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Interaction of Stereo Vision and Optic Flow Processing Revealed by an Illusory Stimulus

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The influence of stereoscopic vision on the perception of optic flow fields was investigated in experiments based on a recently described illusion. In this illusion, subjects perceive a shift of the center of an expanding optic flow field when it is transparently superimposed by a unidirectional motion pattern. This illusory shift can be explained by the visual system taking the presented flow pattern as a certain self-motion flow field. Here we examined the dependence of the illusory transformation on differences in depth between the two superimposed motion patterns. Presenting them with different relative binocular disparities, we found a strong variation in the magnitude of the illusory shift. Especially when translation was in front of expansion, a highly significant decrease of the illusory shift occurred, down to 25% of its magnitude at zero disparity. These findings confirm the assumption that the motion pattern is interpreted as a self-motion flow field. In a further experiment we presented monocular depth cues by changing dot size and dot density. This caused a reduction of the illusory shift which is distinctly smaller than under stereoscopic presentation. We conclude that the illusory optic flow transformation is modified by depth information, especially by binocular disparity. The findings are linked to the phenomenon of induced motion and are related to neurophysiology. © 1998 Elsevier Science Ltd

Optic flow Illusion Binocular vision Induced motion Perception

INTRODUCTION

The traditional view that visual motion is processed by a single channel that acts independently from other visual channels when we perceive the visual world around us has recently been questioned. Several lines of evidence show cross-talk between color and motion (Braddick, 1995), stereo and motion (Qian *et al.*, 1994; van den Berg & Brenner, 1994) or form and motion (Zijiang & Nakayama, 1994; Verghese & Stone, 1996). Here we report a new disparity dependence of a recently described illusory transformation of optic flow fields (Duffy & Wurtz, 1993).

For this illusion, Duffy and Wurtz displayed 300 randomly distributed dots on a screen. Half of the dots underwent a radial motion centered on the screen and the other half of the dots performed a unidirectional motion to the left or to the right. The stimulus thus contained transparent expansional and translational motion at the same time (Fig. 1). When human subjects were asked to locate the center of the expansional motion, they perceived the singular point shifted away from the center. The displacement was in the direction of the translational motion and opposite to the displacement predicted from vectorial summation of the two types of motion. A possible explanation of this illusory shift is that the visual system interprets the translational motion as a reafferent eye movement signal resulting from a horizontal eye rotation. This eye movement component is subtracted from the radial motion in order to compensate for the apparent eye rotation (Duffy & Wurtz, 1993, 1995a).

This explanation is supported by a biologically plausible network model for heading detection from optic flow fields (Lappe & Rauschecker, 1995). Simulation results indicate that the average illusory location of the singular point as reported by human subjects coincides with the direction of heading that is conveyed by this stimulus. This would suggest that the human visual system interprets this stimulus in terms of self-motion parameters, determining the direction of heading while compensating for eye movements. However, model simulations have also shown that a consistent interpretation of this stimulus in such a manner also requires one to implicitly assume a specific layout of the moving dots in three-dimensional space. That is, the translationally moving dots have to be further away in depth than the radially moving dots.

The reason for this becomes clear when one considers the type of self-motion that could simultaneously induce the two components of the illusory optic flow stimulus. Expansion results from a linear forward movement.

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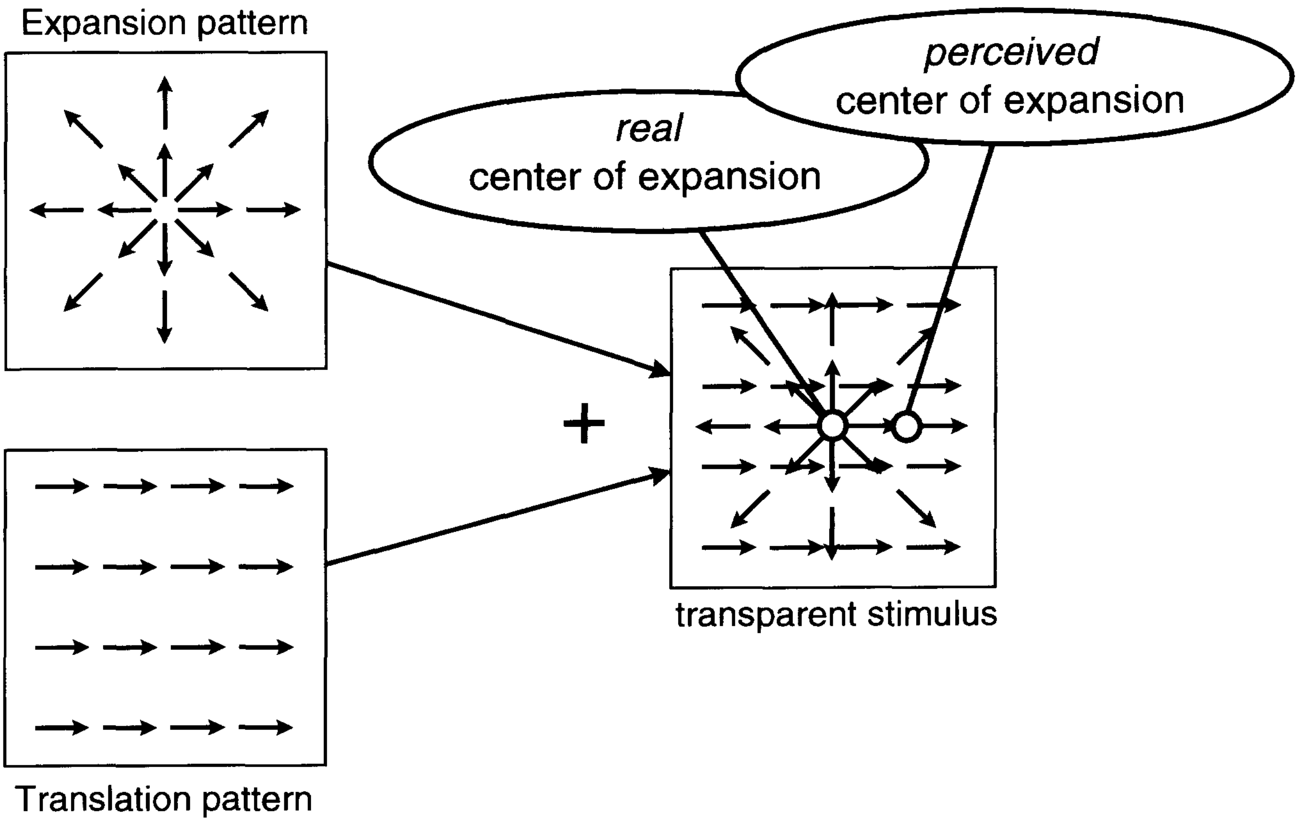

FIGURE 1. The illusory transformation of optic flow fields described by Duffy & Wurtz (1993). Three hundred random dots were displayed on a screen. One half of the dots performed an outward radial motion, the other half a horizontal translational motion. These transparently superimposed dot motions (right) were presented to human subjects, who were asked to locate the center of the expansional motion. In this case the singular point is not perceived at its real position but displaced in the direction of the translational movement.

Translational motion of the visual surround is caused in a first approximation by the observer's eye rotation. However, an eye rotation results in uniform motion of the images of all points in space with equal speed, regardless of their distance in depth. The speed of the radially moving image points, on the other hand, depends on the depth layout of the scene: objects that are near to the observer seem to move faster than objects that are far away (motion parallax). When forward movement and eye rotation are present simultaneously, the ratio of radial to linear motion component is large in the foreground and small in the background. Thus, points in a visual scene that have a large radial motion component should be near, while points performing a translational motion with only a small radial component should be far away.

Thus, we predicted that the magnitude of the illusory shift should depend on the depth arrangement of the radial and linear moving dots in the visual display in the illusory transformation experiment. A separation of the two dot motions should affect the illusory shift, dependent on whether the expansion is shown in front of or behind the translation.

In a natural situation, additional information would be available that could confirm or disconfirm this spatial arrangement. Information about the depth layout of the visual world can be acquired by stereoscopic vision in addition to motion parallax. On the other hand, stereo disparity also has an influence on the perception of transparent motion *per se*, allowing for a better separation of overlapping motion in different directions (Qian *et al.*, 1994). Thus, in the first experiment we investigated the consequences of stereoscopic presentation of the illusory optic flow stimuli.

EXPERIMENT 1: STEREOSCOPIC PRESENTATION

Methods

The stimulus consisted of 300 randomly distributed moving bright dots on a dark background. They were displayed by a video projector on a large tangent screen 70 cm in front of the observer. The dots fell into two equal sized groups differing in their global motion. One half of the dots formed a radial pattern of global motion with the singular point centered on the screen. The second half of the dots underwent a unidirectional motion to the left or to the right. In Fig. 2, the arrangement is shown schematically. The two groups of dots were separated in depth by introducing a relative disparity between them. The radial motion always remained on the tangent screen. The translational motion was presented with relative disparities of 0.6 or 1.2 deg either in front of or behind the radial motion, corresponding to absolute

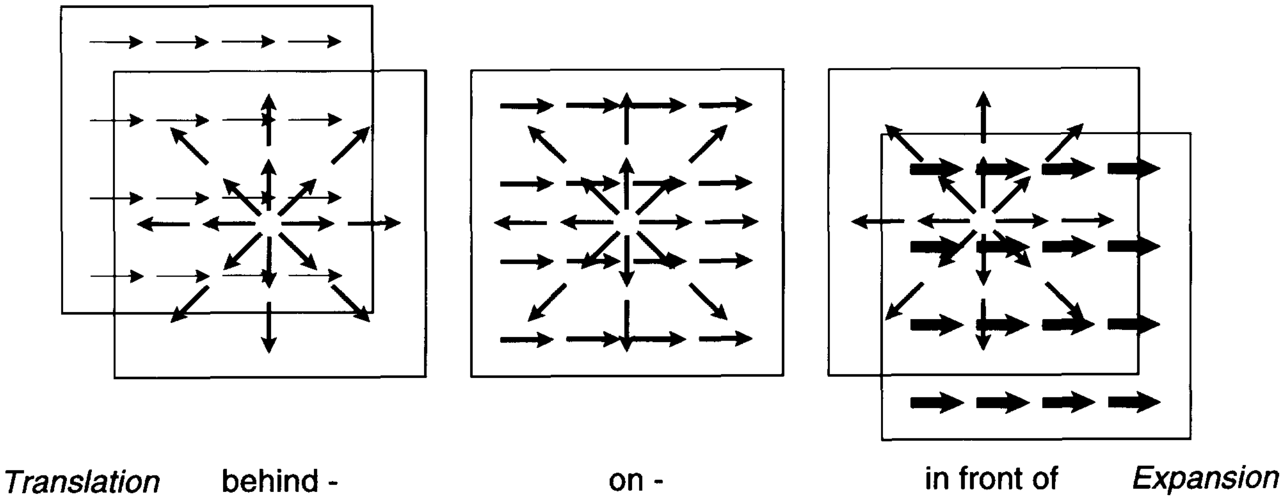

FIGURE 2. Schematic illustration of the stimuli used. Three hundred randomly distributed moving bright dots on a dark background were projected on a tangent screen 70 cm in front of the observer. One half of the dots performed an outward radial motion with the singular point centered on the screen. The other half of the dots underwent a global translational motion to the left or to the right. The two groups of dots were separated in depth by relative disparity. The translational motion was displayed with a relative disparity of 1.2 or 0.6 deg behind (left) or in front of (right) the radial motion or at the same depth (zero disparity, center panel). The task of the subjects was to identify the center of the expansional motion.

distances of 57, 63, 79 or 91 cm, respectively, from the observer. For comparison purposes we also presented a condition where both motion patterns were presented at the screen distance (70 cm), that is with zero disparity.

The stimuli were generated on a Silicon Graphics workstation, using active LCD shutter glasses (CrystalEyes) for the stereoscopic projection. Screen refresh rate was 60 Hz per eye, frame rate was 20 Hz. Screen dimensions were 90 by 70 deg. The visual binocular field was 60 by 70 deg. Dot size was 0.25 deg. The speed of the translational motion was 17 deg/sec. The radially moving dots accelerated with eccentricity. Median speed of the radial motion was 40 deg/sec.

Sixteen volunteers, aged between 22 and 35 years, with normal or corrected-to-normal vision participated in the experiment. Fourteen of them were completely naïve to the purpose of the experiment. The authors also participated, for in preliminary testing as well as in the actual experiment we found no difference between naïve and non-naïve subjects.

The task of the subjects was to identify the singular point of the radial motion. They were asked to concentrate on the radial motion only, because the illusory transformation has been described as a shift of the whole radial pattern. A trial started with the presentation of the static dot pattern for 1 sec to allow the subject to adjust to the stereoscopic presentation. Then the dots were shown in motion for 2 sec. After that, the screen was blanked and the subject had to adjust a previously hidden pointer to the location of the perceived singular point of the radial motion. No fixation was required during stimulus presentation.

The sequence of trials also included trials in which the singular point of the radial motion was truly displaced from the screen center. In these trials, the center of expansion was placed at 10 deg eccentricity to the left or to the right. The different experimental conditions were randomly intermixed. Each condition was presented five times.

Furthermore, to test the precision in pointing, we presented trials in which the speed of the translational motion was zero, i.e., dots were stationary. We found an accuracy of 0.5 deg when the focus of expansion was centered on the screen and of about 2 deg when the focus of expansion was placed 10 deg eccentric from the screen center. These findings are similar to the results of Duffy & Wurtz (1993).

Previous to the experiment we tested the ability of the subjects to generally perceive depth in the display. We presented two planes of randomly distributed static lightpoints with the relative disparities used in the real experiment. All subjects could readily see the various depth arrangements. They had no difficulties in binocular fusion when converging on the respective dot plane. When fixating at screen distance, fusion was not problematic for all disparity conditions except for +1.2 deg (crossed) disparity, where fusion was weak. Despite this the distances of the planes could always be judged in the right order, that is the plane with +1.2 deg disparity as nearest and the one with −1.2 deg disparity as the most distant.

Results and discussion

All subjects reported that they could well distinguish the two groups of dots in all conditions and that separation in depth facilitated this distinction, as expected. If both patterns were at the same depth, i.e. if the relative disparity was zero, we could significantly induce the illusory shift as reported by Duffy & Wurtz (1993) in all subjects (U-Test, $P < 0.05$). The perceived location of the singular point was always shifted into the direction of the translational motion. Consistent with

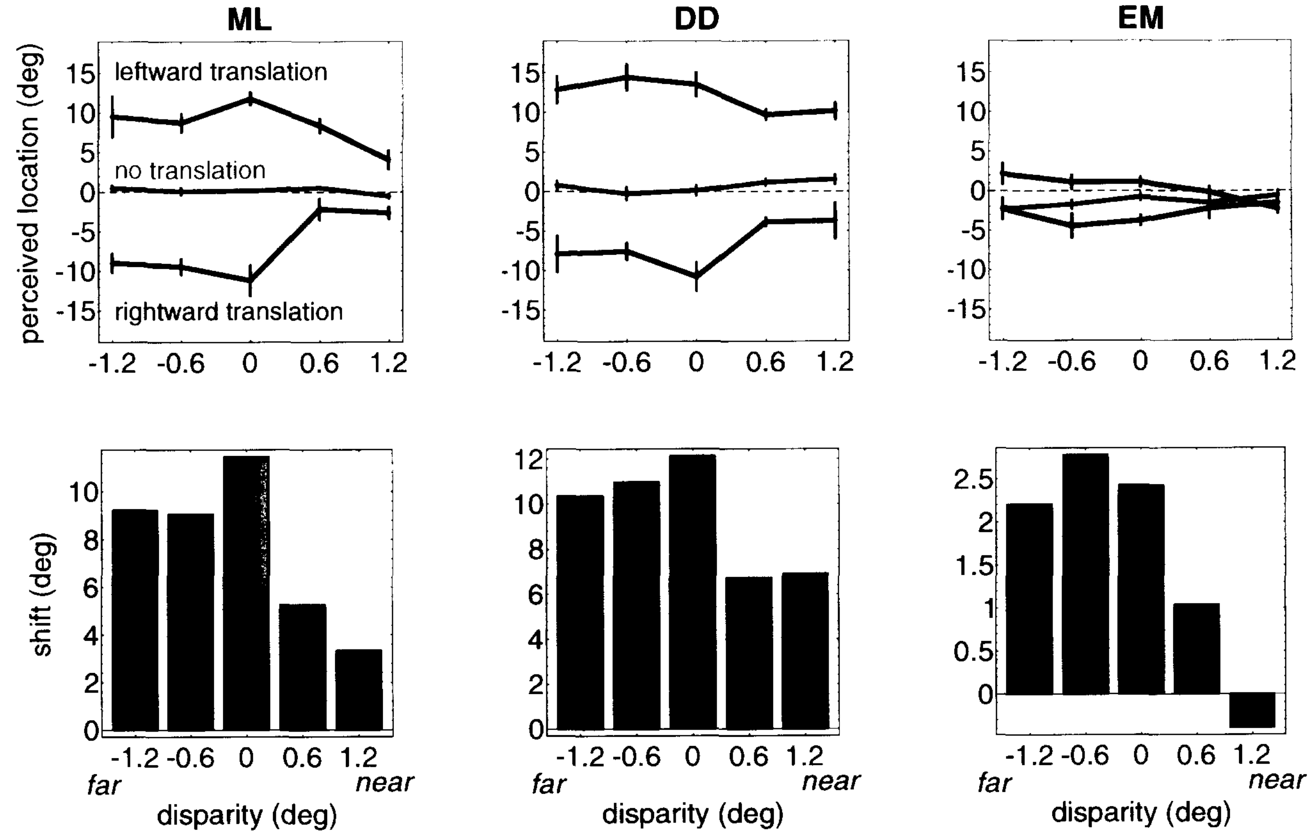

FIGURE 3. Disparity dependence of the magnitude of the illusory shift of the center of expansion. Responses of three individual subjects are shown. Top: Perceived locations were recorded in three conditions differing in the translational motion, which was either towards the left (upper line), towards the right (lower line), or absent (stationary dots, middle line), as well as for five different relative disparities between the two groups of dots. Each condition was presented five times. The graphs plot the means and the standard errors. The broken line indicates the true location of the singular point on the screen. The perceived location of the singular point is always shifted into the direction of the translational motion as previously described by Duffy & Wurtz (1993). A clear effect of disparity can be observed. For uncrossed disparities (−1.2, −0.6 deg), when the translational motion is located behind the radial motion, the illusory shift remains large. For crossed disparities (0.6, 1.2 deg), when the translational motion is in front of the radial motion, the illusory shift is strongly diminished. Bottom: To assess the magnitude of the shift we determined the difference of the mean in the rightward motion condition with the mean in the leftward motion condition. For all subjects the magnitude of the shift for both crossed disparities is significantly different from the magnitude at zero disparity.

previous results, we found the magnitude of the illusory shift to vary strongly between the subjects. It ranged from 2 to 12 deg in different individuals.

However, when we looked at the different disparity conditions, we found a strong dependence of the effect on disparity that was consistent across all subjects. Figure 3 shows responses of three individuals. The magnitude of the illusory shift is given in degrees. The broken line indicates the true location of the singular point, centered on the screen. Perceived locations were recorded in three conditions differing in the translational motion, which was either towards the left (upper line), towards the right (lower line), or absent (stationary dots, middle line), as well as for five different relative disparities between the two groups of dots. The lines connect the means of the five responses in each condition. Figure 3 (top) shows that for uncrossed disparities (−0.6, − 1.2 deg), when the translational motion is located behind the radial motion, the illusory shift remains large. For crossed disparities (0.6, 1.2 deg), when the translational motion is in front of the radial motion, the illusory shift is strongly diminished. To assess the magnitude of the shift we determined the difference between the mean in the rightward motion condition and the mean in the leftward motion condition and divided by 2. As can be seen in Fig. 3 (bottom), for all three subjects the magnitude of the shift for both crossed disparities is significantly different from the magnitude at zero disparity (U-Test, $P < 0.01$), despite the fact that the absolute magnitude of the shift is different for the individual subjects.

The median magnitude of the illusory shift for all 16 subjects, normalized to the shift at zero disparity, is shown in Fig. 4. A Friedman repeated measures ANOVA on ranks confirmed a highly significant effect of disparity ($P < 10^{-6}$). For uncrossed disparities, the illusory shift is slightly lower than for zero disparity. A multiple comparison method revealed that the difference between the disparities 0 and −1.2 deg is significant ($P < 0.05$), whereas the difference between the disparities 0 and −0.6 deg is not significant. For both crossed disparities,

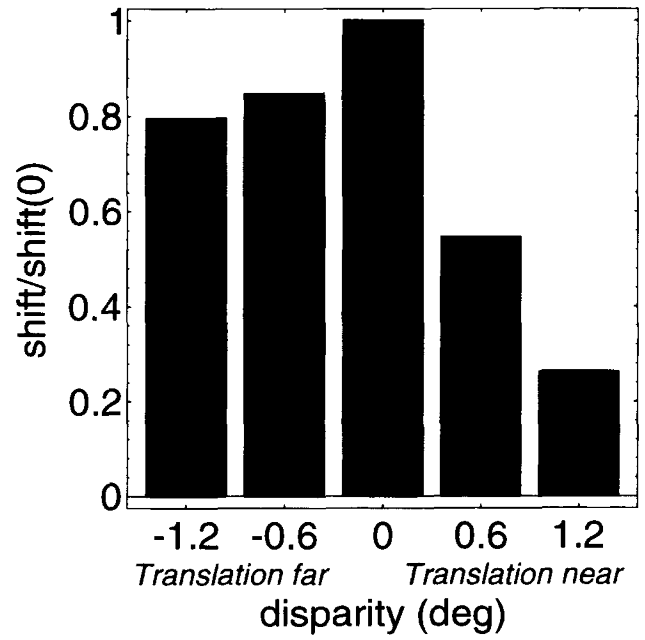

FIGURE 4. Disparity dependence of the median illusory shift, normalized to the shift at zero disparity, for all subjects ($n = 16$). When translational motion is presented behind the radial motion, i.e. uncrossed disparities (−1.2, −0.6 deg), the median magnitude is slightly lower than for zero disparity. When translational motion is shown in front of the expansion, i.e. crossed disparities (0.6, 1.2 deg), the median magnitude drops to only 25% of the value at zero disparity.

the decrease in the magnitude of the illusory shift compared with zero disparity is very large and highly significant ($P < 10^{-4}$). The median magnitude drops to only 25% of the value at zero disparity.

To test the generality of these results we evaluated control trials in which the center of the expansional motion was truly displaced at 10 deg eccentricity to the left or to the right. The results for these trials are shown in Fig. 5. We found the same disparity dependence. The illusory shift decreases significantly only when the translational motion is shown in the front ($P < 0.01$).

In summary, the magnitude of the illusory shift decreases with increasing depth separation between the two groups of dots. However, this decrease is only small when the translational motion is behind the radial motion, but very large when it is presented in front of the expansional motion pattern.

This result is consistent with the interpretation of the stimulus in terms of self-motion. In this interpretation, the pure optic flow signal suggests a self-translation in a direction offset from the center of the radial motion, a simultaneously occurring self-rotation (such as a slow eye movement), and a three-dimensional layout of the visual environment in which the translational dots are far more distant than the radially moving dots (Lappe & Rauschecker, 1995). If binocular disparity also senses the translational motion behind the radial motion, then the stereoscopic depth information is consistent with the three-dimensional layout of the visual scene that results from the assumption of self-motion plus eye rotation. In contrast, if binocular disparity signals that the translational motion is in front of the radial motion, then the stereoscopic information is in conflict with the egomotion scenario. In this case, the presumed self-translation as indicated by the pure visual motion is not valid and the magnitude of the illusory shift is diminished.

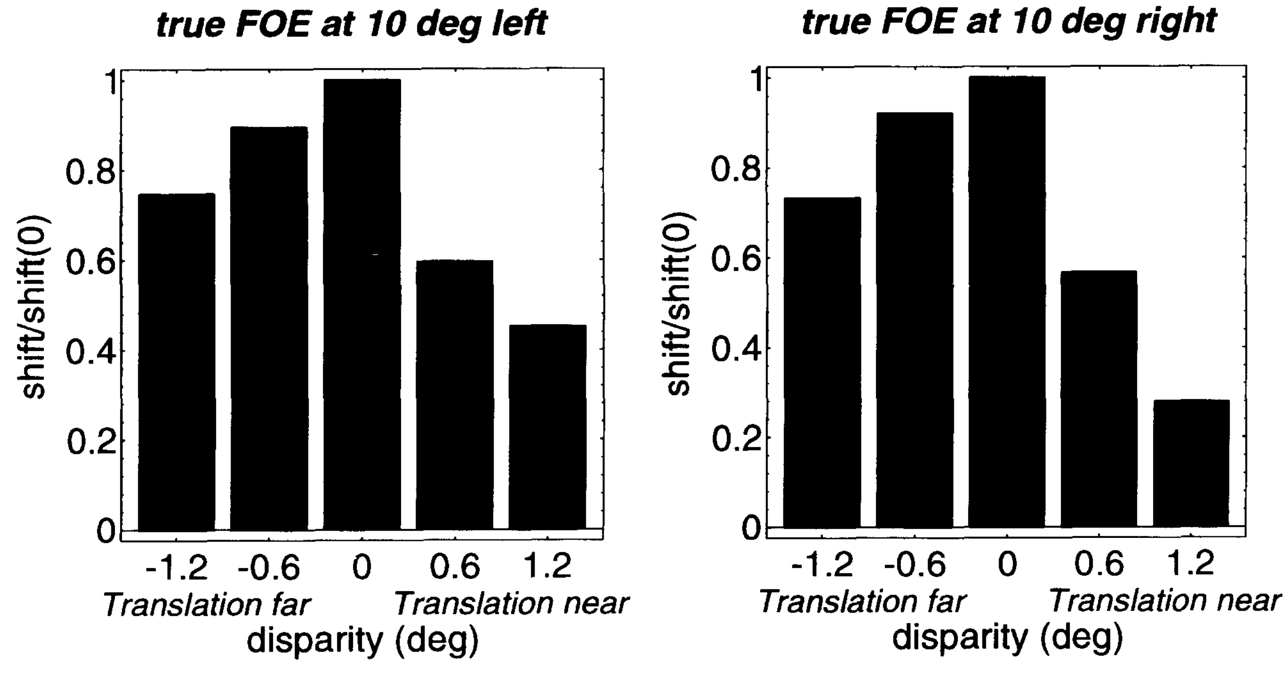

FIGURE 5. Disparity dependence of the median illusory shift ($n = 16$) in trials in which the singular point of the expansional motion was placed 10 deg to the left or to the right of the screen center. All shifts are normalized to the shift at zero disparity. The disparity dependence in both cases is similar to the results in Fig. 4. The occurrence of the shift and the disparity effect are independent of the actual position of the singular point on the screen.

The shift also decreases slightly for uncrossed disparities. This is difficult to explain in the above context, but might be due to an additional effect. Depth separation generally enhances the ability to segregate transparent motion (Qian *et al.*, 1994). Thus, it is conceivable that a better segregation between the two motion patterns might lead to a slightly reduced influence of the translational motion on the perception of the radial motion. Our results show good agreement with predictions from egomotion detection and optic flow analysis. However, it might also be a reflection of a more general mechanism that allows observers to disregard conflicting information in crossed and uncrossed disparity planes. This mechanism might not be specific to optic flow judgements.

One might also think about a more simple explanation for our results. What if difficulties in fusion in the trials with crossed disparity of over 1 deg had allowed the observers to ignore the translational dots more readily than in the trials with uncrossed disparity? First, we can state that one can get reasonable depth effects even if fusion is weak. Prior to the experiment we verified that each subject was able to see depth from our display. We found that even the dots with +1.2 deg disparity were clearly seen in the foreground. Secondly, a significant decrease of the illusory shift already occurred for +0.6 deg disparity, where fusion was not problematic at all. In contrast, for −0.6 deg disparity the decrement was not significant. We take this as evidence for a depth effect, rather than a defect caused by fusion difficulties. Nevertheless, to verify that a lack of fusion does not account for the asymmetric decrement of the illusory shift, we repeated our experiment under disparity conditions where fusion was not possible for both crossed and uncrossed disparity.

EXPERIMENT 2: LARGE DISPARITY

In a second experiment we examined if difficulties in fusing the overlapping transparent motions affect the magnitude of the illusory shift by using disparities well above the limits of fusion.

Methods

Paradigm and parameters of the second experiment were the same as in Experiment 1. This time, however, we separated the two dot planes with a binocular disparity of 2.4 deg.

To test the perception of depth in this display we first presented two planes of static lightpoints with 2.4 deg crossed and uncrossed disparity, respectively. We used seven subjects, none of which had participated in Experiment 1. They were the same age as the subjects used in Experiment 1 and all had normal or corrected-to-normal vision. They were first asked whether they could perceive any depth arrangement and secondly whether they could fuse the dots on the plane on which they did not converge.

In the actual experiment, the two dot planes performed a radial and translational motion, as in Experiment 1. Again the expansional motion was presented at screen distance. The translational motion was separated by 2.4 deg disparity either in the front or at the back and was directed either leftward or rightward. The real center of expansion was located at the center of the screen or truly placed 10 deg to the left or to the right. Each experimental condition was presented five times. As in Experiment 1, the task required the subjects to identify the center of the expansional motion.

Results and discussion

The preliminary testing verified that all subjects perceived the depth arrangement without problems. However, none of them was able to fuse the dots on the plane on which they were not converged.

The results of the localization of the center of expansion are shown in Fig. 6. The median magnitude of the illusory shift, normalized to the value at zero disparity, is plotted against the three disparity conditions. One can clearly recognize the same asymmetric behavior as in Experiment 1. A multiple comparison method yielded that the decrease was significant only when the translation was shown in front of the expansion ($P < 0.01$). The slightly lower decrease compared with that in Experiment 1 (33 vs 25%) is probably due to the different group of subjects. As we found in both

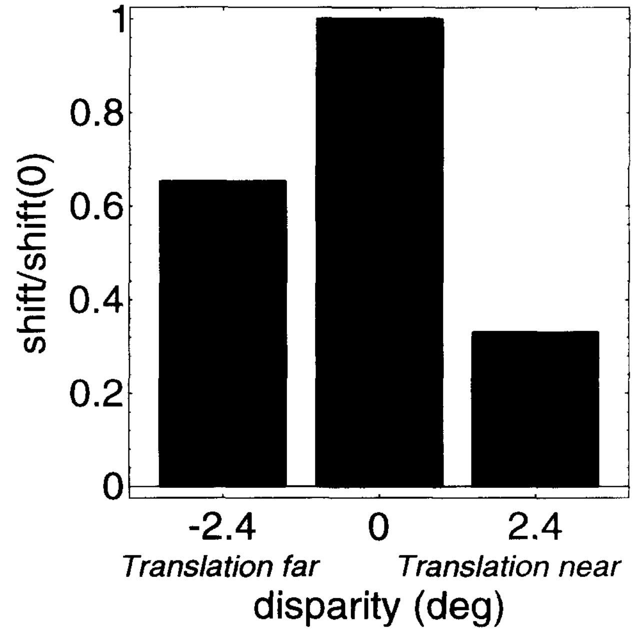

FIGURE 6. Disparity dependence of the median illusory shift of seven subjects when disparity conditions prevented fusion of both dot planes at the same time, because of large disparities. As in Fig. 4, only the trials in which the true center of expansion was located at the screen center are included. All shifts are normalized to the shift at zero disparity. The disparity dependence is consistent with the results from Experiment 1. The illusory shift decreases significantly only for crossed disparity, although for both crossed and uncrossed disparities it was impossible to fuse the dots on the plane on which was not fixated. Since depth was nevertheless perceived easily, this result is evidence for a depth effect and excludes an effect caused by difficulties to fuse.

experiments, the magnitude of the illusory shift differs for individual subjects.

The results of Experiment 2 provide further evidence that the disparity dependence of the illusory shift is due to the depth arrangement of the dot motions and not to an inability to fuse correctly. Fusion in this experiment was impossible for both crossed and uncrossed disparity conditions, while depth was still perceived easily. Yet the illusory shift decreases significantly only for +2.4 deg. Taken together with the observation that the asymmetric effect already occurred at 0.6 deg disparity, where fusion was not problematic at all, we conclude that fusion is not important in the context of the explanation for the effect.

EXPERIMENT 3: MONOCULAR DEPTH CUES

In a third experiment we examined the question, whether similar results are obtained when a depth separation between the translational and expansional dot patterns is indicated by monocular texture-based depth cues.

Methods

We presented the planes of translational and radial motion binocularly at screen distance with a separation in depth simulated by texture cues instead of disparity. These texture cues were based on a difference in dot size and dot density. As illustrated in Fig. 7, the dot size decreases and the dot density increases with increasing distance of a dot plane from the observer. As in the first experiment, we considered five different arrangements of relative depth between the two dot patterns. Dot sizes for the translationally moving dots were 1/2, 3/4, 1, 5/4 and 3/2 of the size of the radially moving dots. The density of the translational dots on the screen was $(1/\text{dotsize})^2$. Thus, the number of the translational dots was 4, 16/9, 1, 16/25 and 4/9-times the number of the radially moving dots. Because the brightness of each pixel was the same, the brightness averaged over the whole screen was the same for each dot plane. According to the size and density parameters, the distance of the translational motion varied between 2/3, 4/5, 1, 4/3 and 2 (i.e. 1/dot size) times the distance of the radial motion. All other parameters were the same as in Experiment 1. Fifteen subjects, different from those used in the previous experiments but at the same age and with normal or corrected vision, participated in the experiment. Again their task was to identify the position of the singular point of the radial motion.

Results and discussion

All subjects reported that they could well distinguish the two groups of dots. None of the subjects, however, reported any perceived depth separation between the two dot patterns during the 2 sec of stimulus presentation. This suggests that the texture parameters, i.e. dot size and dot density, are not sufficient to stimulate an immediate perception of a depth arrangement. On the other hand, the subjects were required to concentrate on the singular point in the stimulus and not on depth arrangements.

Although there was no immediate depth perception during the experimental trials, astonishingly a weak but significant effect of the simulated relative distances could be observed (Friedman ANOVA, $P < 0.05$). The median magnitude of the illusory shift over all subjects is shown in Fig. 8, plotted against the relative nearness between the planes of translational and radial motion. The relative nearness corresponds to the reciprocal simulated relative distance and is given by the size ratio of the translational dots relative to the expansional dots.

The magnitude of the illusory shift decreases significantly when the translational motion is simulated to be in front of the radial motion. But with a decrement down to 80% relative to the equal distance condition, the effect is much less pronounced than the decrease down to 25% found in Experiment 1.

The results show that different depth cues can affect the illusory shift. It decreases significantly when the translational motion is presented in front of the radial motion. However, with texture cues, the decrease is much

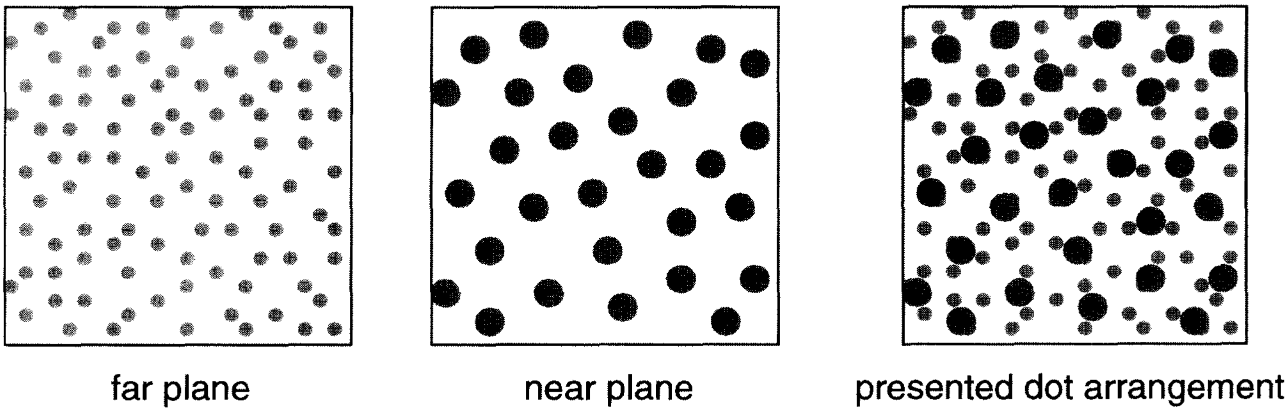

FIGURE 7. Schematic illustration of the monoscopic stimuli used in Experiment 3. The separation in depth between the expansional and translational motion pattern was simulated by monocular depth cues, i.e., changing dot size and dot density. Dot size decreases and dot density increases with increasing distance of a dot plane. As in Experiment 1, we considered five arrangements in relative depth between the two dot planes. The parameters for the radial moving dots always remained constant.

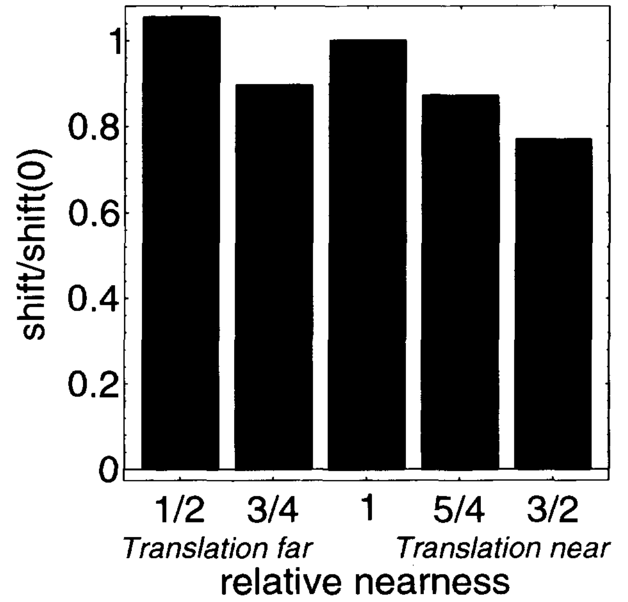

FIGURE 8. Dependence of the median magnitude of the illusory shift on monocular depth cues for 15 subjects. The abscissa gives the relative nearness of the translational dots relative to the expansional dots. It corresponds to the reciprocal relative distance between the planes of radial and translational motion. When the translational motion is simulated in front of the expansion (relative nearness 5/4 and 3/2), a decrease of the magnitude of the illusory shift occurs. With a drop to about 80% it is much weaker than in the case of stereoscopic depth information (Experiment 1).

weaker than with stereoscopic cues. This suggests that the information about depth allows the brain to interpret the flow stimuli correctly, but that stereoscopic information is incorporated more effectively than texture cues in this regard.

A potential problem for the interpretation of the texture depth cues is that our subjects did not perceive any depth order in the displays. Analysis of texture parameters as static depth cues depends on experience and knowledge about, for example, sizes and size ratios of objects in the environment and, therefore, essentially is a cognitive process. The texture parameters in our stimulus obviously are not immediately transferred to depth information when presented only for a few seconds, especially since the task did not require one to report any depth ordering. Nevertheless, the dependence of the illusory shift on these texture cues resembles the disparity dependence in the stereoscopic presentation, albeit to a much lesser degree. Thus, these texture cues affect the illusory shift in the same way as if depth was perceived. It could be that the texture cues we used did modify motion perception in a manner consistent with the simulated depth arrangement, but did not suffice to elicit depth perception *per se*. This might be likely, because the motion stimulus on its own provides kinetic depth cues which could possibly override the texture information. On the other hand, it might be that our texture cues modify the illusory shift simply because they contain fewer translational motion signals when the translation is in the front, because the number of translating dots is reduced.

GENERAL DISCUSSION

Interaction between stereo and motion

The results demonstrate a clear functional interaction between binocular vision and optic flow processing. They suggest that stereoscopic depth information is specifically used as an additional aid in the interpretation of optic flow fields. This is in good agreement with a recent study showing that binocular vision increases the robustness of the visual system in the task of heading detection in noisy optic flow fields (van den Berg & Brenner, 1994).

The effect of the illusory shift nearly vanishes when the translational motion is presented in front of the radial motion. When translational motion is presented behind radial motion, the flow field is consistent with a self-motion flow field that arises when an observer moves forward while performing a horizontal eye rotation. To determine heading requires one to compensate for eye rotation. Consequently, the center of expansion has to be shifted against the direction of the eye rotation, i.e. in the direction of the translational motion. In contrast, a translational motion in front of a radial motion is in conflict with such an ego-motion scenario. The translational motion component of the retinal image due to an eye rotation is independent of the depth layout of the visual surroundings. In contrast, the radial component due to forward translation decreases with increasing depth. Therefore, the movement of points in the background should reflect primarily the translational motion due to the eye movement. In the foreground, on the other hand, the radial component should predominate over the translational component. Thus, a large translational component occurring in the foreground could only be explained by a transparent plane of objects moving sideways on their own while travelling with the observer at a fixed distance, for example, when driving a car and looking through the windshield with raindrops on it drifting aside. To determine one's heading direction then is to evaluate the expansional motion only. Therefore, in this case no shift of the center of expansion occurs.

A dependence on retinal disparity and foreground/background relationships has also been described for smooth pursuit (Howard & Marton, 1992) and optokinesis (Howard & Simpson, 1989) as well as for circular vection (Brandt *et al.*, 1975). But in contrast to the illusory shift in our experiments, the performance of the smooth pursuit system is more severely disrupted when a transparent motion stimulus is presented in front of a pursuit target rather than behind it (Howard & Marton, 1992). However, both cases are similar if one considers whether stereo and motion give a consistent view of a natural situation or not. In the case of smooth pursuit this would be a pursuit over a stationary background rather than the pursuit through a transparent display.

Link to induced motion

The illusory shift has also been linked to the phenomenon of induced motion (Meese *et al.*, 1995; Duffy & Wurtz, 1995a). Induced motion refers to apparent movement of a stationary object (the test object) surrounded by moving objects (inducing objects). The apparent movement is in the opposite direction to the moving surround. Our results strengthen the idea of a link between the illusory shift and induced motion. That is because both are influenced by binocular disparity in the same way. Gogel & MacCracken (1979) investigated induced motion as a function of the stereoscopic separation between a vertical oscillating test point and two horizontal moving inducing points, oscillating in phase with the test point. Because of the induced motion the test point appeared to move on a path slanted in the opposite direction to the horizontal movement of the inducing points. Introducing stereoscopic depth by presenting the test point with certain amounts of relative binocular disparity in front of or behind the inducing objects, caused a reduction of the slant. But the reduction was much more distinct (45% compared with 7%) when the inducing points were in front of the test point. The results are redrawn in Fig. 9. From a comparison with Fig. 4 it is obvious that the depth dependence of induced motion measured by the tilt test is very similar to the depth dependence of the illusory transformation of optic flow fields.

In principle, we can refer to our findings in the context of induced motion. To do this, we consider the translationally moving points as the inducing objects and the radially moving points as the test objects. Each of the latter is influenced by induced motion so that it gets an apparent path component in the opposite direction to the horizontal motion. This results in an apparent shift of the center of expansion in the direction of the translational motion. Interpreted this way we find the same disparity dependence of the illusory shift or induced motion, respectively, as Gogel and MacCracken (Fig. 9). Notice that in their experiment the depth of the test point was varied while the inducing points were presented at a fixed distance. In our experiment the translational dots (the inducer) were separated from the radial motion (the test object), which remained fixed. To simplify the comparison, in IM the negative disparities are shown on the right and the positive disparities on the left. In both experiments a separation in depth of the two planes of motion reduces the magnitude of the induced motion.

Gogel and MacCracken used the "adjacency principle" to account for the asymmetric disparity dependence of the induced motion effect. The adjacency principle states that the influence of the inducing objects on the test stimulus is inversely related to their perceived separation in three-dimensional space. Placing the test point one disparity unit in front of the inducing object results in less depth separation than placing it the same amount of disparity behind. Therefore, the induced motion effect should be less reduced when the test point is presented in front of the inducing points.

However, our results show that the quantitative differences between crossed and uncrossed disparity cannot be referred to the adjacency principle. This is so, because in our experiment the actual depth separation between the horizontal (inducing) motion and the radially moving (test) points was smaller for the inducing points shown in front of the test points. Nevertheless, the reduction of the magnitude of the illusory shift was much larger in this case than in the case of the translational motion presented behind the radial motion. According to the adjacency principle it must have been smaller. Other experiments (Heckmann & Howard, 1991) suggest that the crucial factor concerning the adjacency principle is the depth adjacency of the inducing stimulus and the plane of convergence rather than of the inducing stimulus and the test target. But even this way of consideration cannot explain our findings because our subjects did not have to fixate on a special point or plane, but were free to look around.

Rather, our results suggest a relation to eye movements, which has also been proposed as an explanation for one type of induced motion. Heckmann & Howard (1991) distinguish between induced motion between motion detectors in a retinal frame which is very small, induced motion owing to misregistered eye movements arising from inhibited OKN which is larger, and induced motion arising from vection which is larger still. On the one hand, our results seem to be related to the effect of

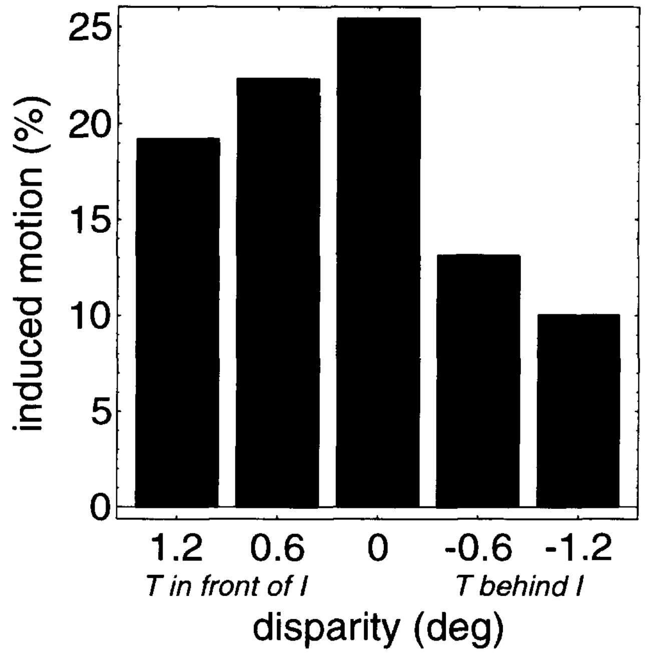

FIGURE 9. Disparity dependence of induced motion measured by the tilt test, redrawn from Gogel & MacCracken (1979). In these experiments, two horizontal moving inducing points (I) were displayed on a screen, oscillating in phase with a vertical oscillating test point (T). Caused by induced motion, the test point appeared to move on a path slanted in the opposite direction to the horizontal movement of the inducing points. Stereoscopic separation of the two kinds of dots in depth reduced the slant. The magnitude of the induced motion is plotted against the disparity of the test point relative to the inducing points, which were presented at a fixed distance. For comparison purposes with Experiment 1, the negative disparities are shown on the right and the positive disparities on the left. The reduction of the slant was much stronger when the inducing points were presented in front of the test point (T behind I, right side). This corresponds to the disparity dependence found in the illusory transformation of optic flow fields.

induced motion due to vection. This comparison holds since vection will be induced by the linear-motion display only when it is beyond the radial-motion display. Thus, the radial-motion display would be apparently shifted when the linear display is seen beyond it. On the other hand, the effect due to inhibition of OKN would be expected most strongly when the radial and the linear display are in the same depth. The effect would become smaller with increasing depth separation of the motions but would still be there, especially when the subjects look at the linear display. This could account for the lowering of the illusory shift when the translational motion is shown further at the back, and for the small but still existent illusory shift when the translational motion is shown in the front.

The similarity between this kind of induced motion effects and our optic flow experiments is remarkable. From our optic flow experiments and their relation to combined eye- and self-motion it is clear why depth separation has to influence the illusory transformation in an asymmetric manner. The same argument might apply to induced motion in general. For this, one has to consider the motion of the inducer as the result of an eye movement and the motion of the test object as the translation of an object at a certain distance from the observer. Visual object motion scales with depth similar to expansional optic flow. Thus, the effect of depth separation between the test object and the inducer should follow the same pattern as the effects of depth separation in the case of the illusory flow stimulus. However, this interpretation cannot fully account for the type of induced motion effect found by Gogel and MacCracken. In their scenario, either of the component motions could be regarded as due to eye movements. Thus, our explanation mainly refers to the studies on induced motion which led Heckmann and Howard to state their thesis of an eye movement-related effect of induced motion. In this context our findings fit in with their results and give a plausible explanation for this type of induced motion.

Relation to neurophysiology

The results of our experiments also bear relevance to the neurophysiology of motion detection. Cells in the medial superior temporal area (MST) in macaque cortex have been shown to respond selectively to the location of the singular point of an optic flow pattern (Duffy & Wurtz, 1995b; Lappe *et al.*, 1996). Together with the middle temporal area (MT), area MST is thought to be involved in motion and optic flow analysis. These areas also carry disparity information, in addition to optic flow signals (Maunsell & Van Essen, 1983; Bradley *et al.*, 1995; Roy & Wurtz, 1990). Especially neurons in MST were found to respond to translational motion in a disparity-dependent manner. These neurons reverse their preferred direction of motion depending on whether a translational motion stimulus is presented in front of or behind the fixation point (Roy & Wurtz, 1990). This effect could be closely related to our findings. It will be intriguing to see how these two neuronal capacities interact on a single cell or population level to account for the effect observed here.

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