Detection of divergence in optical flow fields

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Psychophysical thresholds for the detection of divergence (expansion and contraction) in the presence of a translational component are determined. Stimuli consist of sparse random dot patterns. Lifetime, number of dots, divergence, and translational velocity are varied over a wide range. Moreover, the two major characteristics of a divergence pattern, namely, the direction of and the velocity along the flow lines, are also varied independently. Lifetime and number of dots have only a small influence on performance. Over a wide range the detection of divergence is independent of the translational component. The results indicate that the direction of flow lines is an important, but by no means the only, characteristic in divergence detection. This provides evidence that, at least in these experiments, no use is made of a mechanism selectively sensitive for divergence. © 1996 Optical Society of America

1. INTRODUCTION

During locomotion optically guided behavior such as orientation, navigation, and maintenance of posture is mainly based on information contained in the optical flow field (e.g., Refs. 1 and 2). The relevant information is for the most part given by the structure of the flow field and not by the average direction or velocity of the flow. For such tasks in which the global structure of the environment is of principal importance (e.g., the floor, or walls) it is primarily the first-order (linear) spatial structure that contains the information; for such tasks as shape perception and recognition higher-order spatial structure is involved (the simplest shape properties such as curvature are at least second order). The first-order structure can be decomposed into elementary components such as curl (rotation), divergence (expansion and contraction), and two components of the deformation (dilation and pure shear).[3-5] Although this mathematical decomposition provides an elegant way to describe the optical flow field in as much detail as desired, it is as yet unclear whether it is used by the visual system. The existing studies reported in the literature seem to yield conflicting evidence.

Electrophysiological studies have confirmed repeatedly that cells selectively sensitive to either clockwise or counterclockwise rotation, contraction, or expansion do exist in the medial superior temporal[6-11] (MST) area. Two studies also report the existence of a limited number of deformation-selective cells in MST.[7,8] The presence of such cells in itself is not enough to decide whether or not the visual system analyzes the optical flow in terms of the above-mentioned decomposition. In that case a prerequisite would be that to a certain degree the output of the cells is independent of the possible presence of other elementary components. Orban *et al.*[7,8] and Graziano *et al.*[6] show indeed that the MST cells from which they recorded are more or less insensitive to a translational component when it is added to their stimulus. However, Orban *et al.*[7,8] also report that the same cells were strongly influenced by the addition of a more complex component (e.g., expansion added to rotation). Finally, Graziano *et al.*[6] report the finding of MST cells optimally tuned to spiral motions, from which they conclude that the simple decomposition hypothesis does not appear to be correct.

A number of different experimental techniques (e.g., adaptation, discrimination, and detection) have been used to investigate psychophysical performance with respect to rotation, divergence, and deformation stimuli. Regan and Beverley[12-14] performed a series of adaptation experiments from which they conclude that the visual system shows specific sensitivities for looming, rotary, and shearing motion. De Bruyn and Orban[15,16] performed identification experiments using a number of first-order optical flow components. Correct identifications of rotation and expansion were possible for spiral motions. If, however, rotation and expansion were superimposed transparently, identification was possible only if subjects knew in advance to which component they should attend. Although their experiments do not directly test the existence of mechanisms that detect and analyze the geometric components of the optical flow, they argue that if such mechanisms exist, they should operate in a similar way for the different components. Lappin *et al.*[17] conclude from their detection experiments that first-order flow components are not processed independently, although they find support for the more general hypothesis that the visual system is sensitive to differential structure. Using a masking technique, Freeman and Harris[18] found that detection of expansion was unaffected by the presence of rotation and vice versa, which they consider as evidence for specialized mechanisms for rotation and expansion. Kappers *et al.*[19-21] and te Pas *et al.*[22] showed that first-order components can be detected independently of both each other and translational velocity. However, their experiments indicate that subjects possibly make use of a common factor in the flow components, namely, the direction of the velocity. Finally, Milne and Snowden[23] and Snowden and Milne[24] conclude from their adaptation experiments that whereas there is no evidence for special mechanisms tuned to rotation or expansion, there is evidence for the existence of cells specific for complex motions.

The comparison of the outcome of these experiments is confounded by the variety of descriptions and composi-

tions of the stimuli used. As an illustration we mention a divergence stimulus that is often thought of as synonymous with radial pattern. However, a mathematically pure divergence stimulus should also have a constant relative area expansion (or contraction) over the entire stimulus. A radial flow pattern with dots moving with a constant speed along the flow lines results in a stimulus in which the value of the divergence varies from place to place. Moreover, it is well possible to compose a radial stimulus for which the mathematical value of the divergence is zero (see Section 2). Similarly, one could compose a nonradial stimulus with every possible mathematical value for the divergence. Analogous arguments apply to rotation and deformation stimuli. In their electrophysiological experiments Tanaka *et al.*[10] varied systematically the various aspects of the stimuli that they used to test their rotation- and expansion-sensitive MST cells. Their main conclusion is that the spatial arrangement of different directions of movement is by far the most important factor for the activation of the MST cells. Warren *et al.*[25] report that in their psychophysical experiments the direction of the velocity vectors is sufficient for the perception of heading. Similarly, through our own psychophysical research[20,22] we are also drawn toward the conclusion that the most important information for the observer is contained in the directions.

In this paper we will pursue this topic further while constraining ourselves to divergence stimuli. We will systematically vary the composition of our random dot stimulus in order to determine what aspect of our stimulus is most important for detection. The main characteristics that we distinguish are the direction of and the velocity along the flow lines. Four stimulus categories are tested: (1) pure divergence (Div), (2) decreasing (increasing) velocity along flow lines, which effectively cancels the expansion (contraction) (Div_no), (3) divergence stimulus with straight parallel flow lines (Div_straight), and (4) constant velocity along flow lines (Div_const). Although the stimuli are rather different in appearance and composition, stimulus categories can be compared in terms of equivalent divergence (which will be explained below). If our visual system contains specialized mechanisms sensitive to divergence, responses to Div and Div_straight stimuli should be similar, whereas performance with Div_no and Div_const stimuli should be significantly worse. If, on the other hand, the visual system makes use of the direction of the velocity vectors, performance with the Div, Div_no, and Div_const stimuli should be indistinguishable, whereas performance with the Div_straight stimulus should be worse. In addition, we varied the lifetime of the dots in order to manipulate the local acceleration information. Finally, we also varied the number of dots to obtain an impression of how much information is needed for performance of the detection task.

2. METHODS

A. Apparatus
The stimuli are generated on an Atari MEGA ST4 computer. An Atari SM125 high-resolution monochrome monitor is used (frame rate 70 Hz, white phosphor P4). The monitor is viewed monocularly with a natural pupil

from a distance of 34 cm. The resolution of the display is 400×640 pixels, corresponding to a field of view of 21.1×33.7 deg of visual angle. Thus the pixel separation is 3.2 arcmin.

B. Stimuli
The pseudorandom dot patterns used in this experiment consist of dark dots (3×3 pixels) on a light background. The spatial configuration of the dots is based on a regular hexagonal grid that is slightly perturbed with a two-dimensional Gaussian perturbation vector (spread 1/8 of the grid spacing). The grid spacing is determined by the number and the lifetime of the dots. In Fig. 1(a) an example of one frame of a stimulus is shown. In this case the flow is of course undetermined. We generate moving patterns by stroboscopically presenting sequences of frames. In consecutive frames all individual dots change position in a deterministic way. The diameter of the circular stimulus window (the border of which is not actually shown to the subject) is always 380 pixels (20 deg). The total presentation time is kept constant at 228 ms (i.e., 16 frames).

In our experiments we use the following flow types:

Div: Pure divergence. The Div stimulus consists of a mathematically pure divergence. This divergence indicates the relative area expansion (or contraction) per time unit. The appearance is that of an expanding or contracting radial flow pattern. Along the flow lines the dots either accelerate (expansion) or decelerate (contraction). In order to keep the center of divergence outside the stimulus window (detection of this singularity would be an unwanted strategy), we added a translational component. Examples of such stimuli are shown in Figs. 1(b) and 1(c).
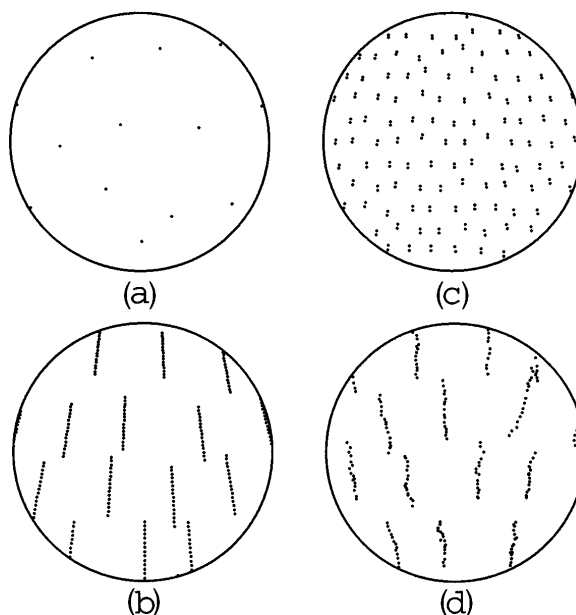

(a)   (c)

(b)   (d)

Fig. 1. Some static examples of the dynamic stimuli used in the experiment: (a) one frame of a 16-dot stimulus; (b), (c), and (d) 16 frames of a 16-dot stimulus superimposed. The examples differ in some aspects: (b) lifetime, 16 frames; noise level, 0; expansion; (c) lifetime, two frames; noise level, 0; expansion; (d) lifetime, 16 frames; noise level, 0.1 deg; contraction. In all three cases the divergence is 1/ s, and the translation is 20 deg/ s. The circular border is not actually shown to the subject.

In order to present static versions of our dynamic stimuli, we have superimposed the 16 consecutive frames of the moving pattern. The velocity inside the window is always directed downward. Thus Fig. 1(b) is an example of an expansion (center of divergence above the stimulus window) with a lifetime of 16 frames, whereas Fig. 1(c) represents an expansion with a lifetime of two frames. In these examples the distances from the center of divergence to the center of the stimulus window are identical. This also implies that in both cases the average velocity of the stimulus is equal.

Div_no: Radial flow pattern without divergence. The Div_no stimulus also consists of a radial flow pattern. Unlike the Div stimulus case, the main characteristic of the Div_no stimulus is that there is no relative area change. Thus for this stimulus the mathematical value of the divergence is always zero (hence the name Div_no!). As a consequence, the velocity of the dots along the flow lines decreases for an expansion and increases for a contraction. The velocity inside the window is always directed downward. Because of the presence of a translational component, the center of the stimulus lies outside the stimulus window. In Fig. 2(a) an example of an expanding Div_no stimulus is shown. The value of the equivalent divergence (which will be explained below) is equal to the value used in Fig. 1.

Div_straight: Parallel flow pattern with divergence. In the Div_straight stimulus the dots move downward along vertical parallel flow lines. Along the flow lines the dots either accelerate (expansion) or decelerate (contraction). When the relative area change is made equal to that of the Div stimulus, both stimuli have the same mathematical value of the divergence. An example of an expanding Div_straight stimulus is shown in Fig. 2(b) [again the value of the equivalent divergence is identical to that used in Figs. 1 and 2(a)]. Since the flow pattern consists of parallel lines, the center of the stimulus is a line instead of a point. In the same way as in the two flow types above, this center is kept outside the stimulus window by the addition of a translation to the flow pattern.

Div_const: Radial flow pattern with constant velocity. The dots of the Div_const stimulus move along radial flow lines, just as in the case of the Div and Div_no stimuli. Unlike the velocities of the Div, Div_no, and Div_straight stimuli, the velocity with which the dots now move is kept constant (hence the name Div_const). Consequently, the value of the divergence cannot be kept constant, and thus it varies from place to place! An example of an expanding Div_const stimulus is shown in Fig. 2(c). Once again the center of the stimulus lies outside the stimulus window. This stimulus serves as a control flow type and is measured by only one of our subjects.

In order to compare the results for the different stimuli, we introduce a quantity that we call equivalent divergence. For both the Div and the Div_straight stimulus this quantity has exactly the same value as the divergence of the stimulus. For Div_no and Div_const this is of course not possible, because for the former stimulus the divergence is always equal to zero and for the latter one the divergence varies over space. A common feature of the Div, Div_no, and Div_const stimuli, the ra-
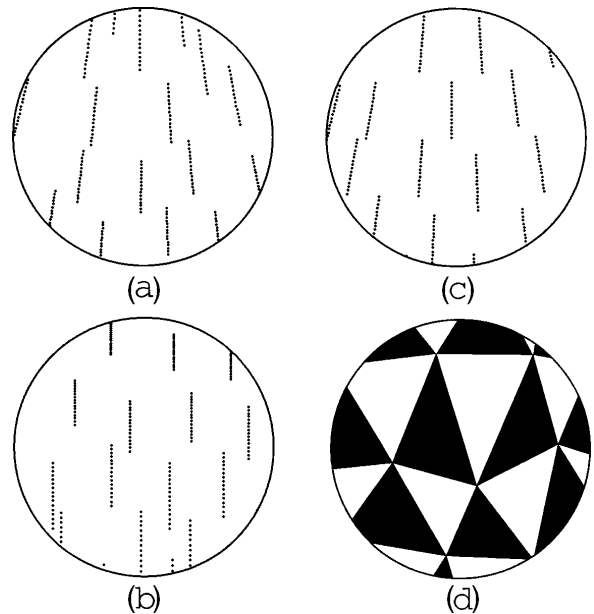

Fig. 2. Some static examples of the dynamic stimuli. In (a), (b), and (c) the number of dots is 16, and the lifetime is 16 frames. The value of the equivalent divergence is in all three cases 1/s, and the translation is 20 deg/s. The examples show an expansion and differ in the following way: (a) Div_no, (b) Div_straight, (c) Div_const. In (d) one frame of the triangle stimulus is shown. See the text for further details.

dial flow field [see Figs. 1(b), 2(a), and 2(c)], can be used in defining the equivalent divergence. Given a fixed choice of the center of the stimulus (determined by the translation), the geometrical distribution of flow lines within the stimulus window depends on the value of the divergence. For equal values of the equivalent divergence this distribution is the same for the three stimulus types. This can be seen by a comparison of Figs. 1(b), 2(a), and 2(c), where the Div, Div_no, and Div_const stimuli are shown for the same values of equivalent divergence (namely, 1/s) and translational velocity (20 deg/s). Figures 1(b) and 2(b) show an example of the Div and the Div_straight stimulus, respectively, with identical values of the translational velocity (20 deg/s) and the (equivalent) divergence (1/s).

Four parameters were systematically varied in the experiment: the lifetime of the dots (2, 3, or 16 frames), the average number of dots per frame (1, 4, 16, or 64), the translational velocity (in the sequel called translation), and the equivalent divergence. For a lifetime of two frames, only the direction and the magnitude of the flow are locally defined. For three or more frames information about the local acceleration is also available (Div, Div_no, and Div_straight stimuli). The wide range of number of dots per frame guarantees a large systematic variation of information density. The translation and the equivalent divergence were measured over the entire range in which it was possible to determine psychophysical thresholds (0.15 deg to 640 deg/s and 0.015 s^{-1} to 64 s^{-1}, respectively). For smaller values hardly any motion can be seen, whereas for higher values motion was undefined because the distance between successive dots was larger than the stimulus diameter. Since the experiments are rather time consuming, it was unfeasible to measure all possible combinations of flow type, lifetime, and number of dots. In Table 1 we give an overview of

Table 1. Overview of the Conditions Measured by Subjects SP and AK[a]

Flow Type	SP	AK
Div	(1, 2), (1, 3), (1, 16)	
	(4, 2), (4, 3), (4, 16)	(4, 2), (4, 16)
	(16, 2), (16, 3), (16, 16)	(16, 16)
	(64, 2), (64, 3), (64, 16)	(64, 16)
Div_no	(1, 2), (1, 3), (1, 16)	
	(4, 2), (4, 3), (4, 16)	(4, 2), (4, 16)
	(16, 2), (16, 3), (16, 16)	(16, 16)
Div_straight	(1, 16)	
	(4, 2), (4, 3), (4, 16)	(4, 2), (4, 16)
	(16, 2), (16, 3), (16, 16)	(16, 16)
	(64, 2), (64, 3), (64, 16)	
Div_const	(4, 2), (4, 3), (4, 16)	

[a] In the parentheses the following values are given: (number of dots, lifetime of dots).

the conditions that the two subjects actually measured. For all these conditions always the full range of translation and equivalent divergence was measured.

C. Some Control Stimuli

A characteristic feature of our stimuli is that they consist of a collection of random dots. In all stimulus types mentioned so far, the size of these dots always remains the same, regardless of expansion or contraction. Thus the information about the relative area change characteristic of the divergence is conveyed only by the distances between the dots, which vary over time. In order to test whether it is essential to performance to have the information about the relative area changes more explicit in the stimulus, we ran some experiments with the stimulus shown in Fig. 2(d). There we show one frame of a stimulus in which the area changes over time are much more apparent than those in the case of the random dot stimuli. The areas between the individual dots are colored alternately black and white. The number of vertices in this stimulus was 8 on average, and the lifetime was 16 frames. Only one of our subjects measured this stimulus condition for Div- and Div_no-type flow fields. This stimulus pushed our Atari to its computational limits.

Another feature of our stimuli is that the movement of the dots is always directed downward. In principle, subjects could use this information and, by attending to the velocity direction of only one dot, perform the task (although not in the Div_straight task). If that indeed were their strategy, they would make local instead of global decisions about the stimulus (see the next subsection). In a first series of controls the movement was made horizontal. Although this does not solve the local/global problem, it checks for a bias in a possibly preferred direction. In a second series the direction of movement was made random, so that the subject was forced to make a global decision (at least two different velocity vectors must be used). A limited number of trials was performed by one of our subjects.

These control experiments are also referred to in Ref. 22.

D. Procedure

After each stimulus subjects had to decide whether an expansion or a contraction was shown. To avoid any ambiguities, we reformulated this question as follows: Is the center of the stimulus located above or below the stimulus window? After a short training session subjects were able to perform this task. In order to measure psychophysical thresholds, we jittered the deterministic positions of the dots by adding a two-dimensional Gaussian perturbation vector. An example of such a perturbed stimulus can be seen in Fig. 1(d). A two-alternative-forced-choice paradigm was used to determine the threshold signal-to-noise ratios, defined as the 75% correct noise levels. (Further details can be found in Refs. 21 and 22.) Thresholds for different flow types were measured in separate sessions. The experiments took place over a period of more than a year. We have no indications that learning effects influenced our results.

Two of the authors participated as subjects. Both subjects are emmetropic. Subjects were seated with their head supported by a chin rest. Viewing was monocular with the subject's right eye (in all cases their dominant eye). Before the stimulus onset the subject had to fixate a cross in the center of the stimulus window. During the stimulus the fixation cross disappeared, but subjects were asked to refrain from making eye movements. Experiments took place in a darkened room.

3. RESULTS

In Fig. 3 we show three representative plots of data points as measured by subject AK. The results of subject SP are similar. The examples show noise level as a function of translation for three different combinations of lifetime and number of dots for the flow type Div. Different curves belong to different values of the divergence. It should be stressed once more that for all conditions we measured the whole possible range. Thus differences in the number of data points in the various plots indicate differences in the measurable range for the different conditions. The starting point of the curves is the mininum translation needed for location of the center of the stimulus outside the stimulus window. This value increases with the value of the divergence. The end points of the curves are determined by the performance of the subject, and in many cases they are characterized by a sharp drop. It should be noted that where such a drop cannot be observed, the actual transition was even sharper. In those cases subjects were not able to measure a threshold at the next value of the translation, not even at the zero noise level!

It follows from Fig. 3 that the noise level as a function of the translation is more or less constant (until the sudden drop in performance for high translational velocities). For higher values of the divergence this noise level also lies higher. In our previous studies[21,22,26] it turned out to be useful to characterize the curves by two parameters: the constant noise level and the maximum translation (see Fig. 4). To avoid unnecessary calculations, we take the maximum noise value of each curve as a rough estimate of the constant noise level. Although this approach certainly leads to an overestimation of the noise level, the parameter itself is useful, since its qualitative
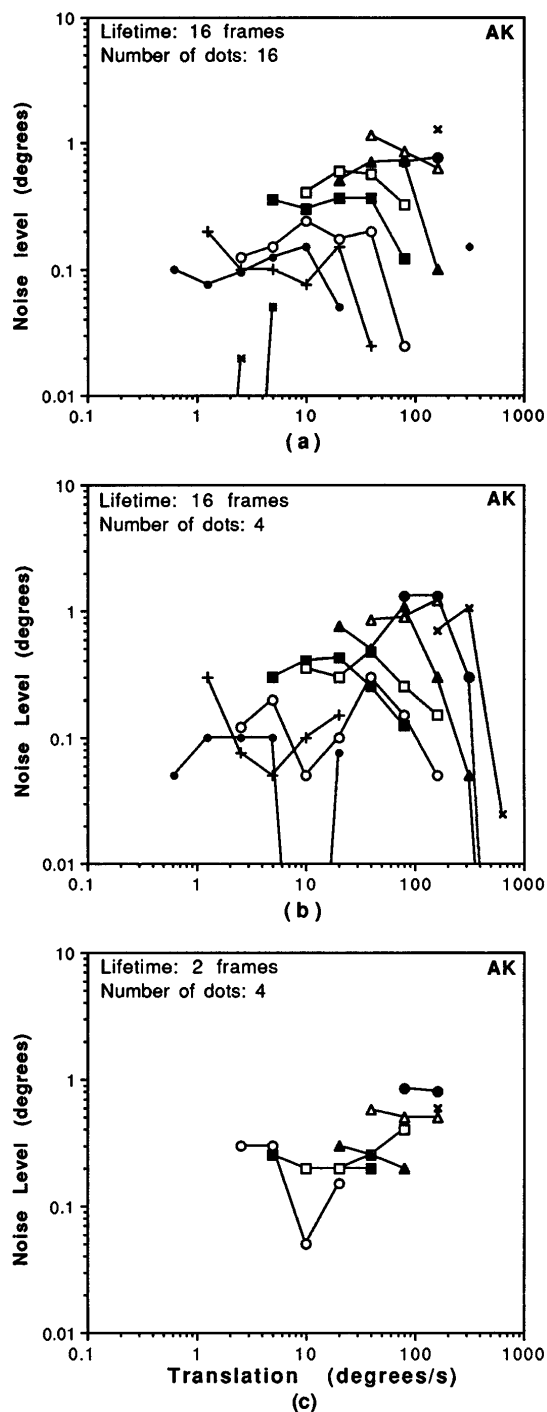
Fig 3. Some data of subject AK. Each curve represents the threshold noise level as a function of translation for a certain value of the divergence. In the three plots the number and the lifetime of the dots are varied. Lifetime: (a) and (b) 16 frames, (c) two frames. Number of dots: (a) 16, (b) and (c) 4. Different values of the divergence (in units of 1/ s) are represented by the following symbols: 0.03: filled squares with small hole; 0.06: crosses with bar; 0.125: small filled circles; 0.25: plusses; 0.5: open circles; 1: filled squares; 2: open squares; 4: filled triangles; 8: open triangles; 16: large filled circles; 32: crosses; 64: open diamonds.

properties are more important than the exact quantitative ones. The final data point (or end point) of each curve determines the maximum translation value. Although ob-

viously coarse, this characterization has the advantage of objectivity and clarity. Figure 3 and the remaining Div data of both subjects (not shown) validate the above description.

Later in this paper we will compare the different conditions of Fig. 3 in more detail by means of the above-mentioned parameters. Here it will suffice to say that the number of dots does not seem to have much influence on performance [compare Figs. 3(a) and 3(b)]. The lifetime of the dots influences the measurable range of divergence values and the maximum translation [compare Figs. 3(b) and 3(c)].

In Fig. 5 we show the results of both subjects for the Div_no and Div_straight flow types. Again each curve represents a different value of the equivalent divergence. In all four plots the average number of dots was 16, and the lifetime of the dots was 16 frames (228 ms). It can be seen that AK's results obtained with the Div_no stimuli [Fig. 5(a)] are remarkably similar to those of the Div stimuli as presented in Fig. 3(a). When we compare the results of the two subjects, we notice only quantitative differences. The measurable range of subject SP is somewhat smaller than that of AK, and SP's noise levels lie slightly below those of AK. This is also true for all other Div_no conditions, which we do not show here. In all cases it is evident that the results can be characterized by schematic curves as shown in Fig. 4.

At first sight the results obtained with the Div_straight stimuli look different from those obtained with the Div and Div_no stimuli. One should bear in mind, however, that for the Div_straight stimulus the value of the minimum translation needed for location of the center (remember: in this case a line instead of a point!) of the stimulus outside the stimulus window (for a given value of the equivalent divergence) is twice that of the Div and Div_no stimuli. This is shown schematically in Fig. 4. Thus, for a fair comparison of the measurable range, one
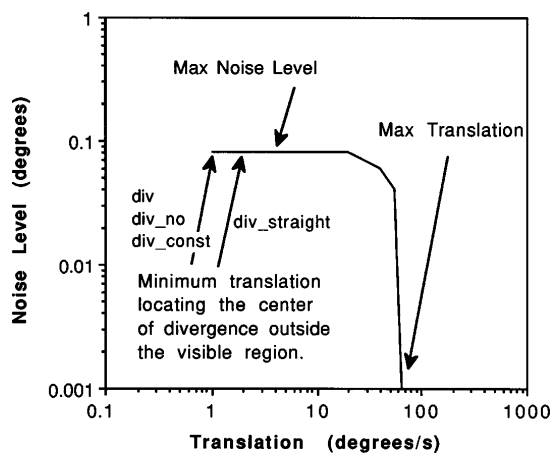

Fig. 4. Schematic drawing of one of the curves of which Fig. 3 consists. Each curve can be characterized by two features: a region of a rather constant noise level (for reasons explained in the text this level is termed Max noise level) and a sudden drop in performance at a certain maximum translation. Also indicated in this figure is the fact that there is a relationship between the starting point of the curve belonging to a certain equivalent divergence and the value of the translation. It is important to note that the starting point for the Div_straight category is higher than that for the other categories.
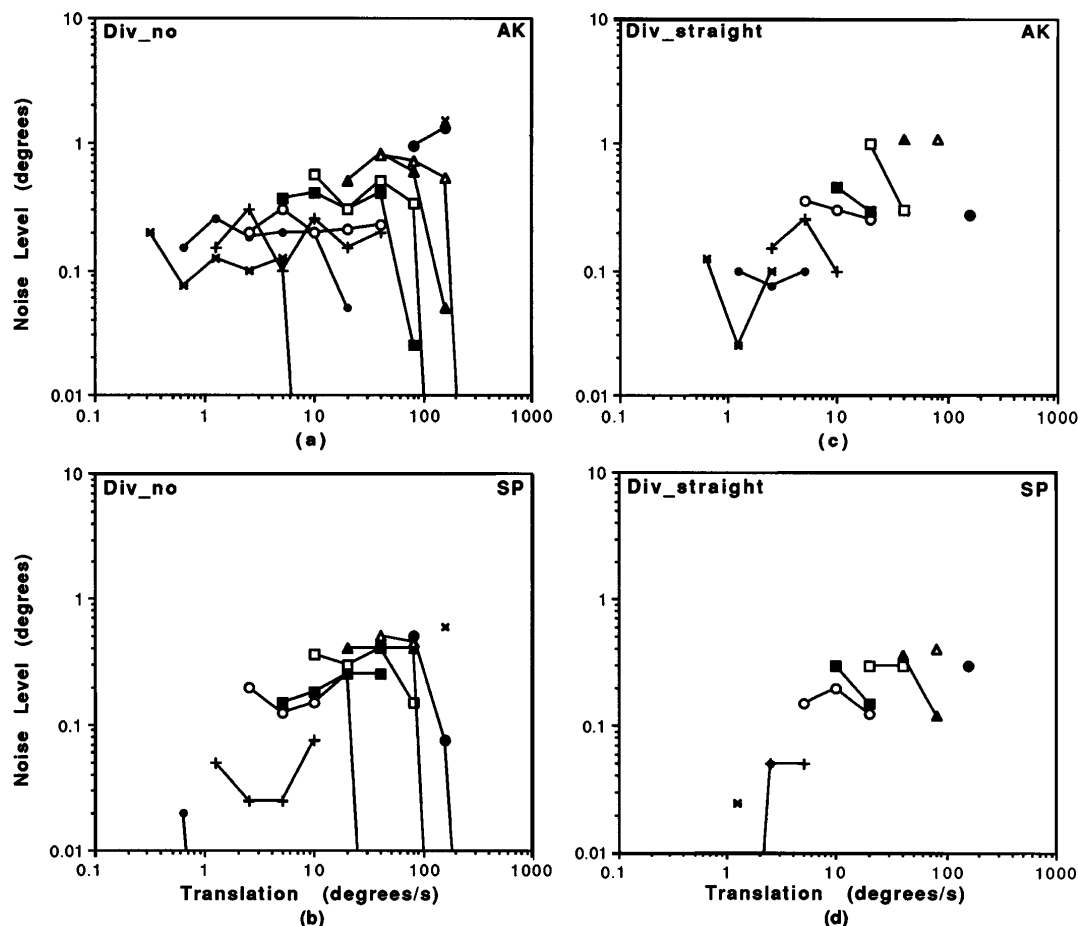
Fig. 5. The upper and lower plots show data of subjects AK and SP, respectively. Each curve gives the threshold noise level as a function of translation for a certain value of the equivalent divergence: (a) and (b) Div_no, (c) and (d) Div_straight. In all four plots the lifetime is 16 frames, and the number of dots is 16. Different values of the equivalent divergence (in units of 1/s) are represented by the following symbols: 0.06: crosses with bar; 0.125: small filled circles; 0.25: plusses; 0.5: open circles; 1: filled squares; 2: open squares; 4: filled triangles; 8: open triangles; 16: large filled circles; 32: crosses; 64: open diamonds.

should ignore the first point of each curve of the Div and Div_no results. In this way the results become more similar, although differences in range remain. This will be analyzed in more detail by means of the two parameters introduced above. Although the choice for these two parameters is less obvious in the case of the Div_straight stimuli, we think it justified to use them as a tool suitable for making comparisons between the different conditions and flow types.

In Fig. 6 we show for both subjects the maximum noise level as a function of equivalent divergence for a number of conditions. Different curves represent different flow types. The two plots on the left show results for the condition in which the lifetime is 16 frames and the average number of dots is 16; in the plots on the right these two parameters are two frames and 4, respectively.

Let us first concentrate on the results presented in Figs. 6(a) and 6(b). Clearly, the maximum noise levels are the same for the three different flow types, Div, Div_no, and Div_straight. The maximum noise level increases as a function of the equivalent divergence, although this increase seems to saturate for higher values of the equivalent divergence. Once again, it can be seen that the maximum noise levels of subject SP lie below those of subject AK, which indicates that SP's

performance is slightly worse. As a consequence, the measurable range of subject SP is smaller. The plots presented in Figs. 6(c) and 6(d) give much the same evidence. There is no difference in maximum noise level for the flow types Div, Div_no, and Div_const (SP only). However, for this more limited condition (shorter lifetime and smaller number of dots) performance with the Div_straight stimuli deteriorates as compared with that of the other flow types. Apparently, the information available in the stimulus cannot be used effectively. For this combination of lifetime and number of dots the measurable range and the attained maximum noise levels are clearly smaller than those in the richer condition (lifetime of 16 frames and 16 dots). Differences between the two subjects are the same as those in Figs. 6(a) and 6(b), although it should be stressed that again these differences are of a quantitative rather than a qualitative nature.

In Fig. 7 we show the maximum translation as a function of equivalent divergence for the same conditions and subjects as those in Fig. 6. The maximum translation increases with the equivalent divergence, but this increase levels off for the higher values. Once more, we can see that the results obtained with the Div, Div_no, and Div_const stimuli are indistinguishable, whereas the Div_straight stimuli lead to lower maximum translations.

This is also the case in the condition in which the lifetime is 16 frames and the number of dots is 16, although this is possibly not significant for subject SP.

Because of space limitations we could show plots of only a restricted number of conditions in the above description of the results. The remaining conditions do not in any way deviate from the results already presented, but they provide extra evidence for the insights that we gained. Summarizing, we can say that for most conditions performance in terms of maximum noise levels is worse for the Div_straight stimulus than for the other flow types with the exception of the rich conditions (i.e., 16 dots or more, lifetime of 16 frames). The measurable range, which is best indicated by the maximum translation, is smallest for the Div_straight stimuli. The number of dots has hardly any influence on performance, provided that there are at least four dots per frame. Only for small values of the equivalent divergence does a smaller number of dots result in a lower maximum translation. Although the effects are only slight, a shorter lifetime results in lower maximum noise levels and lower maximum translations.

Finally, we can report that the results for our control stimuli (black-and-white triangle stimulus and horizontal or random translational velocity directions) do not significantly deviate from the results for our standard stimuli.

4. DISCUSSION

For a visual system that analyzes the optical flow in terms of elementary components such as curl, divergence, and deformation, one necessary condition is that the detection of individual components be independent (to a certain degree) of the presence of other components. Moreover, the stimulus must be mathematically pure. For the divergence stimulus to which we restrict ourselves here this means not only that it is a radial pattern but that there should also be a constant velocity gradient along the flow lines.

The results of our experiments show that the detection of divergence is independent of a translational component up to a certain maximum translation. In earlier work we already showed that this is also true for the detection of vorticity (rotation) combined with translation.[19,21] Te Pas *et al.*[22] extended this work and reported not only that deformation detection was independent of translation but also that rotation detection was independent of divergence and vice versa. Still, we think it premature to conclude that we found evidence for specialized mechanisms tuned to rotation, divergence, and deformation. Similar results might be obtained if subjects use just a subset of the information available in the stimulus, such as, for in-
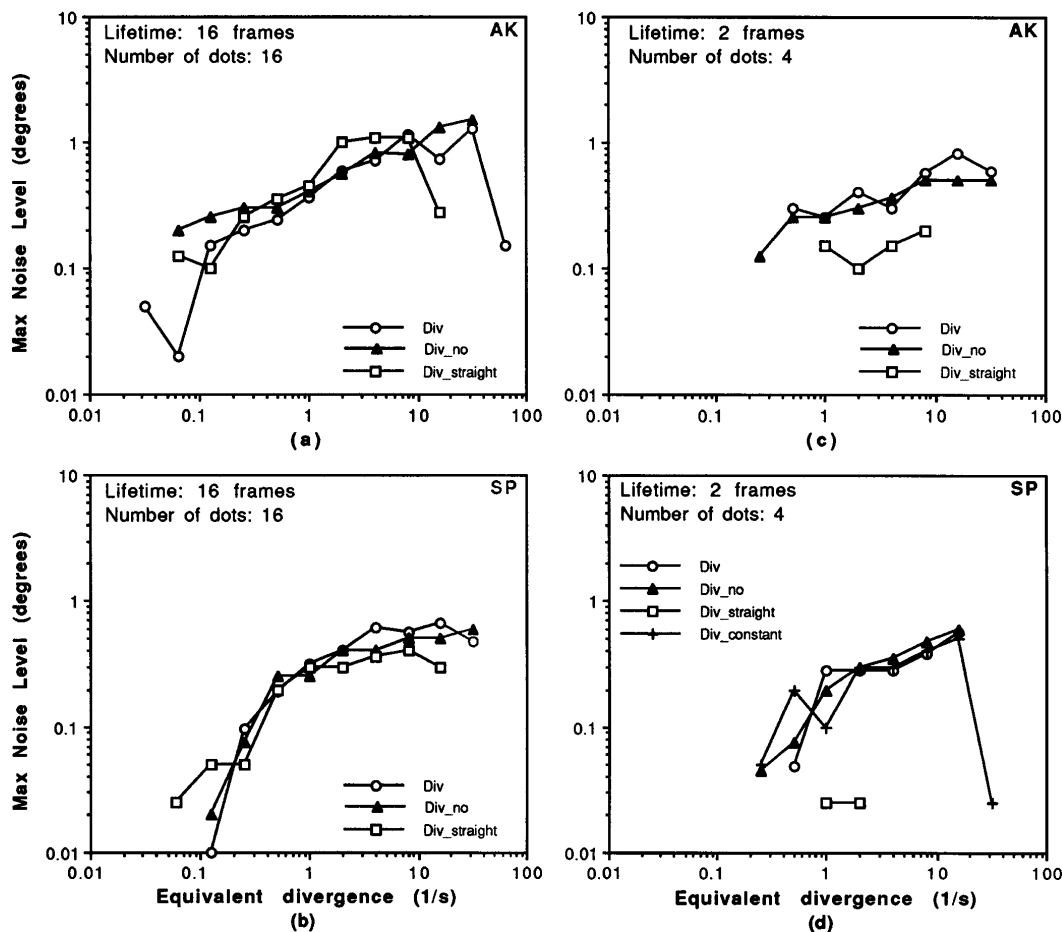

Fig. 6. Maximum noise level (as defined in Fig. 4) as a function of equivalent divergence. (a) and (c) show data of subject AK, and (b) and (d) show data of subject SP. In (a) and (b) the number of dots and the lifetime are kept constant at 16 and 16 frames, respectively. In (c) and (d) the lifetime of the dots is two frames, and the number of dots is 4. In all plots the different curves represent different stimulus categories.
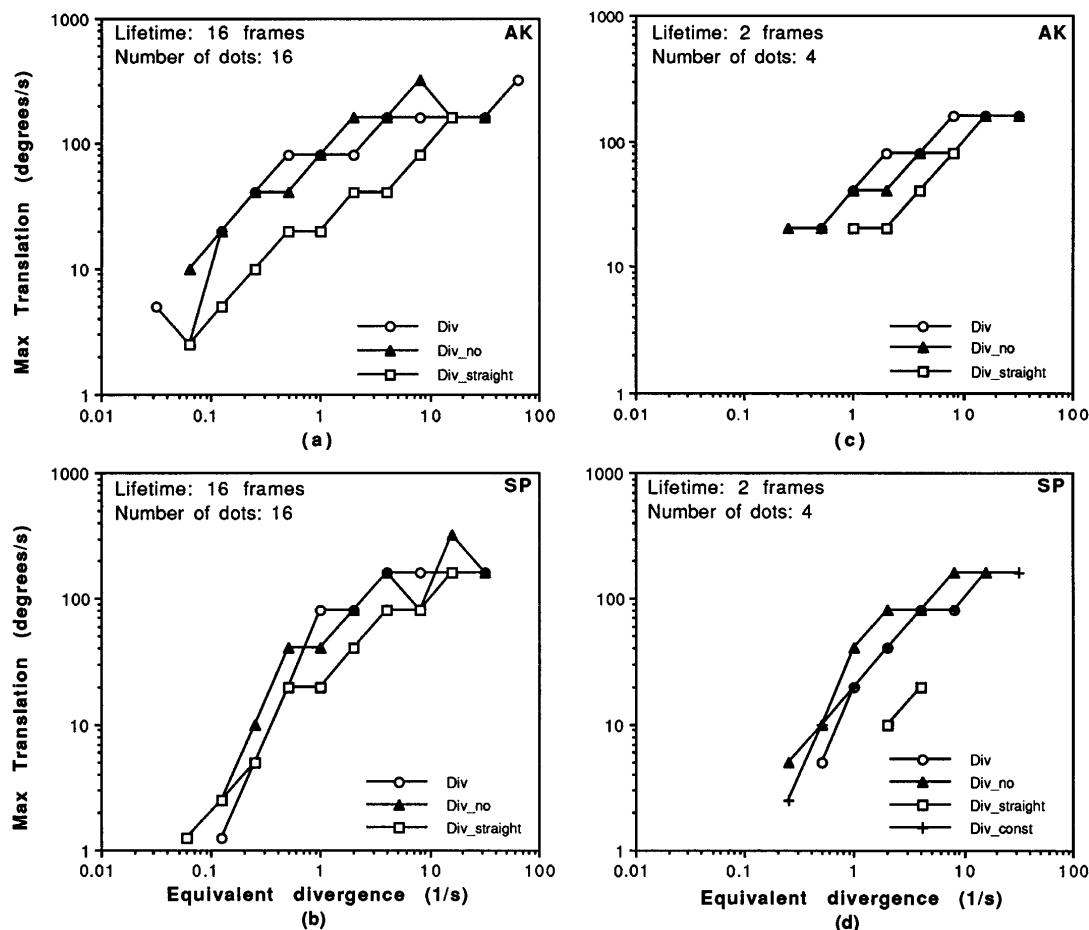
Fig. 7. Maximum translation as a function of equivalent divergence.   (a) and (c) show data of subject AK, and (b) and (d) show data of subject SP.   In (a) and (b) the number of dots and the lifetime are kept constant at 16 and 16 frames, respectively.   In (c) and (d) the lifetime of the dots is two frames, and the number of dots is 4.   In all plots the different curves represent different stimulus categories.

stance, the velocity gradient and the velocity direction. De Bruyn and Orban[15,16] draw similar conclusions from their psychophysical data.

In this paper we focused on the question of what aspects of the stimulus play a major role in divergence detection.   The velocity gradient, the velocity direction, the lifetime, and the number of dots were all manipulated in a systematic way.   If our visual system makes use of a mechanism selectively sensitive to divergence, responses to Div and Div_straight stimuli should be indistinguishable, whereas performance with Div_no and Div_const should be significantly worse.   However, we find that the Div, Div_no, and Div_const stimuli all lead to exactly the same thresholds lying above those for the Div_straight stimulus.   This provides strong evidence that, at least in our experiments, no use is made of a specialized divergence mechanism.

The common factor in the Div, Div_no, and Div_const stimuli, which distinguishes them from the Div_straight stimulus, is the radial flow field.   The velocity along the flow lines is, however, different in the three cases; for Div_const the velocity is constant, whereas Div and Div_no have velocity gradients of opposite sign.   Apparently, the layout of the flow lines is more important than the velocity along them.   Similar evidence comes from the results obtained with different lifetimes.   Although

the influence of lifetime is only small, performance is worse with shorter lifetimes.   When the lifetime of the dots is two frames, there is no information about local acceleration.   This might suggest that local acceleration information plays a role in detection (whereas global acceleration information did not).   However, we prefer another interpretation.   By comparing Figs. 1(b) and 1(c), we see that in the latter case the layout of the flow lines is much less apparent.   As we concluded above that the layout of the flow lines determines performance, it should not be surprising that shorter lifetimes lead to lower thresholds (i.e., noise levels).   This finding, that the velocity direction is a major factor influencing performance, is well in accordance with both electrophysiological work (e.g., Ref. 10) and psychophysical work (e.g., Refs. 15, 16, and 25).

The only aspect of our Div stimulus that was not in agreement with pure divergence was the fact that the dot size remained constant over time and space, although of course the area between the individual dots was subjected to the area changes required by a pure divergence.   As a control condition we performed some experiments in which the dots were replaced by triangular areas.   The results were more or less identical to those obtained with the dots, indicating that the constant dot size did not influence the outcome.   Moreover, since the appearance

of the control stimulus was rather different from our standard stimuli (compare Figs. 1 and 2), we may also conclude that the kind of texture used is not of much importance.

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