanical properties of the lower leg (Holten et al., 2013). Another likely candidate for this anisotropy is the visual system.

Recently, we showed that a motion aftereffect (MAE) caused postural sway in the direction of the perceived MAE (Holten, van der Smagt, Donker, & Verstraten, 2014). When no MAE was reported, no postural sway occurred. Therefore, the internal neural signal responsible for the MAE appears to induce postural sway. It is therefore expected that modulating the strength of this internal neural signal affects the magnitude of postural sway. Manipulating the optical flow structure, or its speed (Holten et al., 2013; Lestienne et al., 1977; Wei et al., 2010), or increasing the size (Lestienne et al., 1977) of a visual stimulus indeed affects the amount of postural sway.

Given the anisotropy in sway magnitude, it is tempting to assume that the *perceptual strength*⁽¹⁾ (eg sensitivity to, conspicuity of, bias towards) of expanding and contracting optic flow differs in that a contracting optic flow stimulus is a stronger inducer than an expanding optic flow stimulus. Some psychophysical studies seem to support this idea. For example, the threshold for detecting contracting optic flow is lower than for expanding optic flow

⁽¹⁾Note that perceptual strength is not synonymous with stimulus strength. We are agnostic as to what causes the difference in perceptual strength. It can be either a difference in sensitivity or conspicuity between stimuli or a bias towards one of the stimuli.

(Edwards & Badcock, 1993; Edwards & Ibbotson, 2007; Raymond, 1994). Developmental studies showed that preferential differences to optic flow directions are already present in 3-month-old infants (Shirai, Kanazawa, & Yamaguchi, 2006, 2008), although the direction of the anisotropy was not conclusive. In one study (Shirai et al., 2006) 3-month-old infants were sensitive to contracting optic flow but not to expanding optic flow patterns. In the other study (Shirai et al., 2008) 3-month-old infants showed an expansion bias at low speeds and no bias between optic flow directions at higher speeds. Studies presenting expanding optic flow to one eye and contracting optic flow to the other eye (resulting in binocular rivalry) reported longer dominance durations for the expanding compared with the contracting optic flow stimulus (Malek, Mendoza-Halliday, & Martinez-Trujillo, 2012; Parker & Alais, 2007). This suggests a greater sensitivity to expansion. Although this result is not in line with our assumption, it is known that mutual interactions related to the relative feature content of the competing images affect binocular rivalry (Stuit, Cass, Paffen, & Alais, 2009; Stuit, Paffen, van der Smagt, & Verstraten, 2011). Such interactions could in turn affect the relative sensitivity to expanding and contracting optic flow, complicating the interpretation of the data.

In the current study we examine the perceptual strength of expanding and contracting optic flow. We determine whether an asymmetry in perceptual strength between radial optic flow directions is similar to the directional asymmetry apparent in postural sway. If this is the case, the perceptual strength of a radial optic flow stimulus could be an explanation for the directional anisotropy in postural sway. We use breaking continuous flash suppression (b-CFS) to test the perceptual strength of expanding and contracting optic flow. During b-CFS, a stimulus presented to one eye is temporarily suppressed by a dynamic stimulus (mask) that is presented to the other eye. The advantage of using b-CFS compared with binocular rivalry is that, by using a b-CFS paradigm, the perceptual strength of expanding and contracting optic flow can be examined in isolation without the occurrence of mutual interactions between these two flow directions. The perceptual strength of a stimulus influences its suppression duration as perceptually stronger stimuli, such as higher contrast stimuli (Tsuchiya & Koch, 2005) or stimuli containing coherent motion compared with incoherent motion (Kaunitz, Fracasso, Lingnau, & Melcher, 2013), are known to break through CFS more readily. As a consequence, we expect that if contracting optic flow is a perceptually stronger visual stimulus than expanding optic flow, it will break suppression earlier than expanding optic flow. In three experiments, we investigated whether this is the case.

2 Experiment 1

In the first experiment we investigated whether there was a difference in the perceptual strength of expanding and contracting optic flow. Observers had to report the motion direction (expanding or contracting) of the radial optic flow stimulus as quickly as possible. We examined whether observers detected contracting optic flow earlier than expanding optic flow.

2.1 Methods

2.1.1 Observers. Ten observers participated in the experiment. All observers had normal or corrected-to-normal visual acuity and were naive to the purpose of the study. The experiment involved healthy participants, and did not utilize any invasive techniques, substance administration, or psychological manipulations. Therefore, compliant with Dutch law, this study only required, and received, approval from our internal faculty board (Faculty's Advisory Committee under the Medical Research Human Subjects Act, WMO Advisory Committee) at Utrecht University. The experiment was conducted according to the principles expressed in the Declaration of Helsinki. By signing the informed consent, observers indicated to have read and agreed with both the rules regarding participation and proper (laboratory) behavior,

and the researchers' commitments and privacy policy. Observers were also informed that they could stop participating in the experiment at any time and that all data would be analyzed anonymously.

2.1.2 Stimuli and apparatus. Stimuli were generated on a MacPro and presented on a linearized 20" LaCie CRT monitor (refresh rate = 100 Hz, resolution = 1024×768 pixels). Observers viewed the stimuli through a mirror-stereoscope that was mounted on a chin-rest. The viewing distance was 57 cm. Stimuli were presented on a gray background (luminance = 23.2 cd m^{-2}); and to facilitate binocular fusion, a rectangle that was composed of randomly assigned black and white (47 cd m^{-2}) pixels surrounded each stimulus (figure 1). One of the stimuli was a radial optic flow pattern (radius of annulus = 3.6 deg) composed of randomly placed dots (diameter = 0.1 deg) with an unlimited lifetime and a dot density of $2.5 \text{ dots deg}^{-2}$. The center (radius = 0.2 deg) of the stimulus contained background luminance with a red fixation dot in the middle (diameter = 0.2 deg). Dots of the optic flow pattern reaching the border of the annulus were randomly replaced within the annulus. The optic flow pattern contained a quadratic speed gradient that simulated observer movement through a circular tunnel (see Holten et al., 2013, for details). The dot speed increased from center (0.01 deg s^{-1}) to periphery (4.1 deg s^{-1}). The stimulus ($7.2 \times 7.2 \text{ deg}$) that was simultaneously presented to the other eye served as a mask and was used to suppress the optic flow pattern for a few seconds. It was created by filtering pink ($1/f$) noise using a rotationally symmetric Gaussian low-pass filter ($\sigma = 1.5$) and by making the resulting grayscale image binary with maximum contrast. Every 100 ms (10 Hz) a new mask was randomly selected from a total of 200 available masks.

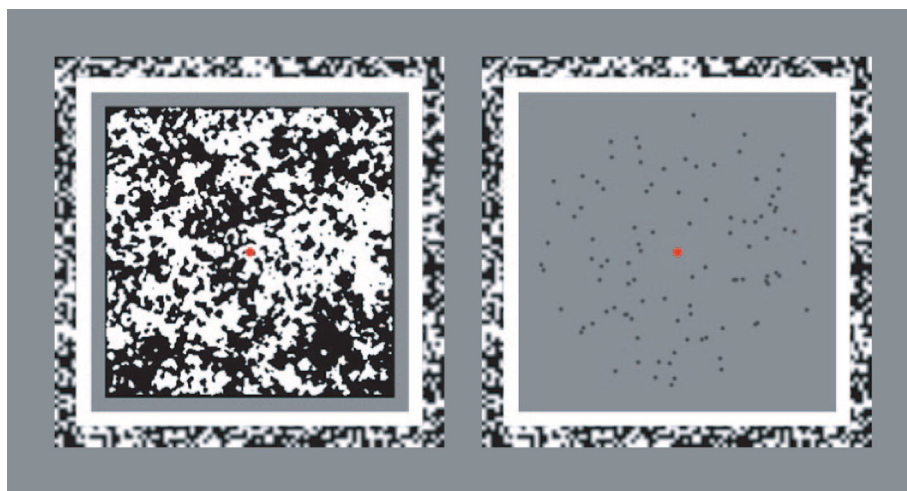


Figure 1. [In color online, see <http://dx.doi.org/10.1068/p7925>] Schematic representation of the stimuli used in the experiment. A mask (refresh rate = 10 Hz) was presented to one eye, while an either expanding or contracting radial optic flow stimulus was presented to the other eye. The mask and optic flow were presented to each eye in counterbalanced order. To facilitate binocular fusion, a rectangle that was composed of randomly assigned black and white pixels surrounded each stimulus.

2.1.3 Procedure. To prevent the optic flow pattern from breaking suppression immediately after stimulus onset, which would result in a floor effect and no observed difference between motion directions, the dot luminance of the optic flow pattern was determined for each observer before the start of the experiment. Observers performed a two-alternative forced-choice QUEST staircase experiment in which two intervals were randomly presented for 3 s. One of the two intervals contained an expanding or contracting optic flow pattern that was presented to either the left or right eye and a dynamic stimulus (mask) that was presented to the other eye. The other interval contained only the mask, which was presented to the same

eye as the mask was presented to in the other interval. Observers had to indicate which interval contained the optic flow pattern. The order of the interval containing the optic flow pattern was randomly determined. The dot luminance was decreased when observers correctly indicated the interval containing optic flow. When observers indicated the wrong interval, the luminance of the dots was increased. To correct for eye dominance and the motion direction of the stimulus, four QUEST staircases were simultaneously executed in the same experiment (4 conditions, ie 2 optic flow positions: left/right eye; 2 motion directions: expanding/contracting). The optic flow pattern and mask were randomly presented to each eye. Every observer performed 120 trials in total, 30 trials per condition. The mean of the QUEST posterior probability density function was calculated to acquire a dot luminance value per condition. The luminance values of expanding and contracting optic flow were averaged to obtain a single dot luminance for the left and right eye separately. These two luminance values were used as the dot luminance of the optic flow pattern for either the left or right eye in the next experiment.

In this experiment observers were instructed to press a key as quickly as possible when they detected the motion *direction* of the optic flow stimulus, which could be either contracting (left arrow) or expanding (right arrow). Each trial lasted maximally 6 s but was aborted as soon as observers pressed a response key. After each trial, observers started a new trial by pressing the spacebar. This allowed observers to take a short break between trials. There were 200 trials in total, 100 per motion direction. For each observer, the order of expanding and contracting trials and the eye it was presented to was randomly determined at the start of the experiment.

2.1.4 Analysis. The RTs of the incorrect trials were not used in the analysis of the data. All observers reported the correct motion direction in more than 75% of the trials. The RT of trials in which the observer did not report any motion direction was set to the maximum duration of a trial (6 s). We included these trials because it indicated that the optic flow pattern was still suppressed at the end of a trial. A larger amount of trials that did not break suppression for one of the optic flow directions indicated that this optic flow direction was more strongly suppressed than the other optic flow direction. Since it is known that RTs are not normally distributed, the median RT for the expanding and contracting trials was calculated for each observer. The data were also normalized to compensate for individual differences in RT. That is, for each observer, the median RT of the expanding and contracting trials, respectively, was divided by the median RT of all trials. After averaging across observers, these averages were multiplied by the overall median RT across all observers, which resulted in a duration in seconds. A paired-samples *t*-test was used to examine a significant difference between the two motion directions.

2.2 Results and discussion

For each motion direction, the averaged median RT across observers is shown in the left panel of figure 2a and the individual median RTs are depicted in the middle panel of figure 2a. Expanding optic flow generated a shorter RT than contracting flow, which indicates that expanding optic flow breaks through suppression faster than contracting optic flow ($t_9 = -2.68$, $p = 0.025$, $r = 0.67$). Normalization of the data does not change this result (figure 2b, $t_9 = -2.93$, $p = 0.017$, $r = 0.70$). For all trials across all observers, the total distributions of the (normalized) RTs when either expanding or contracting optic flow broke suppression are shown in the right panels of figure 2. For the normalized RTs, the peak (number of trials) of the distribution is at a later duration (shifted to the right) for contracting than for expanding optic flow. For the median RTs, this shift of the peak of the distribution for contracting optic flow is less apparent (peak of distribution at 6 s). We expected that contracting optic flow would break suppression earlier than expanding flow, but the results show the opposite. A possible reason for this result is that observers had already perceived dots of the optic flow

pattern before they could indicate the motion direction of the stimulus and that observers had more difficulty with indicating, rather than perceiving, contracting than expanding motion. To exclude this possibility, we changed the task of the observers in a new experiment.

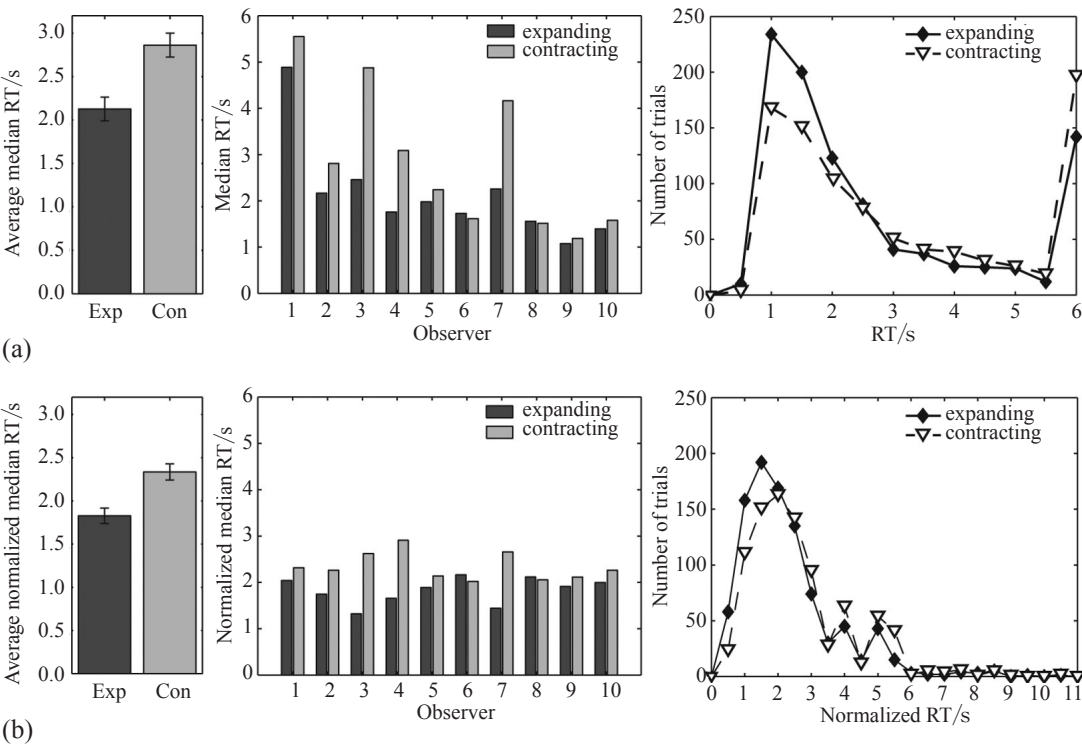


Figure 2. (a) Averaged median and (b) normalized reaction times (RTs) across and for individual observers. The left panels depict the average (normalized) median RT across observers for expanding (Exp) and contracting (Con) optic flow, respectively. The error bars represent the standard error of the mean, without between-subjects variability for graphical purposes only (Cousineau, 2005). The middle panels show the median (normalized) RT of each observer for expanding and contracting optic flow. The right panels show, for all trials across observers, the distribution of the (normalized) RTs when the expanding (black diamonds) or contracting (open triangles) optic flow broke suppression. Note that, due to the normalization procedure, the normalized RT can be longer than the duration of a trial. This occurred when an observer had an RT at a certain trial that was much longer than the median RT of all trials of this observer.

3 Experiment 2

In the second experiment we investigated whether changing the task of the observers would influence their response. Instead of indicating the motion direction of the optic flow stimulus, observers now had to report when they perceived dots of the optic flow pattern, irrespective of perceiving any motion direction. In this experiment we not only presented radial optic flow but also presented translation or random motion to observers. Given that, to the best of our knowledge, no anisotropy in postural sway has been reported between leftward and rightward translation (Ravaioli, Oie, Kiemel, Chiari, & Jeka, 2005; Tsutsumi et al., 2010), we assumed that the perceptual strength of both motion directions would be similar. As a consequence, both motion directions would break suppression after approximately equal durations. If this would not be the case, it would not fit with previously observed postural sway results, implying that in the first experiment observed visual directional anisotropy between expanding and contracting optic flow could also not be compared with previous postural sway results. The random motion condition served as a control condition. The motion coherence of this stimulus is lower than the motion coherence of translation and radial flow. It is known that decreasing the motion coherence decreases the detectability of the stimulus during b-CFS (Kaunitz et al., 2013).

We therefore expected that the random motion condition would be detected at a later moment in time than radial flow and translation.

3.1 *Methods*

The methods of the second experiment are largely identical to the methods of the first experiment. Specific differences are mentioned below.

3.1.1 *Observers.* Ten observers participated in the second experiment of which nine already participated in the first experiment. One of the ten observers had to be excluded from the analysis (see subsection 3.1.3 for the reason why). All observers were naive to the purpose of the experiment and had normal or corrected-to-normal visual acuity.

3.1.2 *Stimuli.* Three motion types were used in this second experiment. The radial optic flow stimulus was identical to the first experiment. The translation and the random motion stimuli were composed of randomly placed dots with an unlimited lifetime and the same dot size and dot density as the radial optic flow stimulus. In the translation condition all dots translated leftward or rightward, while in the random motion condition dots translated in a direction that was randomly determined. To prevent an effect of the speed distribution on the time it took to detect a stimulus, the translation and random motion condition contained the same speed distribution as the radial optic flow pattern. Instead of increasing in speed from center to periphery, all dots of the translation and random motion condition translated with a randomly selected single speed (within the speed range of the radial optic flow pattern, $0.01\text{--}4.1\text{ deg s}^{-1}$) across the aperture. Therefore, some dots translated faster than other dots.

3.1.3 *Procedure.* Observers were instructed to press the right arrow as soon as they perceived dots of the radial optic flow pattern, translation, or random motion stimulus. Experience with the stimuli may facilitate the detection of these stimuli (Gayet, van der Stigchel, & Paffen, 2014). Hence, observers performed some practice trials before the start of the experiment to determine whether the dot luminance of the first experiment had to be decreased, so that dots did not break through suppression immediately after stimulus onset. In total, there were 360 trials of which 300 contained one of the three motion types and 60 trials contained background luminance. These 60 trials were catch trials in which observers were expected not to respond. All but one observer responded in less than 30% of the catch trials. This observer responded in the majority of the catch trials (71%), which indicated that this observer did not do the task correctly and was therefore excluded from the analysis. The motion direction of the stimulus, the motion type, and the eye it was presented to were randomized across trials and observers.

3.1.4 *Analysis.* The RTs of all trials except the catch trials were used in the analysis of the data. The RTs of trials in which the observer failed to respond was set to the maximum duration of a trial (6 s). For each observer, the median RT per condition was calculated (expanding, contracting, leftward translation, rightward translation, random motion). Planned comparisons paired-samples *t*-tests with Bonferroni correction to correct for multiple comparisons were used to examine significant differences between conditions.

3.2 *Results and discussion*

The averaged median RTs across observers for all conditions are shown in figure 3. As in the first experiment, presenting expanding optic flow to observers resulted in a shorter RT than when contracting optic flow was presented ($t_8 = -3.27$, $p = 0.022$, $r = 0.76$). This result shows that changing the task of observers did not alter the outcome of the first experiment. The results of this experiment also show that there is no difference in RT between leftward and rightward translation. Averaging the median RTs of expanding and contracting optic flow resulted in a median RT for radial flow. The median RTs of leftward and rightward translation

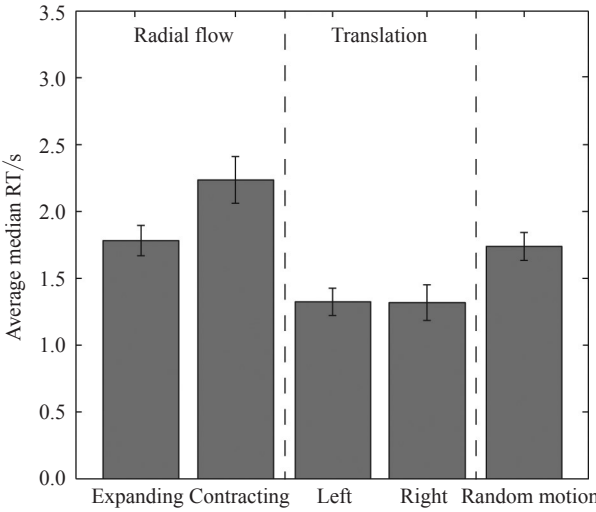


Figure 3. The median reaction time (RT) averaged across observers for different motion types (radial flow, translation, random motion) and directions. The error bars represent the standard error of the mean, without between-subjects variability for graphical purposes only. The radial flow pattern contained a quadratic speed gradient. Dots of the translation and random motion stimuli did not increase in speed but travelled with a randomly selected single speed (within the speed range of the radial optic flow pattern).

were also averaged to obtain an overall median RT for translation. Although it appears that translation generates shorter RTs (average median RT: 1.32 s) than radial flow (2.01 s) and random motion (1.74 s), this difference is not significant (radial flow: $t_8 = 2.86$, $p = 0.063$, $r = 0.71$; random motion: $t_8 = -2.76$, $p = 0.075$, $r = 0.70$). We expected that random motion would cause the longest RT of all conditions. However, the results show that there is no difference between the RT of radial flow and random motion ($t_8 = 1.35$, $p = 0.639$, $r = 0.43$). It is possible that this result is caused by the speed gradient of the radial flow stimulus.

In the current experiment the speed of the radial flow stimulus was not evenly distributed across the annulus because it increased from center to periphery. It is known that an increased difference between the visual characteristics of a stimulus and the characteristics of the mask decreases the suppression duration (Yang & Blake, 2012). As dots at the higher end of the speed distribution of the flow stimulus (ie dots that were assigned a higher speed) deviate more from the mask than dots at the lower end of the speed distribution (ie dots that were assigned a lower speed), they will probably be perceptually stronger and break suppression faster than the dots at the lower end of the speed distribution. Considering the radial flow stimulus, the dots moving at a higher speed were positioned only at the outer edge of the annulus, while those same (higher speed) dots of the random motion stimulus were randomly positioned across the complete annulus. As a consequence, most of the higher speed dots in the random motion stimulus covered a longer distance before reaching a border of the annulus and were therefore presented for a longer duration before being replaced than the same (higher speed) dots in the radial flow stimulus. It is possible that this unequal presentation duration of the dots moving at a higher speed increased the perceptual strength of the random motion stimulus compared with the strength of the radial flow stimuli. Removing the speed gradient will cause all dots of all stimulus types (radial flow, translation, random motion) to travel with an equal speed across the annulus. We assume that this will decrease the strength of the random motion stimulus compared with the strength of the radial flow stimuli. Because the motion coherence is lower for the random motion stimulus than for the radial flow stimulus, we expect that removing the speed gradient will cause a longer RT for the random motion stimulus compared with the radial flow stimulus. In a new experiment we removed the speed gradient and examined whether this is the case.

4 Experiment 3

The results of experiment 2 showed that the random motion stimulus did not induce the longest RT of the three stimulus types. To further investigate this finding, we performed a third experiment in which we removed the speed gradient of the radial flow stimulus, and as a result all dots travelled with the same speed across the annulus. We expected that removing the speed gradient would increase the RT of the random motion condition compared with the RT of radial flow, since the only remaining difference between these stimulus types was the lower motion coherence of random motion and decreasing the motion coherence decreases the detectability of a stimulus during b-CFS (Chung & Khuu, 2014; Kaunitz et al., 2013).

4.1 Methods

The methods of the third experiment are largely identical to the methods of the previous experiment. Specific differences are mentioned below.

4.1.1 Observers. Nine observers, including one of the authors, participated in the experiment. Six observers had also participated in both previous experiments and one observer had participated in only the first experiment.

4.1.2 Stimuli. The stimuli were identical to the stimuli used in the second experiment. The only difference with the previous experiment was that the speed gradient was removed from the radial optic flow stimulus. Therefore, all dots of the three stimulus types (radial flow, linear translation, random motion) translated with the same speed, which was determined by calculating half the area under the quadratic speed gradient curve (see Holten et al., 2013, for details). This resulted in a dot speed of 2.7 deg s^{-1} .

4.2 Results and discussion

The average median RT after stimulus onset across observers is shown for all conditions in figure 4. Although the RT for expanding optic flow (1.68 s) appears to be shorter than for contracting optic flow (1.85 s), no significant difference is observed ($t_8 = -1.57, p = 0.312, r = 0.49$). As in experiment 2, there is also no significant difference in RT between leftward and rightward translation. Comparing radial flow, which is the average median RT of expanding and contracting flow, with the random motion stimulus, shows that observers respond at a later moment in time

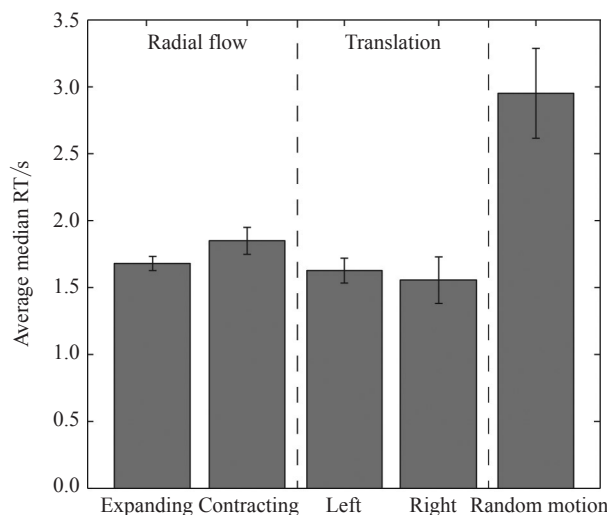


Figure 4. The median reaction time averaged across observers for different motion types (radial flow, translation, random motion) and directions. The error bars represent the standard error of the mean, without between-subjects variability for graphical purposes only. The radial flow pattern did not contain a speed gradient. All dots of all motion types travelled with the same speed.

when random motion is presented than when radial flow is presented ($t_8 = -3.07$, $p = 0.030$, $r = 0.74$). This result agrees with our expectation. The same result is observed when the RT of translation (average of median RT of leftward and rightward translation) is compared with the RT of random motion ($t_8 = -2.98$, $p = 0.035$, $r = 0.73$).

5 General discussion

In the current study we examined whether an asymmetry in perceptual strength exists between expanding and contracting optic flow and whether it mirrors the directional anisotropy apparent in postural sway (more postural sway generated by contracting than by expanding optic flow). On the basis of the anisotropy in postural sway, we assumed that contracting optic flow is a perceptually stronger visual stimulus than expanding optic flow. As a result, during b-CFS, contracting optic flow should be detected earlier than expanding optic flow. However, our results show the opposite: RTs of observers were shorter for expanding optic flow than for contracting optic flow when the optic flow pattern contained a quadratic speed gradient.

5.1 Postural sway

Because both higher contrast stimuli (Tsuchiya & Koch, 2005) and stimuli with a higher spatial frequency (Tsuchiya & Koch, 2005; Yang & Blake, 2012) are not only dominant during monocular presentation, but are also known to break suppression more readily, one can assume that perceptually stronger visual stimuli break CFS faster than perceptually weaker stimuli. The results of the current study therefore suggest that expanding optic flow is perceptually stronger than contracting optic flow. A perceptually stronger expanding optic flow stimulus can possibly be explained from an ecological perspective. A small expanding optic flow pattern, such as used in the current study, could be interpreted as an object that is moving toward the observer. Such a stimulus is possibly more threatening for an observer than objects that are moving away. As a consequence, expanding optic flow might be detected earlier than contracting optic flow. A perceptually stronger expanding optic flow stimulus also agrees with the findings of previous studies. Ball and Sekuler (1980) have shown that the RT to horizontal linear motion away from fixation was shorter than to linear motion toward fixation. It has also been reported that observers needed a larger displacement of a stimulus with an ambiguous motion direction to perceive a reversal from expanding to contracting motion than the other way around (Lewis & McBeath, 2004). Another study has showed that counterphase gratings with equal motion components in both directions appeared to drift foveofugally rather than foveopetally (Georgeson & Harris, 1978). Also, longer dominance durations for expanding optic flow compared with contracting optic flow are reported during binocular rivalry (Malek et al., 2012; Parker & Alais, 2007). However, this apparent greater perceptual strength of expanding motion is opposite to what we expected based on the direction of the anisotropy in postural sway, and it is also opposite to the results of previous studies reporting a lower threshold for contracting than for expanding optic flow (Edwards & Badcock, 1993; Edwards & Ibbotson, 2007).

Nevertheless, the apparent difference in perceptual strength between expanding and contracting optic flow implies that the visual system is in some way involved in the anisotropy in postural sway. Although the CFS paradigm limited our maximum stimulus size and therefore we could not use optic flow stimuli of comparable size with those generally used to induce postural sway, we can speculate on a possible explanation of our findings, by considering them from an ecological perspective by using the concept of the *exposure history* of a stimulus (Held, 1961). This concept has been used previously to explain why removing the speed gradient of an optic flow stimulus causes more postural sway (Holten et al., 2013) or why contracting optic flow induces a stronger vection magnitude than expanding flow (Bubka, Bonato, & Palmisano, 2008). In short: observers compare incoming sensory

information with that of the past, called exposure history. In daily life we more often move forward than backward, causing a large-field expanding optic flow pattern to be perceived more often than contracting flow. As a consequence, the exposure history for expanding flow can be considered *stronger* than the exposure history for contracting optic flow. Exposure to an expanding optic flow stimulus without the corresponding nonvisual input will therefore cause a greater inconsistency with the exposure history than contracting optic flow. As a result, expanding optic flow may induce a compensatory mechanism to a larger extent than contracting optic flow, resulting in less postural sway during expanding flow.

A striking correlation is observed considering the temporal dynamics of the effect sizes of the detection duration of radial flow and the induced postural sway observed by a previous study (Holten et al., 2013). The current study shows that the largest difference in number of trials between expanding and contracting optic flow is between 1–2 s after stimulus onset (figure 2, right panels). The difference in postural sway magnitude for these two flow types is also largest in this time period (Holten et al., 2013).

5.2 Radial flow

Although this study focused on examining a possible explanation for the anisotropy in postural sway, other interesting findings were observed. It is possible that the observed difference in RT between expanding and contracting optic flow is the result of the tuning of cells in higher level visual motion areas. These areas, such as the medial superior temporal (MST) area and the ventral intraparietal (VIP) area are involved in the processing of radial optic flow stimuli (Bradley, Maxwell, Anderson, Banks, & Shenoy, 1996; Duffy & Wurtz, 1991; Schaafsma & Duysens, 1996). It is known that cells in these areas can be tuned to a particular motion direction such as expansion, contraction, or rotation, or a combination of these directions (Colby, Duhamel, & Goldberg, 1993; Lagae, Maes, Raiguel, Xiao, & Orban, 1994; Orban et al., 1992; Saito et al., 1986; Tanaka & Saito, 1989). Previous studies have shown that MST (Graziano & Andersen, 1994; Tanaka & Saito, 1989) and VIP cells (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Schaafsma & Duysens, 1996) tuned to expansion outnumber the cells tuned to contraction. As a consequence, more MST and VIP neurons will probably respond during expanding optic flow than during contracting optic flow and might therefore differentially affect the perceptual strength of both optic flow directions.

Removing the speed gradient of the radial flow stimulus showed that especially RTs of contracting optic flow decreased, resulting in a smaller difference in RT between expanding and contracting optic flow. We do not have an explanation for this result, and one would also not expect this result because most MST neurons, for instance, prefer stimuli with a speed gradient over stimuli with no speed gradient (Duffy & Wurtz, 1997).

The perceived speed of expanding optic flow has been demonstrated to be higher than the perceived speed of contracting optic flow when both flow patterns contain a linear speed gradient and equal physical speeds (Clifford, Beardsley, & Vaina, 1999). Although the current study did not use optic flow patterns with a linear speed gradient, one could argue that a perceived speed difference between radial optic flow directions affects the detection duration of a radial optic flow pattern during b-CFS. However, the results of other studies (Blake, Zimba, & Williams, 1985; Parker & Alais, 2007) make a role for perceived speed in the current study less likely. Specifically, increasing the physical speed of a translating random dot stimulus does not affect the predominance of this stimulus over stationary dots (Blake et al., 1985). This finding makes it unlikely that the predominance is affected by an increased perceived speed. Likewise, when expanding and contracting optic flow patterns were presented dichoptically and engaged in binocular rivalry, the predominance of both patterns was not affected by the looping frequency of each pattern (Parker & Alais, 2007). A similar predominance was observed when both gratings were looped with the same frequency

or with dissimilar frequencies (where higher looping frequencies resulted in higher stimulus speeds). This again shows that an increase in speed does not necessarily influence the rivalry dynamics. All in all, the findings of the above-mentioned studies indicate that a role for perceived speed is highly unlikely in the current experiments.

5.3 Translation

The results of the current study show that observers detected leftward and rightward translation equally fast. We expected this result because in areas involved in the processing of linear motion, such as the middle temporal (MT) area, no distribution bias has been found between MT cells that are tuned to leftward or rightward motion (Churchland, Gardner, Chou, Priebe, & Lisberger, 2003). In addition, the dominance duration of leftward and rightward motion during binocular rivalry has been shown not to differ (Malek et al., 2012). Given that no anisotropy in postural sway is reported between leftward or rightward translatory stimulation (Ravaioli et al., 2005; Tsutsumi et al., 2010) and also no anisotropy in the detection duration of these motion directions is observed, the current results are concurrent with the notion that there might be a relationship between the perceptual strength of a visual stimulus and the amount of postural sway.

5.4 Random motion compared with translation and radial flow

The detectability of random motion did hardly differ from that of translation and radial flow when the dots translated with different speeds. We did not expect this result since we expected that the detectability of a stimulus would decrease with decreasing motion coherence and random motion is less coherent than radial flow and translation. However, our results show that this unexpected result is probably caused by the dot speed distribution across the optic flow annulus, which differed between stimulus types. The difference in presentation duration of the dots at the higher end of the speed distribution has probably increased the perceptual strength of the random motion stimulus, causing a decrease in the RT of the random motion stimulus to a duration that is comparable with the RTs of radial flow and translation. Removing the speed gradient caused all dots of all conditions to travel with the same speed, and therefore it is likely that all dots were of equal strength. This probably has decreased the perceptual strength of random motion compared with radial flow and translation, since the only remaining difference between radial flow and random motion was the lower motion coherence of random motion. As a consequence, RTs of random motion increased compared with radial flow and translation. The shorter RT observed in our study for translation and radial flow without a speed gradient compared with random motion is thus probably caused by the difference in motion coherence. This is supported by previous studies using b-CFS, which reported that decreasing the motion coherence of a radial optic flow stimulus without a speed gradient increased the suppression duration or decreased the detectability of the stimulus (Chung & Khuu, 2014; Kaunitz et al., 2013).

6 Conclusion

The aim of the current study was to investigate whether an asymmetry in perceptual strength existed between expanding and contracting optic flow and whether this asymmetry reflected the anisotropy apparent in postural sway. We showed that this is not the case, since expanding optic flow was detected earlier than contracting optic flow, while previous studies have shown that expanding optic flow generates less postural sway than contracting optic flow (eg Holten et al., 2013; Palmisano et al., 2009; Wei et al., 2010). Our results therefore suggest an inverse relationship between the perceptual strength of a radial optic flow stimulus and the amount of postural sway it generates. We argue that this result may imply that the visuovestibular system compensates more strongly for the more frequently perceived expanding optic flow pattern.

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