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Saccade amplitude disconjugacy induced by aniseikonia: role of monocular depth cues

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Abstract

The conjugacy of saccades is rapidly modified if the images are made unequal for the two eyes. Disconjugacy persists even in the absence of disparity which indicates learning. Binocular visual disparity is a major cue to depth and is believed to drive the disconjugacy of saccades to aniseikonic images. The goal of the present study was to test whether monocular depth cues can also influence the disconjugacy of saccades. Three experiments were performed in which subjects were exposed for 15–20 min to a 10% image size inequality. Three different images were used: a grid that contained a single monocular depth cue strongly indicating a frontoparallel plane; a random-dot pattern that contained a less prominent monocular depth cue (absence of texture gradient) which also indicates the frontoparallel plane; and a complex image with several overlapping geometric forms that contained a variety of monocular depth cues. Saccades became disconjugate in all three experiments. The disconjugacy was larger and more persistent for the experiment using the random-dot pattern that had the least prominent monocular depth cues. The complex image which had a large variety of monocular depth cues produced the most variable and less persistent disconjugacy. We conclude that the monocular depth cues modulate the disconjugacy of saccades stimulated by the disparity of aniseikonic images. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Saccade amplitude; Disconjugacy; Aniseikonia; Monocular depth cues

1. Introduction

Normal subjects are able to change the conjugacy of their saccades after only a few minutes of exposure to an image which is magnified for one eye (Kapoula, Eggert & Bucci, 1995; Van der Steen & Bruno, 1995). Aniseikonic images contain a distribution of disparity that simulates a tilt of the image in 3-D space. However, when the image is uniformly magnified subjects do not perceive such tilt, most likely because of the vertical disparities contained by such images (see Ogle, 1950). Yet, as shown by the above cited studies, saccades become unequal for the two eyes. Saccade disconjugacy allows to reduce the disparity and to obtain single binocular vision of the fixated point despite the

aniseikonia. Both studies reported persistence of the disconjugacy under the subsequently recorded monocular viewing condition. This indicates the presence of a fast learning mechanism.

Eggert and Kapoula (1995) demonstrated that similar rapid and persistent changes in the conjugacy of the saccades can be induced with the use of a stereogram. The stereogram used contained the disparity produced by a natural 3-D object (a wedge) viewed binocularly in real space. The distribution of disparity gave rise to vivid depth perception and called for position-specific changes in the conjugacy of saccades; within a few minutes, saccades to the right became larger for the right eye, while saccades to the left became larger for the left eye just as required by the disparity. Depth perception might have facilitated these remarkably rapid position-specific changes of the conjugacy of saccades. Kapoula et al. (1995); Eggert and Kapoula (1995) suggested that the disparity of aniseikonic im-

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ages or stereograms stimulates the same mechanism as that for fixating targets in real 3-D space that differ both in distance and in direction. Saccades to such targets are known to be naturally disconjugate (Enright, 1986; Erkelens, Steinman & Collewijn, 1989). More recently, Chaturvedi and van Gisbergen (1997) found that saccadic gain plasticity can be specific to depth, suggesting that the saccadic system is sensitive to 3-D information.

The goal of the present study was to examine whether monocular depth cues can also influence the disconjugacy of saccades. In natural situations both binocular and monocular depth cues are available. Disparity is a powerful stimulus and apparently can drive disconjugate eye movements even in the absence of depth perception. Monocular depth cues such as linear perspective can also drive vergence movements that parallel depth perception (see Enright 1987a,b). How disparity-reducing mechanisms regulating the conjugacy of the saccades are operating in the natural environment in the presence of multiple, monocular as well as binocular depth cues is not known. To examine this we performed three aniseikonia experiments using different images: a grid, a random-dot pattern, and a complex image. Because the images were always magnified for one eye (10% uniform magnification), the disparity was the same for all three images. In contrast, monocular depth cues were different: the random-dot pattern had no prominent monocular depth cues except the absence of texture gradient that indicated a frontoparallel plane; the grid contained a single but powerful monocular depth cue, its geometric structure that strongly indicated a frontoparallel plane; finally the complex image contained multiple monocular depth cues (linear perspective, overlapping of items, relative size etc. see Section 2).

As mentioned, the disparity produced by the uniform magnification of one image does not produce perception of tilt. Thus, the conflict between disparity and monocular depth cues is not perceptual but motor: disparity calls for disconjugacy while monocular depth cues (of the random-dot pattern and of the grid) indicate a frontoparallel plane and do not call for disconjugacy. For the complex image the conflict is also motor: the disparity due to 10% aniseikonia call for disconjugacy while the monocular depth cues and the implied distance relationships within the image call for small disconjugacy sometimes in the same direction as the disparity but also sometimes in the opposite direction.

The results show that both disparity-reducing disconjugacy of saccades as well as the retention of this disconjugacy under monocular viewing were diminished for the latter two experiments using images containing a powerful monocular depth cue (grid), or a variety of monocular depth cues (complex image). The findings

support the hypothesis that disparity driven saccade disconjugacy is influenced by monocular depth cues. Preliminary results have been published elsewhere (Egert, Kapoula & Bucci, 1994).

2. Methods

2.1. Subjects

Four subjects participated in all three aniseikonia experiments. Two subjects (SF and TE) were myopes, and performed the three experiments with their spectacles on. The spectacle correction was OS: $-1.25 + 0.25 \times 0$ and OD: $-1 + 0.25 \times 180$ for subject SF, and OS: $-2.25 - 1.25 \times 70$ and OD: -3.25 for subject TE. All subjects have corrected visual acuity of 20/20 and perfect binocular vision (TNO random dot test for stereopsis was 60 s of arc or better). Subjects participated in the experiments after giving informed consent; this study was approved by the French ethics committee CCPPRB N°15.

2.2. Stimulus

Subjects were seated in a dark room in front of a flat translucent screen. The head was stabilised with a bite bar and a forehead support. Two projectors were used to provide each eye with its own image. The beams of the projectors were polarised 90° apart. Subjects viewed through filters which were also polarised 90°. The two images were centred on the screen as shown in Fig. 1A. One image was uniformly magnified by 10%. Each subject performed three experiments using the three different images. In an effort to check for distance effects (see van der Steen & Bruno, 1995) two distances were tested: 1 m from the screen (subjects BM and SF), and 57 cm (subject TE and BC). Each subject participated in three different experiments using the three types of images which was the main purpose of the study. The viewing distance being examined in different subjects this aspect was treated qualitatively only. In all three experiments subjects BM and SF saw the larger image with the right eye, while subjects TE and BC saw it with the left eye. The larger image subtended $33 \times 33^\circ$ for the experiments using 1 m viewing distance and $48 \times 48^\circ$ for the experiment using 57 cm viewing distance.

For subjects BM and SF the required disconjugacy was divergent for rightward saccades and convergent for leftward saccades. In contrast, for subjects TE and BC the disconjugacy was convergent for rightward saccades and divergent for leftward saccades. For all subjects but one (subject SF) the order of running of the experiments was as follows: (i) experiment with the random-dot pattern; (ii) experiment with the grid; and

(iii) experiment with the complex image. For subject SF the order was: (i) complex images; (ii) random-dot patterns; and (iii) grid. To avoid transfer of learning or bias from one session to another the interval between experimental runs was longer than a week.

Fig. 1B shows the image used in each experiment. The three images differ with respect to their local structure, e.g. the number, the size and the density of their elements. Compared to the grid, the random-dot-pattern and the complex image are similar containing a larger number of small elements. The type of monocular depth cues contained by the three images are different. The grid is formed by horizontal and vertical lines and contains letters at the intersection of them; as mentioned, such geometric structure strongly indicates the frontoparallel plane. The binocular disparity depth cues calls for disconjugacy and is in conflict with the monocular depth cues. If for instance the right eye views the magnified grid the distribution of disparity calls for divergent disconjugacy for right gaze positions and convergent disconjugacy for left gaze positions. It does so, even though the disparity due to uniform

magnification does not give rise to tilt perception, and the geometric structure of the grid strongly signals a frontoparallel untilted plane. The absence of the texture-gradient of the random-dot pattern is also a potential monocular depth cue indicating a fronto-parallel plane. However, such a cue is less powerful than the geometric square-structure of the grid. Evidence for this was presented by Stevens and Brookes (1988) in experiments involving spatial judgements of planar surfaces that had conflictual stereo and monocular information. In some experiments the authors compared a grid and a random-dot-pattern, both similar to ours. They found that the linear perspective of the grid interfered more with the stereo information than the absence of the texture-gradient of the random-dot-pattern. The complex image has several irregular geometric forms partially overlapping that provide a rich variety of monocular depth cues (this image was created and used by Busetini, Miles & Krauzlis, 1996). Monocular depth cues in this case were sometimes congruent with the disparity depth cues and other times in conflict, depending on where the eyes land after every saccade.

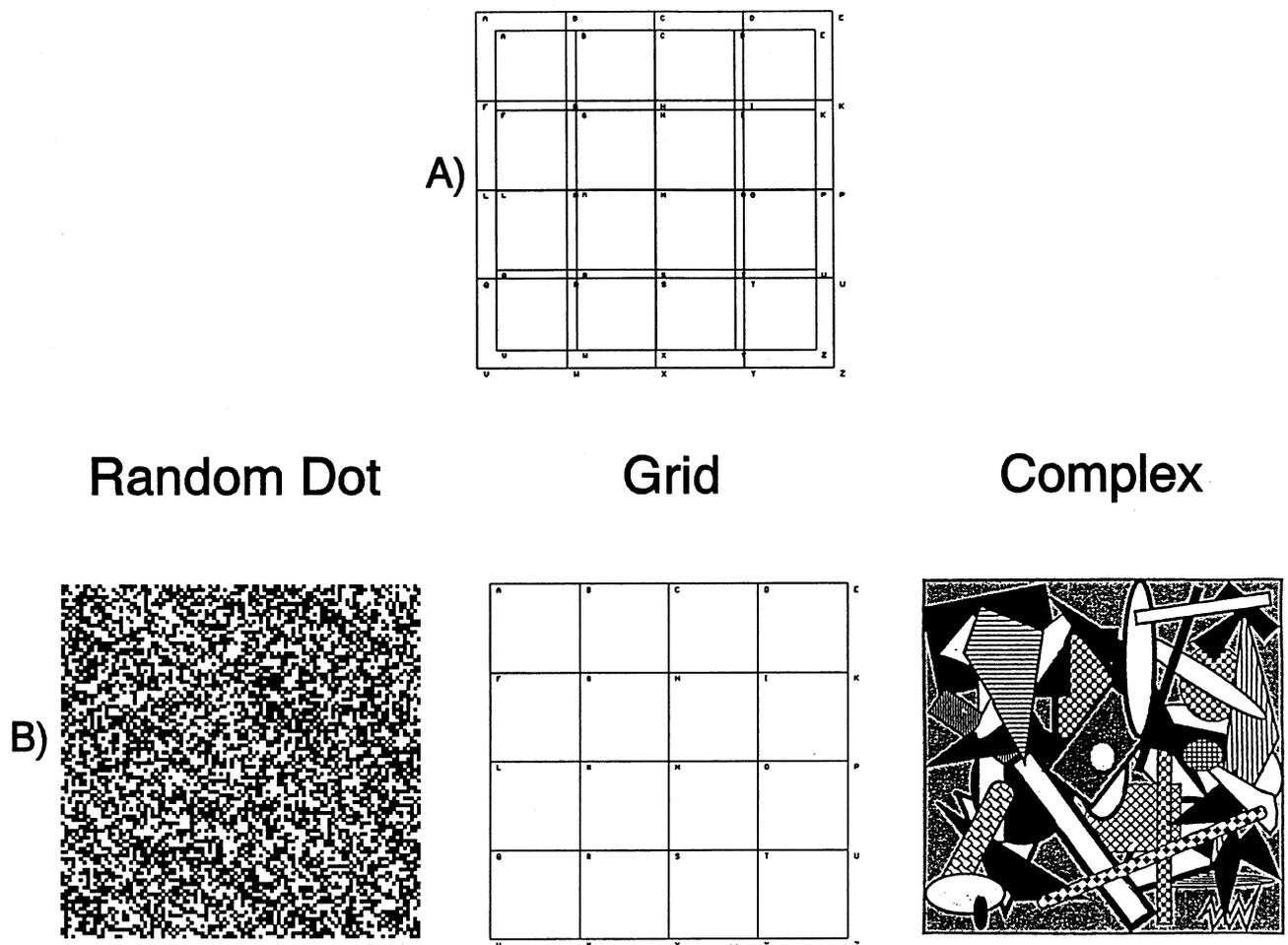


Fig. 1. (A) In a dichoptic viewing set-up a grid was presented to each eye. The two grids are centred on the screen. (B) The images used in each of the three aniseikonia experiments.

In all three experiments subjects were asked to saccade back and forth between the centre and different points of the image along the horizontal and vertical meridians; the extreme edge points of the image and the points half-way were indicated alternately every about 2–3 min. These points corresponded to 8 and 16° from the centre for subjects BM and SF and 12 and 24° for subjects TE and BC. In order to keep the size of the saccades the same, the same target points were indicated for all three conditions and for each experiment (before, during and after training). For the experiment with the complex image these selected points were at similar depth planes corresponding to monocular depth cues. However, if the subject did not fixate very accurately (e.g. 0.5° away), the depth plane implied by monocular depth cues could be different. Thus, for intrinsic physiologic reasons related to the small natural saccade inaccuracy it was not possible to impose that all actually made saccades ended to the same depth plane. Nevertheless, the distance relationships between different points of the image implied by the monocular depth cues were rather small.

2.3. Eye movement recording and data analysis

Detailed description on recordings and data analysis techniques can be found in prior studies (e.g. Kapoula et al. 1995). Briefly, stimulus presentation and data collection were directed by REX, a software developed for real time experiments and run on a PC. Eye movements of both eyes were recorded simultaneously by the search coil-magnetic field method (Robinson, 1963; Collewijn, Van der Mark & Jansen, 1975). The eye position signals were filtered with a bandwidth of 0–200 Hz and digitised with a 12-bit analogue-to-digital converter sampling each channel 500 times per second. Calibration factors for each eye were extracted from saccades under monocular viewing. The calibration data were corrected for the tangent screen projection and fitted by a polynomial function with five parameters. Off-line computer algorithms were used to determine the times of saccade onset and offset: saccade onset was determined at the point where eye velocity reached 5% of the peak velocity; saccade offset was taken at the time when velocity dropped below 10°/s for both eyes.

For each individual saccade we measured in degrees the disconjugacy (LE-RE difference) of the amplitude of the saccade. For horizontal saccades positive values indicate convergent disconjugacy, negative values indicate divergent disconjugacy. For vertical saccades positive values indicate a disconjugacy in the appropriate direction regardless of the direction of the saccade (i.e. larger saccades in the right eye for subject BM and SF, larger saccades in the left eye for subjects TE and BC). Post-saccadic eye drift was measured during the first

160 ms following the end of the saccade; this early drift period was chosen to avoid drift components driven by disparity detected after the end of the saccade. The disconjugacy of the drift was measured by subtracting the amplitude of the drift of the right eye from that of the left eye. For horizontal saccades positive values indicate convergent drift, negative values indicate divergent drift. For vertical saccades positive values indicate drift in the direction required by the disparity of the unequally sized images. Training values average behaviour through the 15–20 min of training. Statistical analyses were performed using the Student's *t*-test.

3. Results

3.1. Horizontal saccades

3.1.1. Qualitative data

Fig. 2 shows typical binocular recordings of leftward saccades from subject BM. Before training leftward saccades showed small divergent disconjugacy due to the abduction–adduction asymmetry (see Kapoula, Optican & Robinson, 1987; Collewijn, Erkelens & Steinman, 1988a). This inherent divergent disconjugacy was present for all subjects and for all conditions (before, during and after training). During training leftward saccades were associated with convergent disparity. In the experiment with the grids, the eyes started diverging at the beginning of the saccade but showed substantial convergent disconjugacy towards the end of the saccade. The net change in the disconjugacy at the offset of the saccade was convergent just as required by the disparity of the unequal images. During training with the random-dot pattern the net change in the disconjugacy at the offset of leftward saccades was even more convergent. In contrast, during training with the complex images, the net change in the disconjugacy of leftward saccades was small albeit convergent. In the example shown, convergent disconjugacy occurred towards the end of the saccade and during the early post-saccadic fixation period.

3.1.2. Time course of saccade disconjugacy.

Fig. 3 shows the disconjugacy for leftward saccades for subject TE during the training period. The baseline value of disconjugacy (shown at the *y*-axis) was close to zero for all experiments. Substantial disconjugacy appeared within the first 2 min of training for all three experiments. The mean of the disconjugacy of the saccades made during the first 2 min of training is statistically different from the mean disconjugacy of baseline saccades (shown at the *y*-axis). This time course is short and confirms prior results (Kapoula et al., 1995; van der Steen & Bruno, 1995). A further increase of the disconjugacy of the amplitude of saccades beyond 6–8

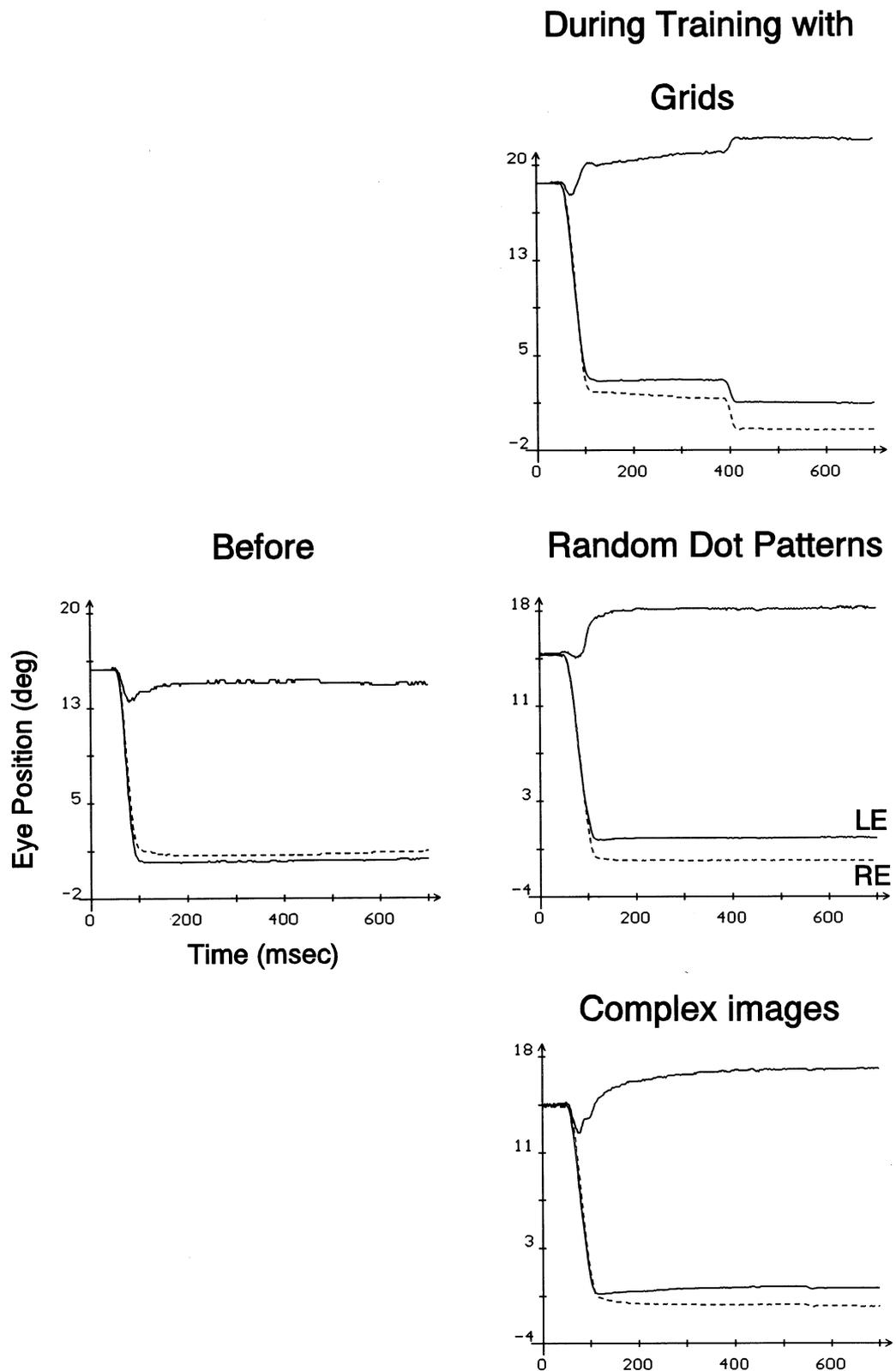


Fig. 2. Typical binocular recordings of leftward saccades before and during exposure to the three different aniseikonic images. The solid line is the position trace of the left eye, the dashed line is that of the right eye; the upper trace is the disconjugacy of the saccade (the difference between the left and the right eye $\times 2$). Data are from subject BM in all three experiments. Before training the subject viewed monocularly, during training he viewed the larger image with the right eye. Leftward saccades were thus associated with convergent disparity thereby requiring convergent disconjugacy. The eyes always start by diverging slightly (due to abduction–adduction asymmetry); this stereotypic pattern is followed by appropriate intrasaccadic convergent disconjugacy.

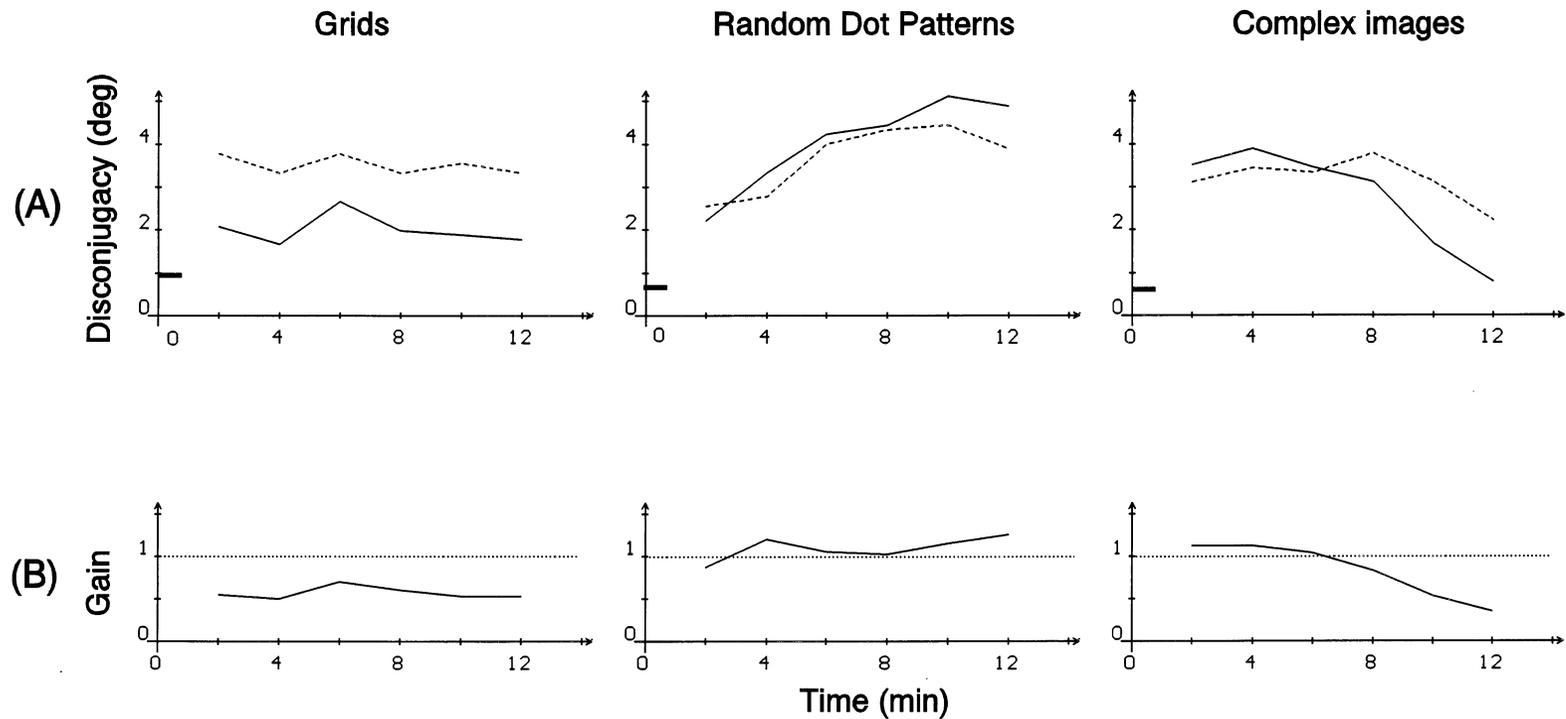


Fig. 3. Disconjucy of the amplitude of the saccades during training with different types of aniseikonic images (each point averages seven saccades, subject TE). (A) The dotted line is the disconjucy required by the unequal images (convergent), that is, the difference between the current vergence angle and the vergence required by the disparity of the target point where the ensuing saccade is directed. The continuous line indicates the actual disconjucy of the saccades. The thick segment-line on each ordinate indicates the inherent disconjucy of saccades before training. (B) Gain (disconjucy of saccades/required disconjucy). Note that the amplitude of the required disconjucy increases with the amplitude of the saccades. The variation of the requirement is due to the variation of the size of saccades performed by the subject at different times during training; recall that subjects alternated the size of their saccades every two-three minutes (see Section 2).

min of training was observed only in the experiment with the random-dot pattern. This is better illustrated in Fig. 3B that shows the gain (saccade disconjugacy/required disconjugacy). Towards the end of the training the gain was above unity and statistically higher than that at the previous points (e.g. those at 8 or 4 min). For the experiment with the grids the disconjugacy increased until about 6 min but no further increase occurred for the remaining training period, even though the disconjugacy was still below the required value. In the experiment with the complex image the disconjugacy reached and slightly exceeded the requirement almost immediately (during the first 2–4 min of training). Surprisingly, however, afterwards, the actual disconjugacy and the gain decreased. This behaviour provides no evidence for a continuous learning process over the 15 min training period.

In conclusion, fast modifications of disconjugacy of the amplitude of saccades occurred in all three experiments. After the first 2 min of training the disconjugacy further increased only in the experiment using the random-dot pattern; this increase suggests the presence of a slower learning process. To confirm the presence of learning we tested for the retention of the disconjugacy in the subsequently monocular viewing condition (see Section 3.1.3).

3.1.3. Quantitative data

Fig. 4 shows all individual changes from normal baseline values of the disconjugacy of saccades. Data are shown for each saccade direction and for each experiment. For all three experiments and for each subject, the changes of disconjugacy was evaluated from saccades that had similar amplitudes for the three conditions (before, during and after training). The mean difference in saccade size between conditions was $1.0 \pm 0.6^\circ$ (range of individual difference $0.1\text{--}2^\circ$).

3.1.4. Experiment with the grid

During training, the disconjugacy changed in the direction required by the disparity of the grids despite the conflicting information from the monocular depth cue; all changes (differences from the baseline values) were statistically significant. Under monocular viewing, recorded after training (in the absence of disparity cues), five of the eight individual changes from the baseline values were also significant. As in prior studies (Kapoula et al., 1995) the amplitude of the disconjugacy both during and after training was subject-dependent (see in Fig. 4 the discrepancy between the requirement and the bars). Subject TE who performed the experiment at close viewing distance showed the largest changes but only for divergent requirement: his ratio of the change in the disconjugacy from the normal value relative to the requirement was 1.16 and 0.85 for the training and for the after-training condition, respec-

tively. However, the other subject (BC) who also performed the experiment at close viewing, showed the weakest response (the ratio was 0.29 and 0.26 for the training and for the after-training condition, respectively). Furthermore, for the convergent requirement, no subject examined at close viewing showed strong changes in the disconjugacy of saccades. Thus overall, the data of the experiment using the grid do not show consistent effects of proximity. The individual differences in the amount of saccade disconjugacy developed are rather idiosyncratic. For the convergent requirement, the group mean change from the baseline condition was statistically significant for the during training condition (0.51°); for the after training condition the group mean change was not significant (-0.13°). In contrast, for the divergent requirement the group mean change was significant for both conditions (-0.85° during training, and -0.75° in the after training condition).

3.1.5. Experiment with the random-dot pattern

During training, saccade disconjugacy changed in the direction required by the disparity of aniseikonic random-dot patterns; all changes except for subject SF, were statistically significant. A significant change in the conjugacy of the saccades was retained even for saccades in the after-training monocular viewing condition (six cases). The subjects (TE, BC) who performed the experiments at close viewing showed the largest changes. For the convergent requirement in the training condition, the ratio of the change in the disconjugacy relative to the requirement was 1.32 and 0.94 for the two subjects (TE and BC) who performed the experiment at close viewing. For the divergent requirement these ratios were also larger than for the other subjects and for both, during training and after-training conditions: 1.29 and 1.73 for subject TE, and 0.57 and 0.93 for subject BC. Thus proximity produced larger changes in the disconjugacy of saccades for the experiment using the random-dot image. The group mean changes were statistically significant for both types of requirement and for both testing conditions. For the convergent requirement the group mean change was 1.33 and 0.95° for the during training and for the after training condition, respectively. For the divergent requirement the change was -1.11° during training, and -0.69° for the after training condition.

3.1.6. Experiment with the complex image

The results in this experiment were highly variable. During training the saccades associated with convergent disparity developed significant convergent disconjugacy for all subjects, the change was close to the requirement. After training, however, only one of these changes (subject SF) persisted. The group mean values showed a significant change for the during training–be-

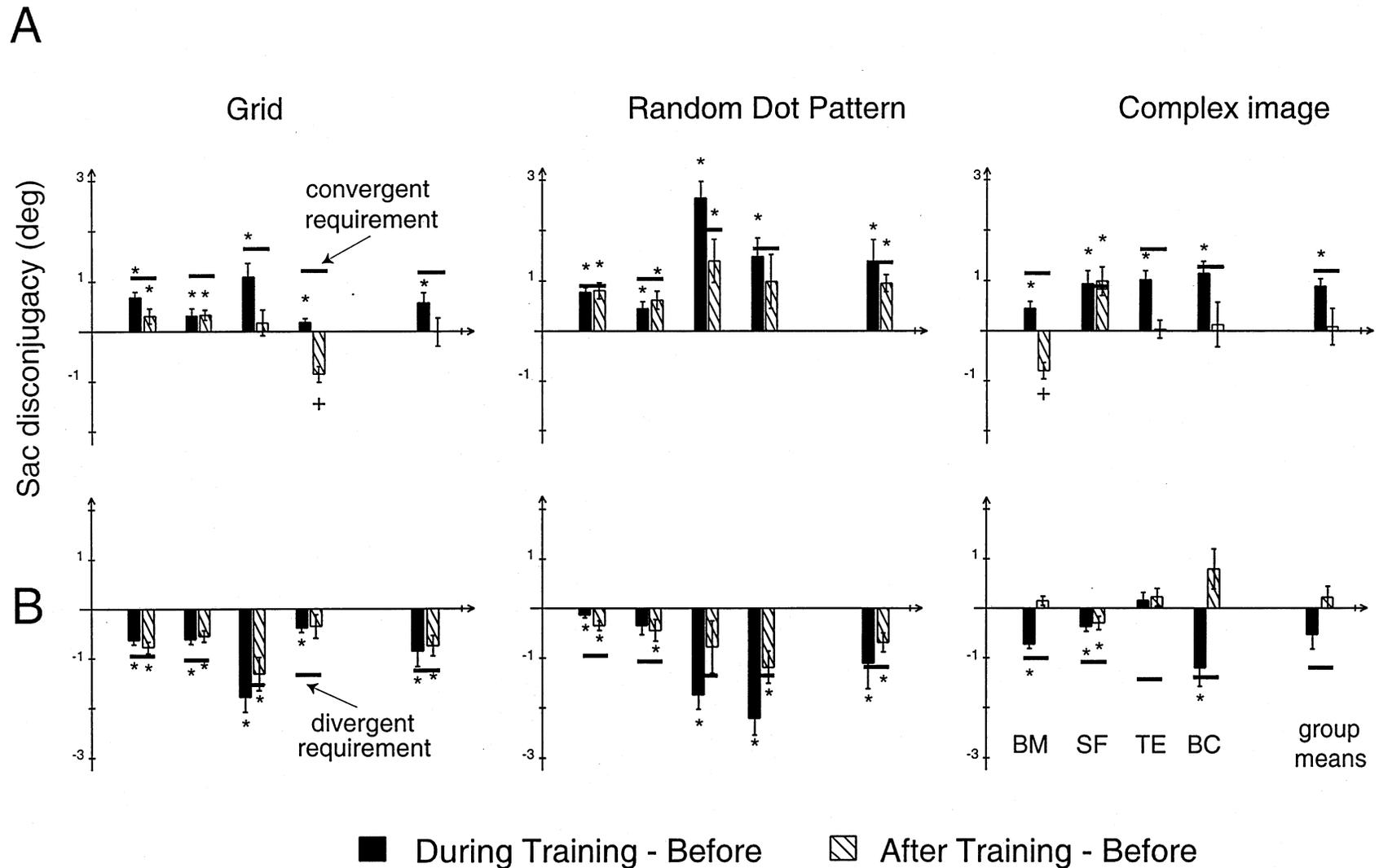


Fig. 4. Individual changes in the disconjugacy of saccades (in deg): solid bars show the difference of the mean disconjugacy of saccades during training from the mean disconjugacy of saccades in the baseline, before training condition; hatched bars show the difference of the mean disconjugacy of saccades before and after training. (A) Changes for saccades associated with convergent disparity, (B) changes for saccades associated with divergent disparity; vertical lines are the standard deviation of each individual change. Individual means are based on 20–75 saccades for pre-training values, 96–397 saccades for during training values, 25–68 saccades for post-training values. Group mean changes are based on the number of subjects (4), vertical lines are standard errors. Horizontal lines indicate the required disconjugacy. * Indicate a significant change ($P < 0.05$) in the appropriate direction (Student's t -test, comparing the baseline before- training means and those during training or those in the after-training condition). + A significant change in the wrong direction.

fore training comparison (0.88°) but no significant change for the after–before–training comparison (0.08°). For saccades associated with divergent disparity appropriate significant changes occurred for three cases. After training, significant persistence of divergent disconjugacy occurred only for subject SF. In general, the changes from the baseline values were weak or in the wrong direction regardless of the viewing distance used for testing. The group mean change from the normal values was divergent (-0.54°) during training, but convergent (0.21° , i.e. in the wrong direction) for the after training condition; neither value was statistically significant.

In summary, for most subjects, short exposure to image-size inequality induced rapidly a disconjugacy for horizontal saccades in all three experiments. The amplitude of the disconjugacy, however, and its persistence in neutral conditions depended on the type of the image. The aniseikonic random-dot pattern that contained no monocular depth cues produced, overall, the largest and longer lasting changes. In contrast, the complex image containing a variety of monocular depth cues produced variable and the least-persisting effects.

3.2. Vertical saccades

Fig. 5 shows the individual changes of the disconjugacy from the normal baseline values for vertical saccades. For all three experiments the changes in disconjugacy were evaluated from saccades of similar amplitude for the three conditions (before, during and after training). The mean difference in saccade size between these conditions was 0.7 ± 0.5 (range 0.1 – 1.9°).

3.2.1. Experiment with the grid

While viewing the two unequal grids all subjects but one (BM), showed a small but significant change in the appropriate direction. Under subsequent monocular viewing the changes were considerably reduced except for subject BC. The group mean change was statistically significant only in the during training condition (0.13°).

3.2.2. Experiment with the random-dot

In this experiment significant changes in the disconjugacy of vertical saccades occurred for three of the subjects. The changes were large in amplitude ($> 0.3^\circ$) and persisted even after training. The ratio of the change in the disconjugacy over the requirement was higher for the subjects examined at close viewing: 0.35 and 0.25 for subject TE during and after training respectively, and 0.65 and 0.91 for subject BC. The group mean change in the disconjugacy from the baseline value was 0.38° for the training condition, and 0.45° for the after training condition; the former was

statistically significant, the latter tended towards significance ($P < 0.1$).

3.2.3. Experiment with the complex image

Similarly to the results for the horizontal saccades, the changes for vertical saccades were highly variable for different subjects and for the two tested conditions. Significant disconjugate changes in the correct direction occurred only for two of the subjects (BM and BC). Subject TE made large significant changes in the wrong direction. The group mean change was 0.38° for the training condition and -0.09° for the after training; none of these values were statistically significant.

In summary, significant changes in the yoking of vertical saccades persisting even under monocular viewing, occurred mainly for the experiment using the random-dot image. The grids and the complex images produced smaller and/or less persistent changes.

3.3. Changes in post-saccadic eye drift

3.3.1. Horizontal post-saccadic drift

For all three experiments, before training horizontal saccades were followed by small disconjugate drift that was consistently convergent regardless of saccade direction. This drift was the continuity of an initial divergent spike occurring earlier at the beginning of the saccade; this pattern is well described by several studies (e.g. Collewijn et al., 1988a; Zee, Fitzgibbon & Optican, 1992). The group mean drift was $0.18 \pm 0.12^\circ$ (standard deviation, $n = 4$ subjects) in the experiment with the grid, $0.16 \pm 0.11^\circ$ in the experiment with the random-dot pattern and $0.28 \pm 0.18^\circ$ in the experiment with the complex image.

The group mean changes in post-saccadic eye drift from these normal values are shown in Table 1. Saccades in the direction associated with convergent disparity developed additional convergent post-saccadic drift. The group mean change was significant for the experiment with the grids and for the experiment with the random-dot pattern; the change for the experiment with the complex image tended towards significance ($P < 0.06$). Saccades associated with divergent disparity developed divergent drift. The group mean change was significant for the experiment using the random-dot pattern and for the experiment using the complex images. Individual changes of drift, however, were always smaller in amplitude than the corresponding changes of the disconjugacy of the amplitude of the saccades (Fig. 4C); changes in post-saccadic drift never exceeded 0.6° .

For the after training monocular viewing condition, the group mean change in post-saccadic drift was significant for the experiment with the grid (convergent) and for the experiment with the random-dot pattern (divergent); individual means were always $< 0.3^\circ$. Thus, in agreement with prior studies the changes in the

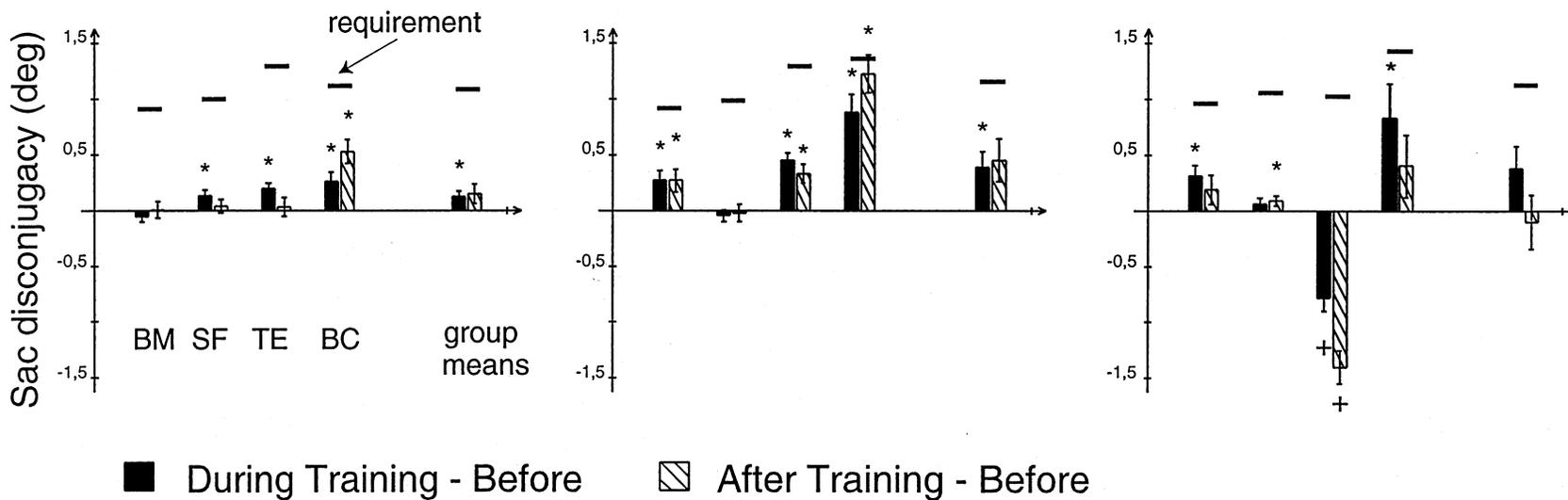


Fig. 5. Individual changes of the disjunctivity of vertical saccades (in deg): solid bars show difference of the mean disjunctivity of saccades during training from the mean disjunctivity in the baseline condition; hatched bars show the difference between the mean disjunctivity of saccades before and after training. Upward and downward saccades are grouped together. Individual means are based on 54–137 saccades for pre-training values, 132–448 saccades for during training values, 42–150 saccades for post-training values. All other notations as in Fig. 3.

Table 1
Group mean changes of the disconjugacy of post-saccadic drift from the normal values; each mean is based on four subjects^a

		Pre-training	Pre-post
<i>Horizontal saccades</i>			
Convergent requirement	Grids	0.350 ± 0.050 ^b (4)	0.108 ± 0.028 ^b (1)
	Random dot patterns	0.389 ± 0.093 ^b (4)	0.144 ± 0.069 (3)
	Complex images	0.232 ± 0.077 (3)	0.021 ± 0.063 (1)
Divergent requirement	Grids	−0.234 ± 0.110 (3)	−0.038 ± 0.089 (1)
	Random dot patterns	−0.243 ± 0.027 ^b (4)	−0.171 ± 0.030 ^b (4)
	Complex images	−0.199 ± 0.011 ^b (3)	−0.106 ± 0.059 (1)
<i>Vertical saccades</i>			
	Grids	0.077 ± 0.017 ^b (3)	0.083 ± 0.009 ^b (3)
	Random dot patterns	0.105 ± 0.016 ^b (4)	0.076 ± 0.008 ^b (4)
	Complex images	0.025 ± 0.010 (1)	0.017 ± 0.049 (1)

^a Numbers in parenthesis indicate the number of subjects for which the change from normal pre values was statistically significant.

^b Indicate a significant change at the level $P < 0.05$ (Student's *t*-test).

disconjugacy of post-saccadic drift were smaller than those in the amplitude of the saccades. Again, the experiment with the random-dot pattern produced the most reliable and consistent over the subjects changes in the disconjugacy of the post-saccadic drift.

3.3.2. Vertical post-saccadic drift

Before training, normal vertical saccades showed small disconjugate post-saccadic drift. The group mean drift (upward and downward saccades together) was $-0.02 \pm 0.08^\circ$ (standard deviation, $n = 4$ subjects) in the experiment with the grid, $-0.04 \pm 0.08^\circ$ in the experiment with the random-dot pattern and $0.03 \pm 0.04^\circ$ in the experiment with the complex image. These values of drift disconjugacy are similar to those reported earlier (e.g. Collewijn, Erkelens & Steinman, 1988b). The changes produced by exposure to aniseikonia are shown in Table 1. They were smaller in amplitude than those described for horizontal saccades. However, they were more consistent over the population, particularly for the experiment with the grid and for the experiment with the random-dot pattern. For these two experiments the group mean changes were statistically significant ($P < 0.05$) for both conditions (during training and after training). In contrast, for the experiment with the complex image the changes were not significant.

4. Discussion

This study shows that the conjugacy of the saccades, horizontal as well as vertical can undergo rapid modification if the images are made unequal in the two eyes. The disconjugacy occurred mainly intrasaccadically; changes in the disconjugacy of post-saccadic drift occurred but were smaller in amplitude. In general, the changes were larger for horizontal than for vertical

saccades, but the latter could be more variable. Significant changes in the disconjugacy of saccades occurred within the first 2 min of exposure to unequally sized images. All these findings confirm prior studies (Eggert and Kapoula 1995; Kapoula et al., 1995; van der Steen & Bruno, 1995). As in the above cited studies, after the 15 min of training the disconjugacy was retained under monocular viewing condition; this is attributed to learning. Our data, however, do not provide evidence for a continuous slow learning process except for the experiment using the random-dot pattern. The learning induced in this study could be better modelled by the buildup of a spatial sensorimotor map rather than a parametric adjustment aiming to reduce an error: subjects learn to associate a certain type of saccade disconjugacy (divergent or convergent) with different gaze positions on aniseikonic images. Subsequently, they are capable of reproducing the disconjugacy even under monocular viewing.

4.1. Effects of viewing distance

This aspect, secondary in our study, was examined in different subjects and thus, it can be treated only qualitatively. Increased saccade disconjugacy as well as better retention for the more proximal viewing distance was found only in the experiment using the aniseikonic random-dot patterns. Our observations are in agreement with the study of van der Steen and Bruno (1995) who demonstrated immediate and large saccade disconjugacy for proximal viewing distance; in that study, however, no retention was observed. Perhaps the difference in the two studies is due to their use of a more proximal distance (33 cm versus 57 cm in our study). The more proximal the distance the less learning would be involved. A noteworthy fact would be that both studies used similar aniseikonic random-dot patterns that do not contain prominent monocular depth cues.

The absence of a consistent effect of viewing distance in our two other experiments using both the grid and the complex images, which have more prominent monocular depth cues, is an interesting new observation. Perhaps, powerful monocular depth cues interfere more with disparity processing at close viewing than at far viewing.

Finally, one should address the importance of accommodation and accommodative-vergence. If viewing distance influences the ability to make disconjugate saccades by means of accommodative vergence then the disconjugate changes should always be higher at close viewing regardless of the type of the image. This was not the case. Perhaps, there is a complex interaction between disparity processing, monocular depth cues and accommodation at close viewing distance. Next we will discuss the possible factors explaining the difference in the induced disconjugacy for the three experiments.

4.2. Effect of the structure of the image

The experiment with the random-dot images produced the most reliable and lasting modifications in the disconjugacy of saccades. The grid experiment produced smaller changes, while the complex image produced the most variable changes and the weakest evidence for retention and learning. The major stimulus driving modification of the conjugacy of saccades is disparity. Kertesz (1981) found that the gain of disparity-vergence movements increases with the complexity of the images. The random-dot-pattern and the complex image had a rich number of small elements allowing disparity to be extracted locally from a larger number of points than in the case of the grid image. Yet, the random-dot-pattern and the complex image produced very different results. Most important, the grid produced better results than the complex image despite its lower density of small elements. Thus, it is unlikely that the differences in the induced disconjugacy of the saccades for the three types of images are due to the structure of the image influencing the disparity evaluation process.

4.3. Effect of monocular depth cues

Preliminary evidence for the ability of monocular depth cues to influence the disparity-driven disconjugacy of saccades was presented by Kapoula et al. (1995). In this study a subject was exposed twice to aniseikonic grids that were either normal or tilted in space; local structures were the same in both experiments. Yet, disconjugate learning was different. The present study provides further evidence for the influence of monocular depth cues as it will be discussed below.

The random-dot pattern had the least prominent monocular depth cue (absence of texture gradient). Thus, during training the evaluation of the required disconjugacy could be based on the evaluation of the disparity without strong conflict from the texture-monocular depth cue. Our findings demonstrate modifications of the binocular coordination of saccades that were consistently in the appropriate direction for the disparity and are in agreement with the psychophysical studies (Stevens & Brookes, 1988).

The square structure of the grid indicated strongly the frontoparallel plane. Apparently, disparity stimulated saccade disconjugacy even in the presence of this strongly conflicting monocular depth cue. Nevertheless the amplitude of the induced disconjugacy was smaller (compared to that observed in the experiment using the random-dot pattern).

The complex image, in addition to disparity, contained a variety of monocular depth cues. The disparity-driven mechanism was still able to function for horizontal saccades and to a lesser extent for vertical saccades. However there was large variability between the subjects and instability of individual behaviours within the training period (Fig. 3). One could argue that the larger intersubject variability observed for both horizontal and vertical directions is due to subjects fixating at different depth planes implied by the various monocular depth cues of the image. This is, however, unlikely as all subjects were instructed to fixate at the same points of the image (see Section 2), thereby fixating at the same depth planes. As mentioned, because of the natural small inaccuracy of saccades, subjects might have fixated slightly off the indicated points, thereby at different depth planes. However, the distance between the planes implied by the monocular depth cues were small and could not explain the differences in the disconjugacy of saccades between subjects; differences could be as large as 1° (see Fig. 4B, complex image subject TE and BC).

4.4. Effect of monocular depth cues in the after-training condition

The question addressed here is to what extent the differences in the disconjugacy of saccades in the after-training condition reflected different degrees of learning for the different images?

A simple explanation would be that the larger the disconjugacy during the training, the larger the disconjugacy in the after-training condition. If this was the case, retained disconjugacy in the after-training condition would be a constant percentage of the response during training. This was not the case. In the experiment with the random-dot pattern the after-training disconjugacy was $100 \pm 12\%$ ($n=4$ subjects) of the disconjugacy observed during training. In contrast, this

value was $182 \pm 87\%$ ($n = 4$ subjects) for the grid experiment, and $62 \pm 89\%$ ($n = 4$ subjects) for the experiment with the complex image. Thus, the after-training disconjugacy was not a gain function of the disconjugacy during the training period.

Another possibility would be that the retained disconjugacy in the after-training condition was directly determined by the strength of interference from monocular depth cues. To examine this we ran four additional experiments using aniseikonic random-dot patterns and a viewing distance of 1 m. In the after training condition the retention was measured not only when the subject viewed one of the random-dot patterns but also when he/she viewed monocularly a grid image (subjects MPB and MG) or a complex image (subjects SP and ZK). For horizontal saccades, the disconjugacy induced with the random-dot pattern was transferred equally well in the after-training condition using the grid or the complex image: the difference of the disconjugacy between this after-training condition and the before-training condition was statistically significant for two of the subjects: $0.18 \pm 0.04^\circ$, $n = 103$ for subject MPB, and $0.24 \pm 0.03^\circ$, $n = 102$ for subject SB. The difference for subject MG was $0.13 \pm 0.08^\circ$, $n = 84$ and tended towards significance, the difference for subject ZK was not significant ($0.11 \pm 0.10^\circ$, $n = 133$). For vertical saccades, the disconjugacy transferred significantly for three of the four subjects: $0.32 \pm 0.05^\circ$, $n = 117$ for subject MG, $0.12 \pm 0.01^\circ$, $n = 100$ for subject SP and $0.21 \pm 0.10^\circ$, $n = 97$ for subject ZK. These results indicate that the disconjugacy seen in the after training condition is primarily due to learning and not to the degree of interference of monocular depth cues in the after-training condition itself. Learning was best for the random-dot pattern, intermediate with the grid images and highly variable and questionable for the experiment using the complex image. We conclude that monocular depth cues influence both, the immediate disconjugacy of saccades during the training period and the learning of such disconjugacy.

4.5. Theoretical considerations and conclusion

The influence of monocular depth cues shown here suggests that disconjugate learning is influenced by all visual cues relevant to vergence and depth perception.

The findings of the present study also have implications for the ecological validity of laboratory situations demonstrating rapid modifications of saccade conjugacy. When disparity is the most prominent feature we show that the modifications of saccade disconjugacy are more reliable and sustained. We also show that monocular depth cues are not ignored and can decrease learning when they are in conflict with disparity. Most likely, the congruence between binocular disparity and monocular depth cues would drive disconjugate learn-

ing more efficiently than binocular disparity alone, however, this needs to be demonstrated. In most natural situations binocular disparity and monocular depth cues are in agreement. Consequently the rapid modification of the conjugacy of saccades shown in artificial laboratory situations with the use of images such as random-dot patterns, reflect, at least partially, the way of functioning of the oculomotor system under natural situations.

Finally, it is noteworthy that monocular depth cues can influence disconjugate learning even for vertical saccades. This is consistent with the idea that the learning stimulated by exposure to aniseikonic images involves sensorimotor remapping of the representation of the image in 3-D space. Remapping would be based on the distribution of disparity, on monocular depth cues and on information from internal loops related to disconjugate movements already performed.

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