# OCULAR RESPONSES TO MOTION PARALLAX STIMULI: THE ROLE OF PERCEPTUAL AND ATTENTIONAL FACTORS

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**Running Head:** OKN and motion parallax

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**ABSTRACT**

**When human subjects are presented with visual displays consisting of random dots moving sideways at different velocities, they perceive transparent surfaces, moving in the same direction but located at different distances from themselves. They perceive depth from motion parallax, without any additional cues to depth, such as relative size, occlusion or binocular disparity. Simultaneously, large-field visual motion triggers compensatory eye movements which tend to offset such motion, in order to stabilize the visual image of the environment. In a series of experiments, we investigated how such reflexive eye movements are controlled by motion parallax displays, that is, in a situation where a complete stabilization of the visual image is never possible. Results show that optokinetic nystagmus,and not merely active visual pursuit of singular elements, is triggered by such displays. Prior to the detection of depth from motion parallax, eye tracking velocity is equal to the average velocity of the visual image. After detection, eye tracking velocity spontaneously matches the slowest velocity in the visual field, but can be controlled by attentional factors. Finally, for a visual stimulation containing more than 3 velocities, subjects are no longer able to perceptually dissociate between different surfaces in depth and eye tracking velocity remains equal to the average velocity of the visual image. These data suggest that, in the presence of flow fields containing motion parallax, optokinetic eye movements are modulated by perceptual and attentional factors.**

**INTRODUCTION**

To an observer's translation through the environment corresponds a complex, continuous, transformation of retinal images, which depends both on the characteristics of the observers trajectory and on the three-dimensional environmental structure (Gibson 1954; Gibson et al. 1955) Such an optical flow field may be further complicated by the fact that at a specific retinal location, several optical motion might occur simultaneously, a situation called motion transparency. A fundamental problem in perception is understanding how the visual system segregates and groups motion signals in the optic flow field, in order to achieve the perception of a three-dimensional layout.

The ability to sort out the different motion components in the optic flow field extends to the oculomotor system. Primates have reflexive visual tracking systems that help stabilize the eyes in a moving visual world. Several studies in both human and monkeys have suggested that some of these reflexive visual tracking mechanisms, also called optokinetic reflexes, are cortically-mediated and able to deal with complex optic flow fields (Miles et al. 1986; Gellman et al. 1990; Busettini et al. 1991; Busettini et al. 1996) When the observer is presented with a flow field containing motion parallax, the visual stabilization of gaze must solve a "bottleneck problem" (Ferrera and Lisberger 1995) Although multiple motion signals enter the visual system, they correspond, at any given moment, to a single eye movement velocity. Therefore, as the global motion of the image cannot be offset by any appropriate eye movement, the tracking system must be able to single out a particular motion signal to be canceled. Such integration, segmentation and selection mechanisms might depend both on automatic and attentional,

perception-based processes.

There are different ways to investigate how the primate oculomotor system deals with visual motion in a three-dimensional environment. First, several studies suggest that the visual motion-processing system involved in the control of eye movements integrates different depth cues, in order to single out the motion of a selected object. For instance, several studies have demonstrated a link between stereoscopic mechanisms and the optokinetic system (Howard and Simpson 1989) In both human and monkeys, this link affects automatic, low-level, motion detection as demonstrated by the disparity-tuning of short-latency ocular following responses. The response to a visual scene moving outside the binocularly-fused plane of fixation is decreased relative to that observed when the movement is presented in the plane of fixation (Busettini et al. 1996) Such properties may be explained by the presence of disparity-sensitive motion detectors at various stages of the primate visual cortex (Poggio and Talbot 1981) The optokinetic system might also use other visuo-spatial cues, such as motion boundaries or dynamic occlusion, in order to select the motion of a given depth-plane (Gellman et al. 1990) Another approach is to try to understand whether high-level, perceptual or attentional processes are involved in the selection mechanism. For instance, Kowler, van der Steen, Tamminga and Collewijn (1984) have demonstrated that subjects are able to voluntarily pursue a moving textured field in the presence of a superimposed stationary field. However, most of these studies have been concerned with the ability to select the local motion signal driving voluntary smooth pursuit eye movements and to ignore other motion signals arising from the moving visual surroundings during pursuit (Collewijn and Tamminga 1984; Yee et al. 1983; Masson et al.

1995) In particular, these studies do not provide information about how reflexive eye movements are controlled in complex flow fields.

The specific aim of the present work was to investigate whether the control of reflexive tracking eye movements depends on the visual processing of differential motion parallax and/or on the perception of three-dimensional structure from motion. Many studies have demonstrated psychophysically that the segregation of different surfaces lying at different distances from the observer can be based on the perception of velocity differences ( and Braddick 1982; Braunstein 1966; Rogers and Graham 1979; Braunstein and Andersen 1981; Braunstein and Title 1988; Andersen 1989) Most of these studies used random-dot optical flows, in which no other cues to depth than differential motion parallax were present. A classical method to build such displays is to randomly position dots throughout the visual field and to set them into motion at different velocities, randomly distributed across the dots. Such displays generate the perception of moving elements lying at different distances from the observer. They also lead to the perception of motion transparency. For instance, when a subject faces a stimulus where two motion signals occur at each specific retinal location, s/he usually reports the perception of two independent transparent surfaces sliding over each other. Moreover, the fact that subjects usually report that one surface (the one which is associated with faster moving dots) is seen in front of the other, suggests a functional link between the perception of transparency and the perception of depth from motion (Kersten *et al.* 1992)

In the following experiments, we investigated both psychophysical and oculomotor responses to transparent, motion parallax stimuli. Optical flows were computer-designed and projected on a tangent screen, in such a way that binocular disparity or distance information remained constant across conditions. Such displays always triggered optokinetic nystagmus (OKN), consisting in a succession of tracking eye movements in the direction of visual motion (slow-phase of OKN) and fast resetting saccades in the opposite direction. We used the characteristic slow temporal build-up of the perception of structure-from-motion (Treue *et al.* 1991) to explore the properties of tracking eye movements during the first, initial eye velocity rise, that is before the perception of structure-from-motion occurred, and during the steady-state OKN triggered by long-lasting stimuli when subjects were asked to pay attention to the global optic flow or to a given component in the velocity flow field. Tracking eye movements were analyzed during the slow-phase of OKN.

## GENERAL METHODS

*Visual stimuli*

Random-dot optical flows were computer-generated using a micro-computer (HP 486 DX2, 66 MHz) expanded with an image processing system (Matrox Board SM 1281, 1280 * 1024 pixel resolution). The stimuli were projected on a tangent, flat white screen using a trichrome video projector (Electrohome 3001), at 60 Hz frame rate. The flat screen was homogeneously white without any visible textural structure. The visible display size was 3.2 m horizontally and 2.6 m vertically, and straight ahead of the subjects' eyes. Subjects were seated in front of the screen, at a viewing distance of 3m. At this distance, the visual stimulation covered a rectangular visual field sustaining 56 x 47 deg along the horizontal and vertical meridians, respectively. Subjects were placed in total darkness, inside a large black booth.

Except for velocity field structure, all physical parameters (contrast, luminance, ...) remained identical during the experiments. Optical flow patterns consisted in rightward motion of a set of 100 randomly distributed dots. Except for the experiment using limited dot life-time, as soon as a dot disappeared on the right side of the screen, it was replaced on the left end side. Each dot covered 0.044 deg of visual angle. Dot density was 0.04 dots/deg2. Luminance of the dots was 4 cd/m2 and background luminance was 0.002 cd/m2.

Four different types of optical flow patterns were used across the different experiments. All consisted in a translational flow field where the number of motion signals in the velocity field, the magnitude of velocity differences and, in one experiment, dot life-time were manipulated. Vision was always binocular. Neither texture gradients (change in dot size or dot density with simulated distance from the observer), binocular disparity (all the dots were in the same actual plane of the screen) or dot luminance were manipulated.

Single-velocity optical flows consisted of an homogeneous rightward motion of all the dots, at constant linear velocity. Single-velocity flow fields resulted in the perception of a rigid vertical plane moving rightward at constant velocity. The different velocities used in single-velocity flows were combined to generate either double-velocity or triple-velocity flows. Double- (triple-)velocity flow fields resulted in the perception of a rigid structure composed of two (three) vertical planes lying at two (three) distances from the observer, with distance being inversely related to velocity. Finally, multi-velocity flows were generated by having dot velocity ranging from a lower to an upper boundary. When facing such optical stimulation, subjects perceived a moving cloud of dots extending in depth from them. The different velocities were equally and randomly attributed to the dots in the display.

*Data recording*

Eye movements were recorded with an infrared reflection system (Iris Skalar Biomed. Inc.). Eye position signals were low-pass filtered (DC-100 Hz, -3 dB), digitized using a 12-bit A-D converter, collected at a frequency of 250 Hz and stored for off-line analysis. Although vision was binocular, only horizontal positions from the left eye were recorded. Head stability was achieved using a bite bar and an impression of the subject's teeth made with a dental impression compound. Before each experimental session, the eye movement recording system was calibrated by having the subject look at ten different targets located at known positions (from -25 to 25 deg, with 5 deg steps), presented in random order. Linearity of the conversion from inputs from the A-D converter to angular values was checked before the beginning of each session (the correlation coefficient had to be greater than .995). If this was not the case, captors were readjusted and the calibration procedure was repeated until satisfaction of the linearity criterion.

In one experiment, subjects were asked to identify the 3D structure specified by the visual stimulation. Reaction time was measured by recording the response of the subject on a three button computer-mouse, at 60 Hz (locked to frame rate).

**EXPERIMENT 1.**

**Method**

*Visual stimuli:* Two conditions of optic flow were used in this experiment. Single-velocity flows were used as control stimuli to investigate the gain and the distribution of slow-phase eye movements evoked by a stimulus with a single motion vector. There were 5 conditions of single-velocity flow: 5, 11, 21, 42 and 84 deg/sec ("straight ahead" optical velocities). Three conditions of triple-velocity flows were used. Velocities were either 84-42-21 deg/sec, 42-21-11 deg/sec and 21-11-5 deg/sec, respectively. Each of these 8 conditions was presented twice. Single- and triple-velocity flow conditions were randomly interleaved. In each trial, a stimulus remained stationary for 1 sec and then moved for 30 sec. The screen was then blanked out for 5 sec during which subjects remained in total darkness.

*Subjects and procedure:* . Five young subjects, aged between 19 and 27 years, participated in the experiment. None had a history of neurologic or ophthalmologic disease, and they were all emmetrope according to the Snellen's visual acuity test. Three subjects were familiar with oculomotor experiments, but they were all naive regarding the purpose of the present study. All subjects gave their informed consent before the experiment. Instruction was given to the subjects to pay attention to the global visual motion without attempting to pursue a particular feature in the visual scene.

*Data analysis: .* Saccadic eye movements were automatically discarded from the eye position data by a computer algorithm using an acceleration criterion. Mean eye tracking velocity was computed by fitting a linear regression across the successive eye positions between two saccadic eye movements. The slope of this linear regression was an estimate of the mean eye velocity. Mean eye velocity and middle of the time-interval between the two saccades were computed for each slow phase of OKN. These data were then gathered across a number of slow phases and over trials of similar stimulus conditions. A mean slow-phase velocity and its standard deviation was computed for each subject and each condition. However, as illustrated in Figure 1, OKN triggered by a triple-velocity flow typically consisted in a succession of slow-phase eye movements with different velocities. To assess the contribution of each motion vector on the control of the steady-state OKN, we computed, for each subject and each condition, the distribution of slow-phase velocities (expressed as a percentage of the total number of slow phases in a given condition). Individual distributions were averaged across subjects, in order to obtain a mean distribution profile for each experimental condition. In such distributions, the spreading of the distribution is dependent upon both inter-subject variability in the average eye velocity of slow phases and intra-subject variability across eye velocity during each given trial.

**Results**

Figures 1a and 1b illustrate typical optokinetic responses recorded in one subject facing a single- and triple-velocity flow, respectively. We can see that a 21 deg/sec single-velocity flow elicited a strong, regular, OKN where eye tracking velocity closely matched stimulus velocity. When the subject was presented with a flow field composed of three motion vectors (21, 11 and 5 deg/sec), eye movements consisted in an irregular OKN. As illustrated by the velocity profile, slow-phase velocity was more irregular, with a clear dominance toward the slowest velocity in the motion parallax field.
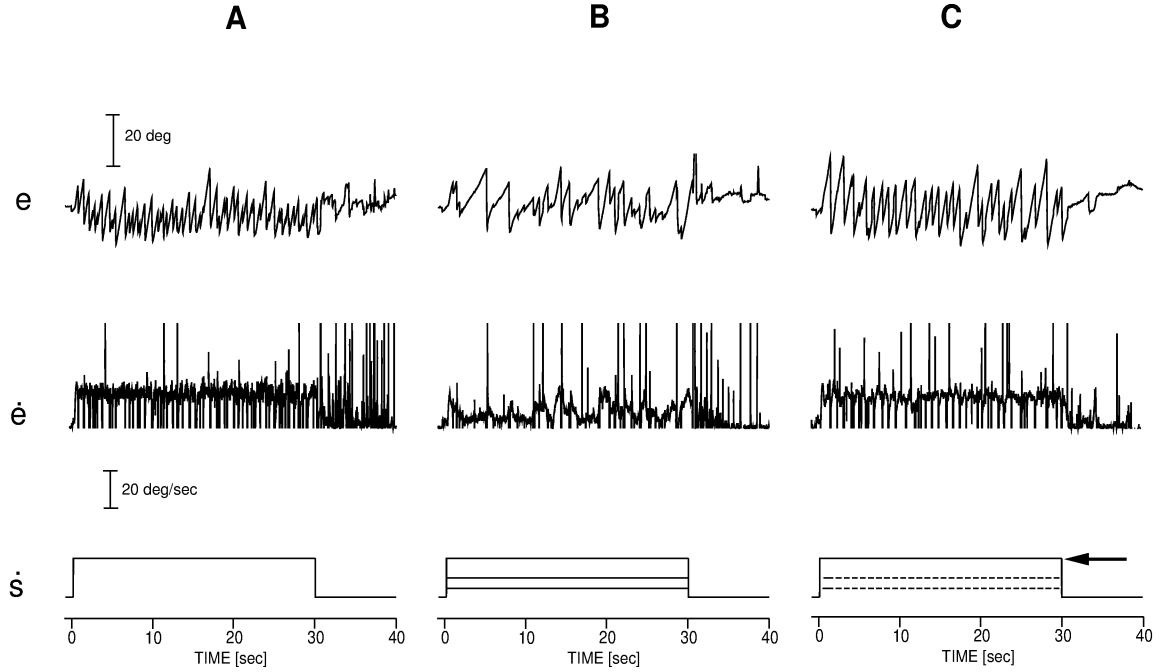
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Figure 1. Eye movements elicited by (a) an optical flow with a single visual velocity (21 deg/sec) specifying rightward motion of a vertical plane, (b) an optical flow containing three velocities (5, 11 and 21 deg/sec), specifying three moving vertical surfaces, separated in depth. The subject was asked to pay attention to global motion. (c) the same triple-velocity flow when the subject was asked to pay attention to the surface specified by a velocity of 21 deg/sec, as indicated by the arrow. e : horizontal eye position. $\dot{e}$ : horizontal eye velocity. $\dot{s}$ : stimulus velocity. Velocity of saccadic eye movements are clipped.

## Optokinetic responses to single-velocity flows:

Single-velocity stimuli elicited regular, consistent involuntary OKN with slow phase eye velocity close to flow velocity for velocities up to 40 deg/sec. Figures 2a illustrates average distribution profiles obtained for the five optical flow velocities. For a velocity of 5 deg/sec, the peak of the distribution was centered on the optical flow velocity. For velocities of 11 and 21 deg/sec, the peak of distribution was shifted towards lower velocities and the spreading of the distribution increased. For a velocity of 42 deg/sec, the distribution peak is barely visible (around 30 deg/sec) and the distribution spreads from 10 to 40 deg/sec. Finally, for a velocity of 84 deg/sec, no peak was evident and the distribution spread from 5 to 60 deg/sec.

An analysis of variance conducted on slow phase average velocity revealed a significant effect of flow velocity ($F[4,16] = 13.73$; $p<.001$), meaning that average slow-phase velocity increased as a function of optical flow velocity. Figure 2b shows that average slow-phase velocity was close to stimulus speed for velocities up to 21 deg/sec. For higher velocities, average slow phase eye velocity was less than optical flow velocity. Notably, the difference between 42 and 84 deg/sec was no longer significant ($p>.60$). Figure 2b also shows that inter-subject variability increased for velocities greater than 40 deg/sec. An analysis of variance conducted on the standard deviation of slow phase velocity (calculated for each subject and each condition) also revealed a significant effect of flow velocity ($F[4,16] = 8.39$; $p<.01$), meaning that intra-subject variability of slow phase eye velocity increased when optical flow velocity increased. From these results, we can note that the evolution of distribution profiles associated with increases of optical flow velocity is due to a weakening of the oculomotor response to optical flow for velocities greater than 40 deg/sec and to an increase in inter- and intra-subject variability in slow phase eye velocity.
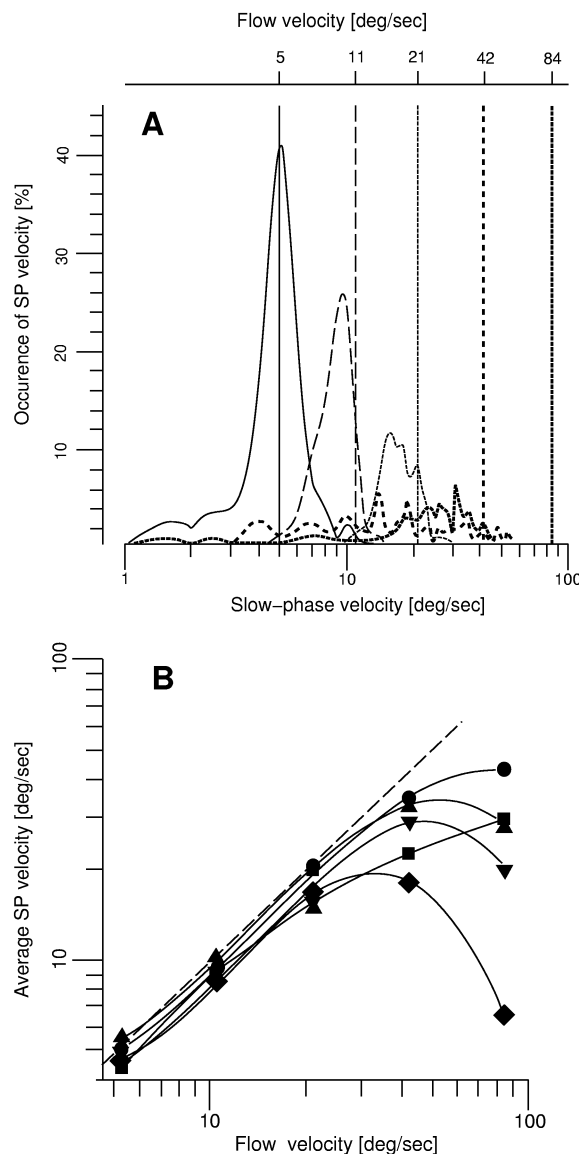
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Figure 2. Optokinetic response to a single-velocity flow. (a) Distributions of the occurrence of slow-phase (SP) velocity (expressed as a percentage of the total number of slow-phases, averaged across subjects), as a function of SP velocity (in deg/sec), for five different stimulus velocities. (b) Average slow-phase velocity, for each subject, as a function of stimulus velocity. The dotted line corresponds to an optimal ratio of 1 between eye and stimulus velocity.

*Optokinetic responses to triple-velocity flows:*

When subjects were simply asked to pay attention to global motion in a triple-velocity flow, slow-phase eye velocity distribution profiles were centered around the slowest velocity in the optical flow (Figure 3a-c). However, the spreading

of distribution profiles was always significantly larger for triple-velocity flows than for single-velocity flows of comparable (slowest) velocity (compare figures 3a, b, c and 2a).

Concerning average slow phase velocities (Figure 3d), an analysis of variance revealed that, with a triple-plane flow with velocities equal to 5, 11 and 21 deg/sec, the average slow phase velocity was significantly higher than that observed with a single-plane flow with a velocity equal to 5 deg/sec (F[1,4]= 47.32; p<.002), not significantly different from those observed with a single-plane flow with a velocity of 11 deg/sec (p>.90), and significantly lower than that observed with a single-plane flow drifting at 21 deg/sec (F[1,4] = 151.9; p<.001). With a triple-plane flow including velocities of 11, 21 and 42 deg/sec, the average slow phase velocities were significantly higher than those observed with a single-plane flow of 11 deg/sec (F[1,4] = 23.55; p<.008) and significantly less than those observed for a single-plane flow drifting at 21 deg/sec (F[1,4] = 744.88; p<.0001). Finally, with a triple-plane flow with velocities equal to 21, 42 and 84 deg/sec, the average slow phase velocities were not significantly higher than that observed with a single-plane flow moving at 21 deg/sec (F[1,4] = 6.77; p>.05).

These results indicate that, when subjects were simply asked to pay attention to a display containing motion parallax, slow phases of OKN were not controlled by the average velocity of the motion parallax flow field. On the contrary, results show that slow-phase tracking eye movements were controlled by motion components present in the flow field, with a strong bias toward the slowest velocity. However, residual retinal velocities appear to trigger some faster slow phases, increasing the average slow phase velocity. This argument is also supported by the increased spreading of the distribution profiles, when comparing ocular responses to single- and triple-velocity flows.

**EXPERIMENT 2**

In this control experiment, we tested the nature of tracking eye movements observed in the first experiment. Were they driven by global motion or voluntary tracking eye movements of single elements in the display (one of the slowest dots in a triple-velocity flow for instance).

**Method**

The experimental conditions were similar to Exp.1, except that three different life-time durations were used. In the first condition, reproducing the conditions of Experiment 1, life-time was "infinite": any single dot lasted for its whole displacement from the left side to the right side of
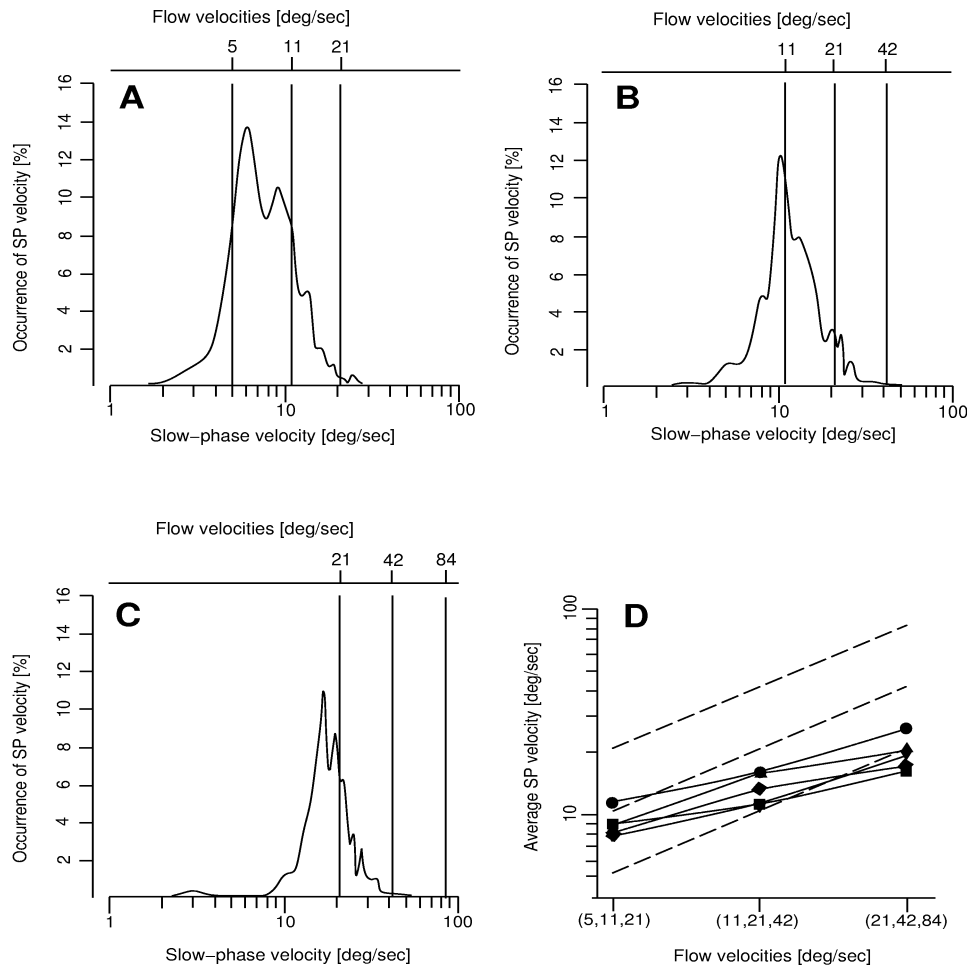
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Flow velocities [deg/sec]



Figure 3. Optokinetic response to a triple-velocity flow. Distributions of the occurrence of slow phase (SP) velocity (averaged across subjects), as a function of SP velocity (in deg/sec), when subjects were simply asked to pay attention to global motion, when presented with velocities of 5, 11 and 21 deg/sec (a), of 11, 21 and 42 deg/sec (b), of 21, 42 and 84 deg/sec (c). (d) Average slow-phase velocity, for each subject, as a function of optical flow velocities. Dotted lines correspond to a ratio of 1 between slow phase eye velocity and each of the optical velocities in the optic flow. From the bottom of the figure, the three dotted lines correspond an optimal ratio of 1 between eye velocity and the lowest, intermediate or highest velocity, respectively.

the screen. In this case, the life-time of each dot depended on its optical velocity. For a maximal velocity of 46 deg/sec, dot life-time was approximately equal to 1 sec. Otherwise, each dot was displayed for a pre-selected duration, defined as its lifetime (83 or 166 msec, that is 5 or 10 frames at 60 Hz). At the end of its lifetime, a dot disappeared and randomly reappeared at a new location on the screen to begin a new trajectory. Dot lives were interleaved, such that, if dot lifetime was equal to x frames, 1/x of the dots were replaced on each frame. This method rendered highly improbable the persistence of a spatial pattern of dots over successive frames. Subjects were asked to stare at a display containing dots moving at 12, 23 and 46 deg/sec (triple-velocity flow) or only one of these velocities

(single-velocity flow). Dot life-time conditions and motion conditions were randomly interleaved. Stimulus presentation, eye movements recording and data analysis were the same as in Experiment 1.

*Subjects and procedure:* Four new naive subjects, all emmetropes according to Snellen's test, participated in the experiment. As in Exp. 1, they were asked to pay attention to global motion. If the subjects actually tracked global motion, no main effect of dot-lifetime on the oculomotor behavior was expected. A slight decrease in the gain of the slow phase responses might be expected due to the noise added in the display by decreasing dot life-time. On the contrary, if the subjects voluntary selected and

tracked a given dot, the duration of tracking eye movements should be related to dot life-time.
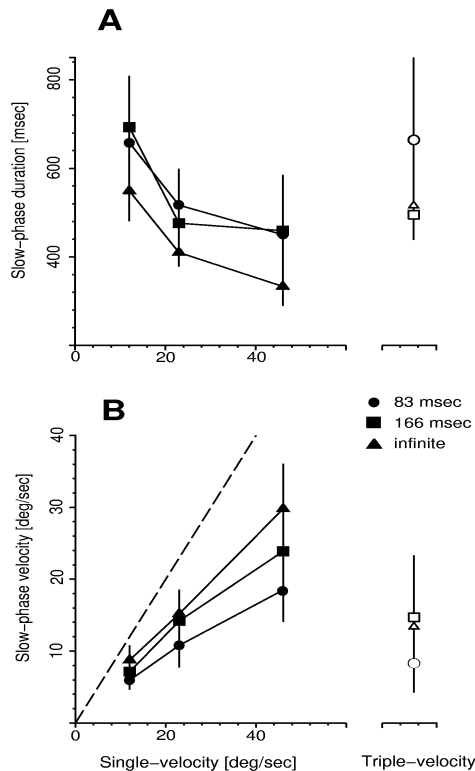
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*Figure 4. Effects of dot life-time on slow-phase duration (a) and velocity (b) of OKN (averaged across subjects) for single-velocity flows, for velocities of 12, 23 or 46 deg/sec and for a triple-velocity flow, containing these three velocities.*

## Results

For infinite life-time conditions, as in Exp. 1, subjects correctly perceived the three-dimensional structure specified by the visual stimulation. However, the manipulation of dot life-time clearly decreased the signal-to-noise ratio in the display. With a 166 msec dot life-time, subjects still perceived the three-dimensional structure. Such perception was lost for the 83 msec dot life-time condition.

Figure 4 illustrates the effects of life-time on the average slow-phase duration and slow-phase velocity across subjects. As shown in Figure 4a and 4b, decreasing dot life-time resulted in a significant increase in slow phase duration (F[2,6] = 9.06, p<.02) and in a significant decrease in slow phase tracking velocity (F[2,6]=8.36, p<.02). Such an increase in slow phase duration when dot lifetime is reduced cannot correspond to voluntary tracking of individual dots, which would result in the opposite effect. Post-hoc analyses revealed that

mean slow-phase velocity was only significantly reduced for a dot life-time of 83 msec, as compared to the two other life-time values (F[1,3]=20.66, p<.02). As can be seen in figure 4b, this effect was maximal for a triple-velocity, in which the reduction in slow phase velocity was equal to 40 %.

## EXPERIMENT 3

In experiments 1 and 2, we demonstrated that, when subjects were simply asked to stare at motion parallax displays, tracking eye movements were driven by global motion and spontaneously matched the slowest velocity component in the optic flow. However, the selection of a specific global motion signal might also be modulated by attention. We already know that optokinetic eye movements depend on the instructions given to the subject before the stimulus onset (Honrubia *et al.* 1968) Thus, selective attentional processes may determine the motion signal to be tracked in motion parallax displays. We investigated this point by asking the subject to pay attention to a given "depth plane", perceived from the velocity field. The same three triple-velocity flows as in Experiment 1 were used. The procedure, data recording and analysis were also identical. "Planes of attention" were defined as the closest, the middle or the farthest plane in the display, corresponding to the fastest, the intermediate and the slowest velocity field, respectively. Each triple-velocity flow was presented 6 times (3 "attention" conditions x 2 repetitions) in random order, for 30 seconds.

Subjects were the same as in Exp. 1. They easily detected the different depth planes. No subject reported failure to select a plane and to direct his/her attention towards it.

## Results

As illustrated in Figure 1c, when the subjects were instructed to pay attention to a particular depth plane in a triple-velocity flow, steady-state OKN was still observed, with slow-phase eye velocity matching the velocity of the selected plane. Therefore, the average distribution of slow phase eye velocity was centered on the velocity of the selected plane, for optical velocities up to 40 deg/sec, as illustrated in Figures 5a-c. This pattern of data was greatly similar to that observed when subjects were viewing single-velocity flows drifting at a similar velocity (compare Figures 5 and 2).
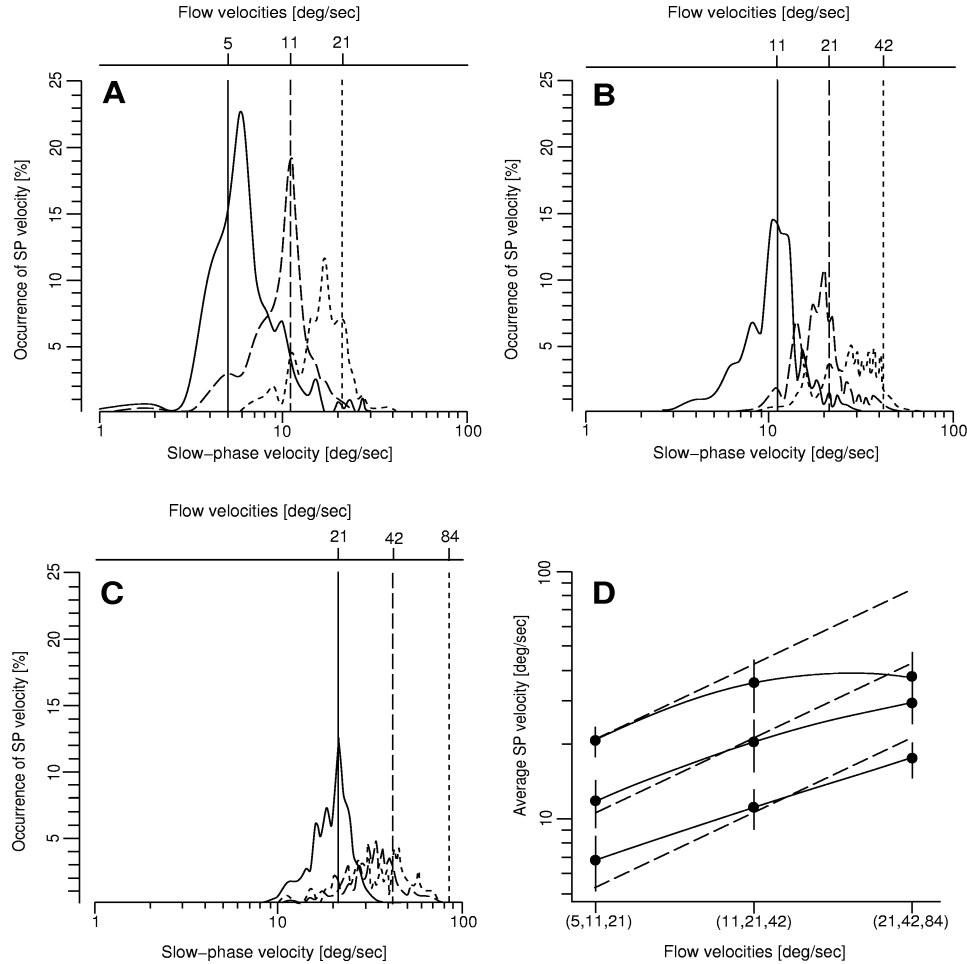
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Figure 5. Distributions of the percentage of occurrence of slow phase (SP) velocity (averaged across subjects), as a function of SP velocity, when observers are presented with triple-velocity flows, and asked to look successively at each plane specified by the motion field. (a) The optical flow field contains optical velocities of 5, 11 and 21 deg/sec. The three distributions (from left to right) correspond to conditions where subjects are asked to look at the farthest plane (5 deg/sec), the intermediate plane (11 deg/sec) and the closest plane (21 deg/sec). (b): The optical flow field contains velocities of 11, 21 and 42 deg/sec. (c): The optical flow field contains velocities of 21, 42 and 84 deg/sec. (d). Average slow-phase velocity, averaged across subjects, as a function of optical flow velocities. From bottom to top, subjects are asked to look at the farthest (slowest), intermediate and closest (fastest) plane, respectively. Vertical lines indicate standard deviation.

Consequently, average slow phase eye velocity of the OKN was close to the velocity of the selected plane, for velocities up to 40 deg/sec (Figure 5d). Interestingly, when subjects were instructed to look at the plane defined by the slowest velocity in a triple-velocity flow with velocities of 5, 11 and 22 deg/sec, the average velocity was significantly less than that observed when subjects had to stare at the same triple-velocity flow (F[1,4] = 9.79; p<.04) while paying attention to global motion (see Exp.1), but was still significantly greater than that observed when subjects looked at a single-velocity flow drifting at 5 deg/sec (F[1,4] = 12.6; p<.02)

(compare Figures 7d, 4d and 3b). For velocities greater than 11 deg/sec, the average slow phase velocity observed when subjects looked at a given plane was not significantly different from that observed when subjects looked at a single-velocity flow of similar velocity. This result indicates that, even if residual retinal velocities of the two other planes might trigger some faster slow phases when subjects focus their attention on the slowest plane, this is only true for a low velocity of 5 deg/sec and this effect is significantly reduced, as compared to the situation where subjects simply looked at a triple-velocity flow.

## EXPERIMENT 4

In this experiment, both oculomotor behavior and perceptual discrimination of structure-from-motion were investigated simultaneously. We designed a simple experimental task in which subjects had to discriminate between optical flows, specifying either a single vertical plane (single-velocity flow), two vertical planes separated in depth (double-velocity flow) or a "cloud" of dots extending in depth (multi-velocity flow). Numerous studies have already demonstrated the ability of human observers to perceive depth from motion accurately in transparent dot-displays. To do so, subjects must extract the depth structure from relative global motions. However, it might be possible to perform a discrimination task using only local motion cues. The subjects may look for the presence of more than one velocity in a small local region of the display. To avoid this potential artifact, we interleaved double-velocity flows, in which only two velocities were present and multi-velocity flows, in which more than 10 different velocities were present. In these two flows, there was more than one velocity in a local region. However, and also because we used low density random dot kinetograms, the correct discrimination between a cloud of dots and two planes required differential global motion analysis.

### Method

Subjects were presented with three different types of optic flow field: single-velocity, double-velocity and multi-velocity flows. Six single-velocity flows were used: 9, 12, 17, 23, 35 and 46 deg/s. Three different double-velocity flows were used : (9,12), (17,23) and (35,46) deg/s. Finally, a multi-velocity flow was generated, in which velocities ranged from 9 to 46 deg/s with at least 10 steps of velocity, randomly distributed over the random dot pattern. Subjects were asked to discriminate between one plane, two planes or a cloud of dots by depressing one of the three buttons of a computer mouse.

Visual stimuli were presented stationary for 2 seconds. Motion was always to the right. Visual stimulation and data acquisition were stopped 3 sec after the discrimination of structure-from-motion, and the screen went blank. Inter-trial delay was approximately 5 sec. The three different types of flows were interleaved during 5 blocks of 72 trials. To ensure equi-probability between each type of flow, each single-velocity flow was presented 3 times, each double-velocity flow was presented 6 times and the multi-velocity flow was presented 18 times, across one block.

*Data analysis:* Reaction time for the discrimination task was defined as the time elapsing from the onset of the motion to the onset of the psychophysical response. Eye movements were recorded monocularly for the entire trial. Two successive analyses were applied to eye movement recordings. First, the initial rise of eye velocity was analyzed. Eye position data were digitally low-pass filtered and then differentiated. All the velocity traces for a single condition were displayed with a videographic interactive program. All the trials containing a saccadic intrusion between 50 msec before and 400 msec after the stimulus onset were discarded. This method ensured both no contamination of the velocity profiles by micro-saccadic eye movements and a fixed time window independent of the time of the first saccadic eye movement. Because we were interested in the time required for the visual processing of the optic flow, this time-window method was more accurate than the measurement of the velocity reached just before the occurrence of the first saccadic eye movement. Unfortunately, because of the poor dynamic resolution of the infra-red recording method, velocity analysis during the very first, open-loop, part of the oculomotor response was impossible. After deletion of the selected trials, velocity profiles were averaged to obtain a mean velocity profile for each subject and each condition. Quantitative measures were obtained for the maximal velocity reached during the initial eye velocity rise in the same time window (-50 to 400 msec), for each trial. The mean and standard deviation of the peak velocity were computed for each subject and for each condition. Changes in slow phase eye velocity during a trial were further investigated by computing the mean velocity of each slow phase occurring between the onset of the first saccadic eye movement and the end of the stimulus, 3 seconds after the psychophysical response.

*Subjects:* Three subjects, including the two authors, participated in the experiment. The third subject was unaware of the purpose of the experiment.

### Results

*Reaction time for structure-from-motion discrimination:* . The three subjects tested were able to discriminate between the three types of optic flow at the 90-100% correct level. As previously reported in numerous studies, the discrimination of structure-from-motion requires a long processing-time as illustrated by the long reaction times (longer than 1 sec., Figure 6c).
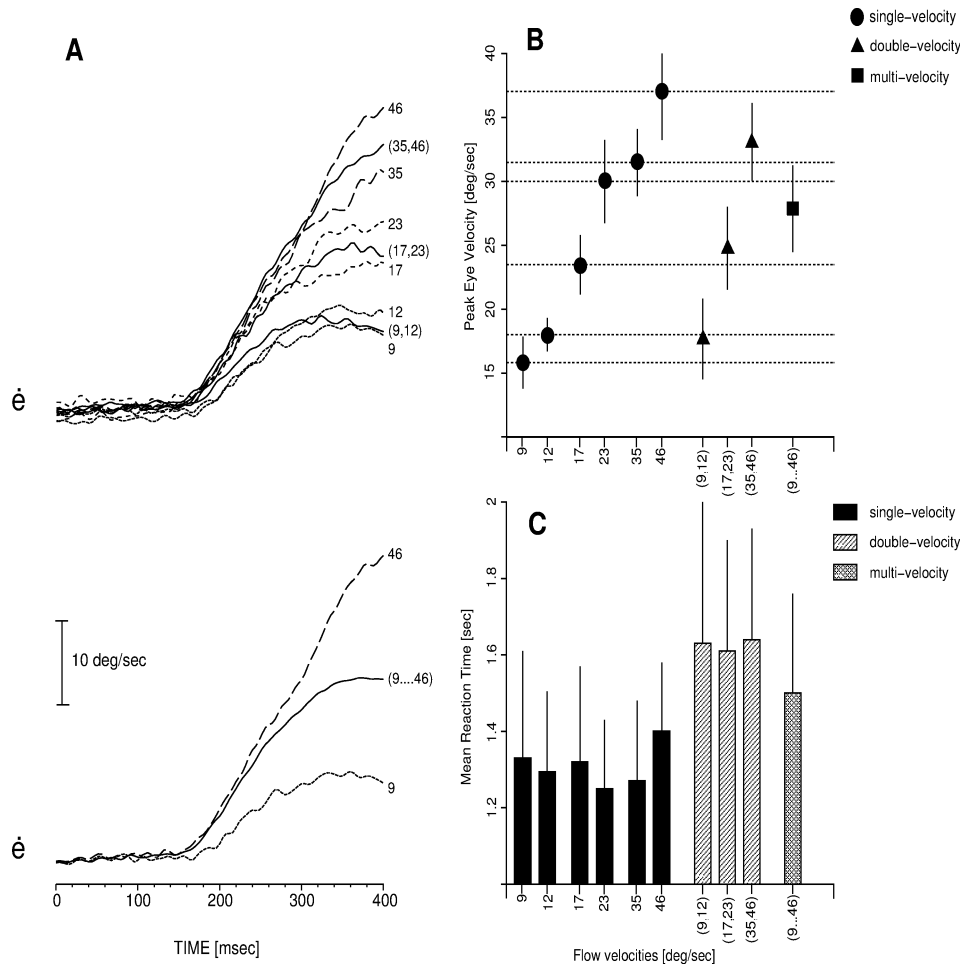
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*Figure 6. Initial oculomotor tracking behavior and psychophysical reaction time induced by single-, double- or multi-velocity flows. (a) Initial eye velocity profiles for one subject. Each curve represents the average of 10 to 40 trials. In the upper plot, the initial eye velocity elicited by flow fields containing two velocities lies between the eye velocities elicited by each of their velocity components. In the lower plot, the initial eye velocity elicited by a multi-velocity flow containing velocities ranging between 9 and 46 deg/s lies around the average velocity of responses elicited independently by its velocity components. Only the responses to the highest and slowest velocity are represented. (b) Peak eye velocity reached by the eye 400 msec after the onset of the stimulation (averaged across subjects, ± s.d.), as a function of flow conditions. Horizontal dashed lines correspond to each of the peak velocities reached with single-velocity flows. They are used as reference lines for the peak eye velocities obtained with double-velocity or multi-velocity flows. (c) Average Reaction time (averaged across subjects, ± s.d.) obtained when subjects were asked to discriminate between one surface (specified by a single-velocity flow), two surfaces (specified by a double-velocity flow ) and a cloud of dots extending in depth (specified by a multi-velocity flow).*

Mean reaction time for the identification of a single plane ranged between 1.64 +/- 0.3 and 1.09 +/- 0.13 sec. Average reaction time across subjects was 1.3 +/- 0.18 sec and no significant differences were found between the different velocities in single-velocity flows. Reaction times were significantly shorter for single-velocity than for double- or multi-velocity flows. Average reaction time across velocities was 1.62 +/- 0.28 sec for a double-velocity flow, and 1.51 +/- 0.26 sec for a multi-velocity flow. No significant differences in reaction time were found between the different velocities in the double-velocity condition or between the double- and multi-

velocity conditions. Data from a fourth, naive subject, obtained without the recording of eye movements, showed a similar pattern, with long reaction times and high correct response levels.

*Initial velocity rise of optokinetic eye movements:* Figure 6a illustrates the average velocity profiles of the initial tracking phase of OKN for one subject. Similar profiles were observed for the two other subjects. For a stimulus with more than one velocity, the initial velocity rise of OKN was intermediate between those evoked by the same velocities presented separately. For instance, 400 msec after the

onset of a double-velocity stimulus with two velocities of 35 and 46 deg/sec (Figure 6b), eye velocity was intermediate between the eye velocities evoked by single-velocity stimuli of 35 and 46 deg/sec. Similarly, with the multi-velocity stimulus, eye velocity after 400 msec was intermediate between the velocities evoked by the different single-velocity flows moving at a velocity ranging between 9 and 46 deg/sec.

For each subject and each trial, the peak eye velocity between -50 and 400 msec relative to the onset of the random dot kinetograms was computed. Figure 6b illustrates the mean (± SD) of the peak velocity for each condition. As illustrated, maximal velocity during the initial oculomotor response when the visual stimulus was either a double- or multi-velocity flow was roughly the average of the maximal velocities reached by the eye when the subjects faced the different corresponding single-velocity flows. For instance, with a double-velocity flow including velocities of 46 deg/sec and 35 deg/sec, the initial maximal eye velocity was significantly less than the maximal eye velocity observed when subjects were presented with a single-velocity flow drifting at 46 deg/sec ($F[1,2] = 46.25$; $p<.02$) and significantly greater than the peak eye velocity evoked by a single-velocity flow of 35 deg/sec ($F[1,2] = 29.79$; $p<.03$). Similarly, for the multi-velocity flow, the maximal eye velocity was on average equal to 28 ± 4 deg/sec, and not significantly different from the maximal eye velocities evoked by single-velocity stimuli of either 17 or 23 deg/sec ($p>.10$).

*Time-course of optokinetic eye movements:* After the initial phase of the ocular response, eye movements consisted of a regular OKN. After the psychophysical response was established, tracking eye velocity tended, for double-velocity flows, to be close to the slowest velocity in the flow field. Thus, for the first double-velocity stimulus (35 & 46 deg/sec), eye velocity was significantly less than that observed when subjects were presented with a single-velocity flow of 46 deg/sec ($F[1,2] = 44.79$; $p<.02$) and not significantly different from that observed when subjects were presented with a single-velocity flow of 35 deg/sec ($F[1,2] = 8.17$; $p>.10$). Similarly, with the second double-velocity stimulus (17 & 23 deg/sec), eye velocity was significantly less than that observed with a single-velocity flow of 23 deg/sec ($F[1,2] = 59.51$; $p<.02$) and not significantly different from that observed with a 17 deg/sec single-velocity stimulus ($F[1,2] = 2.13$; $p>.20$). For the third double-velocity stimulus, slow-phase eye velocity was between those observed with a 12 deg/sec and a 9 deg/sec single-velocity flow, and not significantly different from either ($p>.05$). Finally, with the multi-velocity stimulus, average eye velocity was 19 ± 4 deg/sec, and not significantly different from that observed with either a 17 or a 23 deg/sec single-velocity flow field ($p>.15$).

We further investigated the change in slow phase velocity between the first saccadic eye movement and the end of stimulation. By pooling all individual data and fitting a linear regression to eye velocities plotted as a function of time (for a duration of about 4.5 sec, between stimulus onset and 3 seconds of stimulus duration after the subjects' response (occurring at about 1.5 sec), we found that the only significant correlation coefficients were found with double-velocity flows ($p<.02$ or better). Regression coefficients were not significant for single- and multi-velocity flows. This pattern of results demonstrates that, with double-velocity flows, eye velocity decreased over time to finally match the slowest velocity in the flow field, whereas slow-phase eye velocity remained constant and equal to the average velocity of the stimulus with either single or multi-velocity flows (Figure 7).
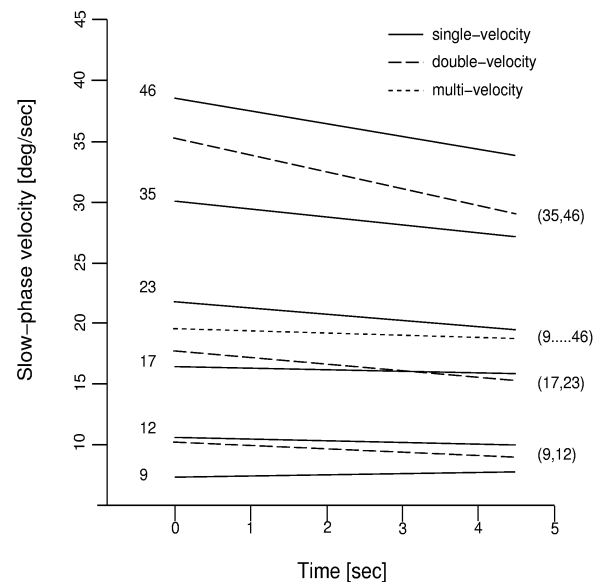
G .sp -.5



*Figure 7. Schematic representation of the evolution of slow phase velocity, as a function of time and of the different flow types. Regression lines have been fitted through the actual data. Regression coefficients are significant only for double-velocity flows, meaning that eye velocity is then reduced over time. For single- and multi-velocity flows, regression coefficients are not significant (eye velocity remains more or less constant over time).*

**EXPERIMENT 5**

In the fourth experiment, we demonstrated that, before the detection of structure-from-motion, the velocity of tracking eye movements equaled the average velocity of the flow field. After psychophysical detection occurred, eye velocity decreased to reach the slowest velocity in stimuli containing two velocities and specifying two planes in depth. This decrease was not observed with multi-velocity flows which contained more than ten velocities. One might

then ask whether it takes longer for the oculomotor system to move down to the slowest velocity when many motion signals are present, or whether the fact that slow phase eye velocity remains equal to the average velocity is related to the failure of the system to segregate the optic flow into its motion components. In the latter case, this result might be related to the limited ability of the human visual system to represent several motion signals simultaneously. Andersen (1989) demonstrated that subjects were unable to perceive more than three different motion-defined surfaces. To investigate whether this constraint extends to the oculomotor system, we recorded eye movements elicited by four different types of random dot kinetograms : single-, double-, triple- and multi-velocity flows.
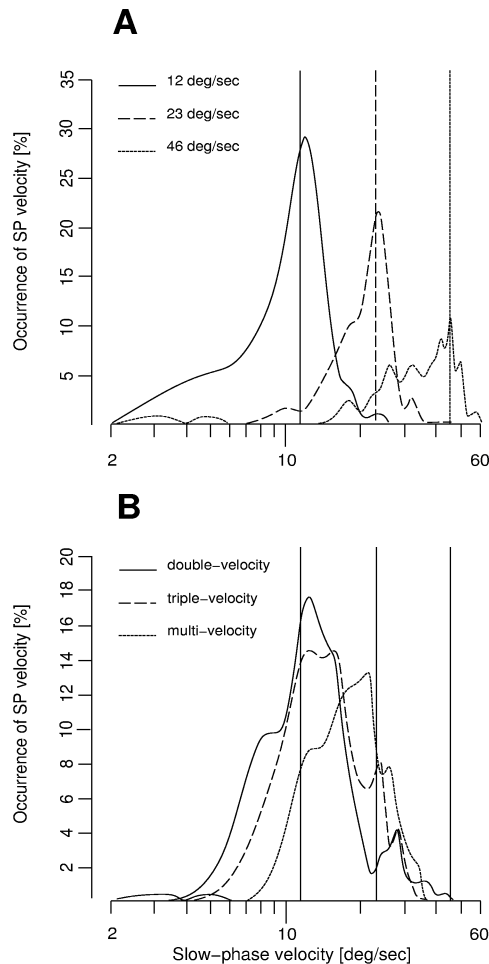
G .sp -.5



*Figure 8. Distributions of the percentage of occurrence of slow-phase velocity (averaged across subjects), as a function of SP velocity. (a) When observers are presented with single-velocity flows, the distribution is centered on the optical velocity (12, 23 or 46 deg/sec). (b) When observers are presented with a double-velocity flows containing velocities of 12 and 46 deg/sec, the distribution is centered on the slowest velocity (12 deg/sec). The same pattern is observed with a triple-velocity flow containing*

velocities of 12, 23 and 46 deg/sec. Finally, when observers are presented with a multi-velocity flow with velocities ranging from 12 to 46 deg/sec, the distribution is centered on the average optical velocity (23 deg/sec).

## Method

*Visual stimuli and procedure:* Random dot kinetograms were computed and displayed exactly in the same way as in the previous experiments. The four different types of optic flow were randomly interleaved and displayed for 30 sec after 1 sec of stationary presentation. At the end of the stimulus, the screen was blanked out for 5 sec before the beginning of the next trial. Three different single-velocity flows were used as controls (46, 23 and 12 deg/sec). The triple-velocity flow was composed of these three motion components randomly distributed over the random dots, while the double-velocity flow was composed of two velocities (46 and 12 deg/sec). Finally, the multi-velocity flow contained more than ten velocity components ranging between 46 and 12 deg/sec (mean velocity, 23 deg/sec). Each type of optic flow was presented four times to provide a large number of slow phase eye movements for each subject and condition.

*Subjects, Data recording and analysis:* Eye movements were recorded in three head-fixed subjects (the two authors and one naive subject). Average velocity and velocity distribution of slow phase eye movements were computed for each subject and each condition, across the two trials for a same optic flow condition to give a large total number of slow phase eye movements. Analyses were performed in a way similar to Experiment 1. Subjects were simply asked to stare at the display.

## Results

As previously demonstrated, the distributions of slow phase eye velocity when subjects faced a single-velocity flow were centered on the velocity of the display (figure 8a). Slow phase eye velocity distributions elicited by a motion parallax display are plotted in Figure 8b. For the multi-velocity flow, the occurrences of slow-phase eye velocity followed a unimodal distribution centered around the mean velocity of the optic flow (23 deg/sec). On the same graph are plotted the occurrences of slow-phase eye velocity evoked by a double- or a triple-velocity flow. The peaks of both distributions are centered on the slowest velocity in the motion field (12 deg/sec).

## GENERAL DISCUSSION

During relative motion between an observer and a rigid three-dimensional environment, different optical velocities occur in the same or neighboring parts of the visual field, due to variable distances of objects from the observer. One consequence is that, contrary to what happens with rotational motion of the observer, no single eye movement can offset the global image motion. The purpose of the experiments reported here was to investigate how the oculomotor system solves the problem of selecting one motion signal in a motion parallax flow field. Several previously published studies have demonstrated that additional depth cues, such as disparity, may help the oculomotor system to single out the motion signal related to the plane of fixation (Howard and Simpson 1989; Busettini *et al.* 1996) However, as suggested by Busettini *et al.* (1996) , subjects may wish to select a plane of attention different from the current plane of fixation. Such behavior requires the processing of differential motion. In the present series of experiments, we studied oculomotor behavior when human subjects were presented with translational optic flows containing motion parallax. We were careful to avoid segmentation cues such as the partitioning of the visual field into central and peripheral areas (Abadi and Pascal 1991; Gellman *et al.* 1990) Motion transparency allowed us to present visual stimuli specifying a tridimensional structure consisting of several "depth planes" specified by several optical velocities.

### Segregation of motion and oculomotor control

When subjects are presented with transparent displays containing motion parallax, they tend to track the slowest plane of motion. Such spontaneous behavior was observed only when subjects were instructed to pay attention to the global scene. This result suggests that a pre-attentional segregation process is involved in the control of visual stabilization. By default, the slowest velocity output of the segregation mechanism is then selected to drive optokinetic eye movements. Such a bias might reflect a low speed dominance in the velocity tuning of underlying visual processes. It might also be that, in our conditions, the lower speed also defined the most robust motion signal contained in the display (due to refresh rate for instance). In other words, our results might simply reflect a particular instance of the response of the ocular system to the most robust signal in a given display.

However, Niemann, Ilg and Hoffman (1994) reported a velocity dominance of OKN evoked by transparent stimuli. Their results revealed that velocity dominance was tuned to the slowest velocity in their display, apart from one condition (visual velocities of 6 and 12 deg/sec in the display). In experiment 1, we also found that the velocity dominance of OKN was systematically adjusted to the slowest velocity, except for the combination of 5, 11 and 21 deg/sec where the average slow phase velocity was between 5 and 11 deg/sec. Niemann *et al.* (1994) argued that this velocity dominance (around 12 deg/sec in their conditions) might reflect a "general function of the optokinetic system". Without discarding their suggestion, we suggest a more functional explanation, which remains partial with regard to the available data. The role of the optokinetic response is to reduce the retinal slip of a moving visual environment. The optimum choice in a 3D environment might then be to stabilize the slowest moving elements, since this strategy will maintain the direction of motion of faster elements, thus avoiding shearing motion (motion signals with opposite signs). By stabilizing the zone of slowest motion in the optical flow, the optokinetic system might contribute to the perception of heading during translational self-motion, as the focus of radial outflow is, by definition, motionless and corresponds to the instantaneous direction of self-motion (Warren and Hannon 1988)

Aside from this "preference" for the slowest plane of motion observed with long lasting stimulation, we found two situations where tracking eye movements were controlled by the average velocity in the flow field : during the initiation of the ocular response (up to 400 ms after stimulus onset) with any type of flow and during steady-state OKN when more than 10 different velocities were displayed simultaneously. We suggest that such an averaging process reveals two constraints of the pre-attentive differential motion processing enabling the segregation and, consequently, the selection of a given motion in a complex flow field: a slow temporal build-up and a limited ability to segregate and simultaneously represent multiple motion signals.

Motion averaging for tracking eye movements is reminiscent of depth-averaging for vergence eye movements when two disparities are simultaneously presented in a random dot stereogram (Mallot and Arndt 1992) or direction averaging for saccadic eye movements toward multiple targets (Findlay 1982; Findlay and Harris 1993) These averaging processes support a population coding scheme hypothesis. Several neurophysiological data recorded in monkeys' area MT and MST support the idea of integration of motion over short reaction times in the absence of segmentation cues (Bradley *et al.* 1995; Snowden *et al.* 1991; Qian and 1994; Recanzone and 1994) Motion averaging may underlie the behavioral data presented here for the initiation of the ocular response, which depends, in primates, on the integrity of the same areas (Dürsteler and Wurtz 1988)

Further studies are required to determine the properties of the spatio-temporal motion integration involved in the initiation of tracking. Noteworthy, no data are currently available concerning the spatial and temporal windows over which the oculomotor system integrates motion to drive eye movements. Psychophysical results suggest that to discriminate the direction of global motion, the visual system integrates visual motion over long periods of time (up to 450 msec) and over large spatial areas (up 60 deg2) (Watamaniuk and Sekuler 1992) Moreover, Watamaniuk and Duchon (Watamaniuk and Duchon 1992) also demonstrated that, when presented with short duration stimuli (between 250 and 450 msec) containing several velocities, human subjects tend to perceive the average velocity. This suggests that the human visual system is able to achieve a spatio-temporal integration of different velocity signals in the flow flied. By investigating the properties of the initial phase of tracking, we may be able to describe the characteristics of the spatio-temporal integration of visual motion in the oculomotor system and its relationship to the spatio-temporal integration of visual motion in perception.

**Similarities between perceptual judgments and oculomotor processes.**

Qualitative similarities between the control of eye movements in motion parallax flow field and perceptual judgments suggest, furthermore, that similar computations, including segregation and segmentation processes, underlie perceptual judgments and oculomotor behavior.

One similarity between structure-from-motion (SFM) perception and the control of eye movements is the long duration of the evolution of both processes over time. We found that, whereas the initial phase of OKN (before SFM perception) is controlled by the average velocity in the flow field, eye velocity of the subsequent slow-phases (after SFM perception) decreases and stabilizes around the slowest velocity present in an optic flow specifying two or three planes in depth. In the present study, depth perception was characterized by a long discrimination time. Accordingly, all previously published psychophysical results on tridimensional structure-from-motion perception emphasized the very long decision times usually observed (Braunstein and Andersen 1981; Andersen *et al.* 1990; Hildreth *et al.* 1990; Treue *et al.* 1991) These results indicate that the human visual system requires an extended period of time to reach an accurate perception of structure from motion. Thus, a brief observation of a moving pattern sometimes yields a perceived structure which is flatter than the "true" structure of the projected object (Hildreth *et al.* 1990) An incremental rigidity scheme using either position (Ullman 1984) or velocity (Grzywacz and 1987) information has been suggested to explain this

slow temporal build-up of perception. The present results confirm that the identification of a tridimensional structure based on relative motion requires an extended time window, which contrasts with the short time-window (about 80-100 msec) over which single image motion is measured (McKee and Welch 1985) A comparison between the time-course of modifications in tracking eye velocity and the build-up of perception might provide further insight about the nature of segregation and integration processes and about their temporal dynamics. No attempt to correlate the change in the oculomotor behavior and the perceptual build-up has been previously reported. For instance, Ringach, Hawken & Shapley (1996) studied vergence responses to the kinetic depth effect after the subject had reached a "steady-state" representation of the surface. From the present study, we suggest that, by looking at the relative time-course of oculomotor behavior and perception, we may understand how high-level processes, such as the representation of a tridimensional structure, are involved in the control of tracking eye movements. The relationship between the time-constant of the slow-phase eye velocity decrease and the perceptual build-up must be further and more precisely investigated, using the present approach.

Secondly, we demonstrated that, when more than ten different motion vectors were displayed simultaneously in the flow field, the distribution of the slow-phase velocity during steady-state OKN was centered on the average velocity of the flow field. This "average" ocular response may be related to the limited ability of the visual system to sort out and represent several motion signals simultaneously, over the same spatial area. Supporting this hypothesis are previous results showing that human subjects cannot discriminate more than three transparent surfaces when more than three different velocities are displayed in random-dot displays (Andersen 1989) Andersen suggested that this inability cannot be explained by the reduced dot density of each surface or by the smaller velocity increment between two "adjacent" surfaces, as the number of surfaces is increased. On the contrary, he argued that the fact that subjects could not discriminate more than three planes might be the result of a limitation in the number of channels for information processing in both the temporal and spatial domains. The present results suggest that similar limitations exist for both oculomotor behavior and perception. Further studies are needed to demonstrate whether such similarities are due to low-level motion channels shared by both oculomotor behavior and 3D perception or to a direct control of perception over the oculomotor responses to complex flow fields.

Additional similarities may be found between the dependency of ocular following responses on dot life-time found in the present

study and previously published data on differential motion processing. Computational and psychophysical studies have already suggested that dot lifetime in a random-dot display is an important constraint for the perception of structure-from-motion (Siegel and Andersen 1988; Siegel and Andersen 1988) Treue *et al.* (1991) demonstrated that subjects cannot discriminate between structure and no-structure below a point lifetime of ˉ60 msec. Peak performance was reached at a point lifetime of ˉ125 msec. In Experiment 2, we did not precisely measure the effect of dot life-time on depth perception. Nevertheless, for dot lifetimes of 85 msec a dramatic reduction of SFM perception was reported by the subjects. Similarly, changes in oculomotor behavior were observed, namely a significant decrease in slow-phase eye velocity. Such effects of dot lifetime can also be accounted for by an increase in the velocity noise level in the display. In contrast, no significant changes were observed between "infinite" and 160 msec dot life-time. Moreover, by manipulating dot life-time, we demonstrated that the observed eye movements consisted in tracking of global motion signals and not voluntary tracking of single elements in the motion field.

In summary, the present results suggest that the control of reflexive eye movements is correlated with the subject's perception of depth from motion. More precisely, integration and segmentation of global visual motion into distinct motion fields seem to play a key-role in both processes. Nevertheless, we did not demonstrate that the visual stabilization of gaze in a motion parallax flow is controlled by the perception of depth-from-motion. To do so, it would be necessary to show that a change in eye movements related to depth, such as vergence eye movements, can be caused by the transition of tracking eye movements from one motion field to another. Recently, Ringach *et al.* (1996) demonstrated that the perception of a rotating three-dimensional structure from motion is sufficient to elicit vergence eye movement. It is clear from their study that high-level percepts and mechanisms can drive oculomotor behavior which is directly related to the three-dimensional structure of the environment.

**Modulations of the optokinetic response by attentional processes**

Visual attention is one mechanism that enables us to distinguish important objects or spatial locations from less important ones. It is known that properties of the optokinetic response vary according to the subject's attitude to the task (Braak 1957; Pola and Wyatt 1993) In our study, subjects had to stare at either the whole motion pattern (experiment 1) or at an actively-selected motion-defined depth plane (experiment 3). This enabled us to study the

effect of attentional processes on the same display and the same basic oculomotor behavior. The present results demonstrate that when attention is allocated to the global pattern, the distribution of slow phase eye velocity is centered on the slowest velocity and not on the average velocity of the optical flow field. However, when attention is paid to one of the motion fields, distribution profiles are centered on the velocity of the actively selected field, within velocity upper-limits similar to those observed when subjects stare at a single velocity flow. The results support the assumption that cognitive input does not affect the process of segregation of the flow field into its velocity components, but rather contribute to the selection of which component will be tracked. Thus, we suggest that the optokinetic response is driven by motion-parallax sensitive neuronal inputs, which segregate the global velocity field. Thereafter, the optokinetic response spontaneously selects the slowest velocity in the optical flow, determining a spontaneous gaze stabilization strategy in a translational optical flow. Only the active selection of a given depth plane is cognitively oriented from the perception of structure from motion. Ferrera and Lisberger (1995) have suggested such a network where attention only biases the selection process by which one object is attributed as the target to be pursued. Such a network implies that the different objects in the field have been independently and pre-attentively represented, prior to selection. Recently, Treue and Maunsell (1996) provided some insight about the putative mechanisms for such attentional biases, by demonstrating that, early in the motion pathway hierarchy, as in area MT, an attended stimulus takes greater control of cells' responses than does the unattended stimulus.

In summary, we demonstrated that optokinetic eye movements depend, in complex optical flow fields, on the segmentation of visual motion into distinct motion fields. Further research will focus on the causal links between the perception of depth and the control of conjugate and disconjugate eye movements. Precise comparative measurements of the time-course of perceptual judgments and oculomotor behavior might also give some insight into the temporal aspects of visual motion processing.

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