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journal homepage: www.elsevier.com/locate/visresParadoxical fusion of two images and depth perception with a squinting eye[☆]S.I. Rychkova^{a,1}, J. Ninio^{b,*}^aEye Microsurgery Clinic of S. Fyodorov, Lermontov Street 337, 664033 Irkutsk, Russia^bLaboratoire de Physique Statistique, Ecole Normale Supérieure, 24 rue Lhomond, 75231 Paris cedex 05, France

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ABSTRACT

Some strabismic patients with inconstant squint can fuse two images in a single eye, and experience lustre and depth. One of these images is foveal and the other extrafoveal. Depth perception was tested on 30 such subjects. Relief was perceived mostly on the fixated image. Camouflaged continuous surfaces (hemispheres, cylinders) were perceived as bumps or hollows, without detail. Camouflaged rectangles could not be separated in depth from the background, while their explicit counterparts could. Slanted bars were mostly interpreted as frontoparallel near or remote bars. Depth responses were more frequent with stimuli involving inward rather than outward disparities, and were then heavily biased towards “near” judgments. All monocular fusion effects were markedly reduced after the recovery of normal stereoscopic vision following an orthoptic treatment. The depth effects reported here may provide clues on what stereoscopic pathways may or may not accomplish with incomplete retinal and misleading vergence information.

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1. Introduction

A strabismic eye often develops a peripheral sensitive zone in its retina, which allows the eye to capture, in the deviating position, the portion of space to which it should have attended in the non-deviating position. This phenomenon is usually accompanied by an inhibition of the foveal signals. In some cases however, the fovea remains sensitive and the squinting eye may even produce double images arising from different regions of space, a phenomenon known as ‘monocular diplopia’ (e.g., Bielschowsky, 1898; Ramachandran, Cobb, & Levi, 1994a, 1994b; review in Howard, 2002, chap. 7).

In the course of routine examinations made in an orthoptic service, we made an intriguing observation: strabismic patients who perceived two images simultaneously with the same squinting eye could, under favourable geometric conditions, produce a fused image percept. Here we describe the conditions under which this monocular fusion is observed (Section 3.1) and describe some properties of the perceived image in relation to the differences in contrast, colour or geometry between the two images to be fused. The results are compatible with the hypothesis that the observed

monocular fusion and depth perception effects are mediated by stereoscopic pathways working under unusual conditions. If this is the case, our results bring into focus fundamental issues about stereoscopic mechanisms, in particular about the “depth sign” issue: how the brain associates crossed or uncrossed disparities with close or remote positions in depth.

2. Materials and methods

2.1. Subjects

All subjects in this study were strabismic patients undergoing an orthoptic treatment aimed at improving their binocular vision. Out of about 550 patients 44 were found able to fuse two images monocularly, as reported in Section 3.1 below.

The 44 patients were young (9–32 years, 15.8 years on average). 29 patients had normal visual acuity, 15 patients had modest amblyopia with 0.4–0.7 (+0.4 logMAR to +0.15 logMAR) acuity in the weakest eye. The deviations of the subject’s eyes were determined with an accuracy of 1–2° using Hirschberg’s method in which a spot of light is projected on the eye’s cornea, and the distance from this spot to the other eye’s pupil is measured. 27 patients had a cross-eyed squint (15 on a single eye, 12 on both eyes in alternation) 17 patients had a divergent squint (11 on a single eye, six on the two eyes in alternation). See the [Supplementary material](#) for additional clinical details.

The patient’s natural propensity to use binocular vision in the 1–5 m range was determined according to Worth’s colour test in which two green, one red and one white circular areas patched

[☆] S.R. performed all the clinical work and made the initial observations on paradoxical fusion. J.N. suggested to extend the work to lustre and stereoscopic effects and designed stimuli. S.R. and J.N. interpreted the results and wrote the article.

* Corresponding author. Fax: +33 1 44 32 34 33.

E-mail addresses: rych.sv@mail.ru (S.I. Rychkova), jacques.ninio@lps.ens.fr (J. Ninio).

¹ Fax: +7 3952 42 20 35.

on a black disc are examined through anaglyphic red and green filters mounted on special glasses (see Fig. 1 in the Supplementary material). The responses are interpreted in terms of four visual behaviours: normal binocular vision, anomalous binocular vision (the patient reports the normal fusion pattern, while his eyes are in the strabismic condition), neutralization (one image is suppressed), and diplopia (there are two unfused images). Diplopia was found in five patients, neutralization in four patients, but without scotoma. The other 35 patients had binocular vision at least up to a distance of 1 m.

Binocular vision can be stimulated by presenting two images in rapid alternation to the two eyes, then simultaneously at various frequencies on a synoptophore (See Fig. 2 in the Supplementary material). This is the basis for a classical orthoptic treatment of strabismus, which was followed by our patients (Section 3.5 below). A person who neutralizes one image according to Worth's test may nevertheless be able to binocularly fuse two images on the synoptophore. By varying the directions of the two arms of the synoptophore which hold the images, one can determine whether or not the patient is able to use normal binocular vision, anomalous binocular vision, or both. By convention, a person has normal retinal correspondence (NRC) when he/she is able to binocularly fuse two images falling on the foveal regions of the two eyes. When the person can fuse an image captured by the foveal region of one eye with an image captured by the second sensitive zone of the other eye, he/she is said to have abnormal or anomalous retinal correspondence (ARC). The angle between the two arms of the synoptophore under which ARC is observed is determined with an accuracy of about 1°. It roughly agrees with the deviation angle determined by the method of Hirschberg.

All 44 strabismic patients in this study were able to fuse two images under the stimulating conditions of the synoptophore, yet they were unable to perceive depth according to two classical clinical tests: the Lang's test which uses a random-dot stereoscopic pair and the Titmus fly test, in which a stereoscopic pair of images of a fly is viewed through polarizing glasses.

All the examinations were carried out routinely as part of the clinical work. All 44 patients in this study agreed to participate as subjects in further testing (described below), for the purpose of our scientific inquiry.

2.2. Viewing apparatus, stimuli and testing conditions

The stimuli to be fused are presented with an apparatus called the binarimeter (see Fig. 3 in the Supplementary material). The two images are held on a chariot which can be displaced on a 1-m long graduated rack. The chariot has rotating buttons that allows the separation of the images to be adjusted from about 2 cm to about 12 cm. The subject's head is fixed with a chin rest. The orthoptist faces the subject and checks the positions of the eyes. The distance of the two images from the eyes is set within the accommodation range of the subject. Their angular separation is chosen to allow an extrafoveal capture of one image by the squinting eye while he/she fixates the other image. A finer adjustment of the separation, to promote the monocular fusion of the two stimuli, was performed at each presentation of a new stimulus or stimulus variant.

The stimuli for fusion, lustre and colour effects are shown in Fig. 1 and the stereoscopic stimuli are shown in Fig. 2. The images were presented as small circular areas, 1.5 or 2.5 cm in diameter, or as small square domains, 1.5 cm or 2.5 cm wide. The small extension of the images was related to the necessity of presenting them under a small angular separation, corresponding to the deviation angle of the tested strabismic eye. In a number of cases subjects viewed images of the two sizes and responded similarly to both. The images were presented at a 15–70 cm distance and, typically,

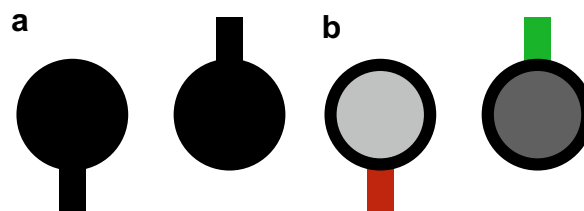


Fig. 1. Fusion stimuli. (a) Standard stimulus. When the two images are correctly fused, one must see the two bars aligned and going through the central disc. (b) Modified stimulus. The discs in the left and right images have different levels of grey, giving rise to a lustre effect upon fusion. The colours of the bars are usually maintained upon fusion, but occasionally, both bars are perceived with the colour of the foveal one.

with 4–6 cm separation. Typically, an image 1.5 cm wide presented at a distance of 30 cm subtends an angle of about 3°. Six subjects were tested on the six stimuli 2a–2f, and 24 subjects were tested on the 13 stimuli 2a–2m.

In a typical session, the subject would undergo a detailed optometric examination on the synoptophore. He/she would then undergo a testing session on the binarimeter, the stimuli being presented in a constant order: first the lustre and colour stimulus of Fig. 1b, then the stereoscopic stimuli of Fig. 2 in their alphabetic order. More precisely, each stimulus of Fig. 2 was presented in two versions, that shown in Fig. 2 and the related variant obtained by exchanging the left and right images, in random order. For each stimulus in each version, the viewing conditions followed an invariable order: left eye fixates the left image, left eye fixates the right image, right eye fixates the left image, right eye fixates the right image. For each condition, the subject had to describe in his own words what he perceived on the fixated image, the non-fixated image and eventually on an intermediate image. Details were subsequently requested, if necessary. The responses were written down, then encoded in standard form. There was a 3-way classification for intensities: no effect, weak effect, strong effect, which was subsequently reduced to two (no effect versus weak or strong effect) for the computer analyses.

3. Results

3.1. Occurrence of monocular fusion

Binocular vision was routinely characterized in nearly 550 strabismic patients using simple fusion stimuli (for instance, two images of the same cat, one without tail and the other without ears) presented on a synoptophore (see Supplementary material, Fig. 2). Most strabismic patients are unable to perceive one of the two images, they neutralize it. This neutralization scotoma can exist over a more or less extended spatial domain. It is accompanied by a loss of acuity in the central part of the visual field of the squinting eye, acuity remaining normal in the periphery (Siriteanu, 1982). Nearly 400 among the 550 patients had a neutralization scotoma, and thus were not able to use binocular vision at the time of the first examination. The remaining patients were able to binocularly fuse two images, through normal (NRC) or anomalous (ARC) retinal correspondence (see the definitions in Section 2.1). The binocular competence of these patients was then tested on a binarimeter. While the images are viewed at infinity on the synoptophore, their distance to the observer (in the 15–70 cm range) and their separation are independently adjusted on the binarimeter.

As a routine control, expected to give a negative result, our patients were asked to view the images of a nonius fusion test (Fig. 1a) with each eye occluded in turn. To our great surprise, we found that a number of patients could form a fused image even

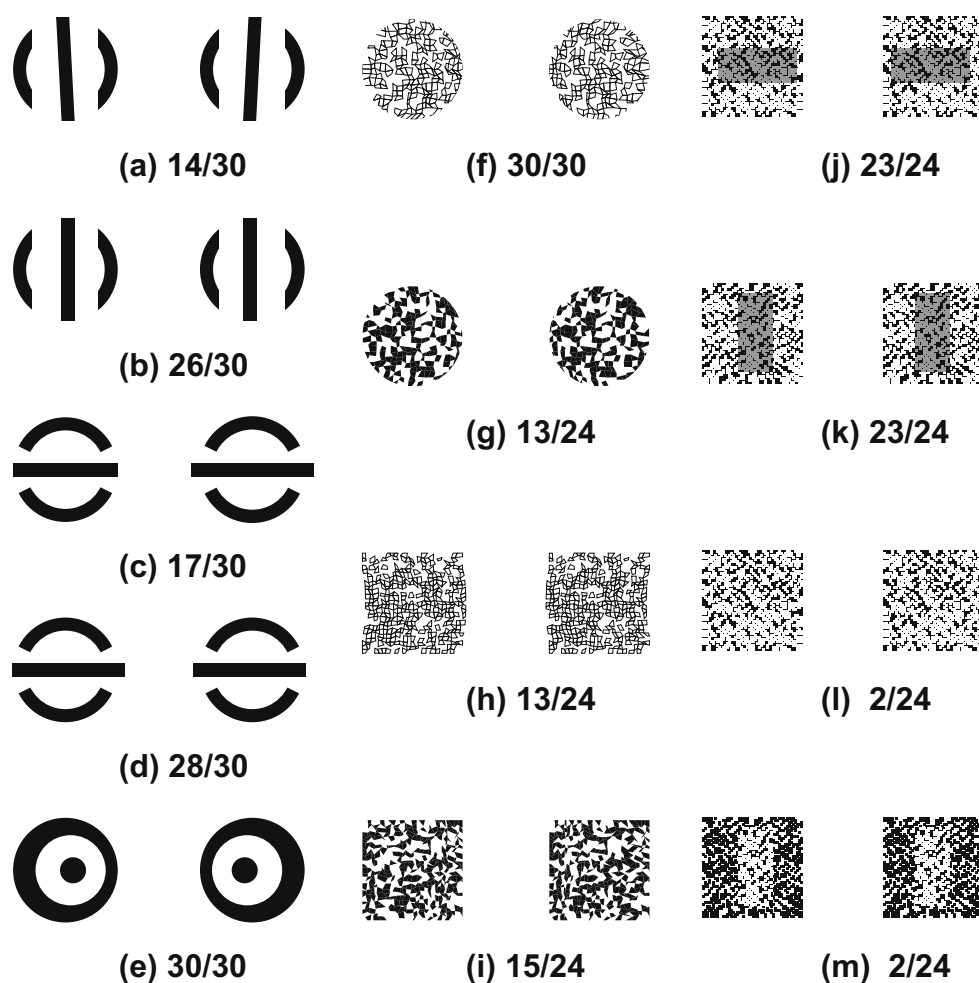


Fig. 2. Main stereoscopic stimuli used in this study. All the subjects were tested on stimuli (a)–(f), and 24 of them were tested on (g)–(m). The number of subjects who reported depth in at least one of the testing situations is indicated for each stimulus in the numerator, the denominator indicating the number of subjects tested on the stimulus. In normal binocular vision, the stimuli represent slanted (a) or frontoparallel (b), vertical bars, slanted (c), or frontoparallel (d), horizontal bars, a central disc above or below background (e), a dome (f), a dome with a depression in the centre (g), cylindrical surfaces with a horizontal (h), or vertical (i), axes, explicit horizontal (j), or vertical (k), segments above or below background, and their camouflaged counterparts (l and m). Stimuli (f)–(i) use distorted square grids (Ninio, 2007). For each geometric condition, they were designed both in the outline drawing style, as in (f) or (h), and in filled quadrangle style, as in (g) and (i). The subjects responded equally well to the two versions of each stimulus.

under the control condition, with a single eye, the other eye being occluded by interposition of an opalescent screen (see the [Supplementary material](#), Fig. 4). The monocular fusion phenomenon occurred when the separation of the images more or less matched the separation between the fovea and the secondary sensitive zone of the squinting eye, as indirectly estimated by the Hirschberg deviation angle, and the ARC angle on the synoptophore. In a first survey, based on an initial set of 450 patients, 37 patients (20 with convergent 17 with divergent squint) could fuse the nonius stimulus of Fig. 1a monocularly (Rychkova & Malyshev, 2007). We then widened the scope of the tests, including stimuli for lustre (Fig. 1b) or depth (Fig. 2).

Within an extended set of 550 patients, we identified 151 patients who could experience binocular fusion under the stimulating conditions of the synoptophore. Out of these, 44 were able to monocularly fuse nonius (Fig. 1) or stereoscopic (Fig. 2) stimuli or both on the binarimeter, and were retained for further studies. In this subset, 14 had NRC, 13 had ARC and, remarkably, 17 had both NRC and ARC (i.e., they could fuse an image captured foveally by one eye with an image captured by the other eye, be it by the fovea or by the second sensitive zone of this eye). Among the remaining 107 patients who could experience binocular but not

monocular fusion, 81 had NRC, 26 had ARC but none had both NRC and ARC. Having both NRC and ARC thus appears to be a sufficient but not a necessary condition for the occurrence of monocular fusion. This feature drew our attention to a fact that we had not noticed previously: all the patients who were competent for monocular fusion were *inconstant* squinters, i.e., they alternated between deviating and non-deviating eye conditions.

It then becomes clear that monocular fusion occurs almost invariably in strabismic patients who fulfil three conditions: (i) they have no neutralization scotoma, (ii) they are capable of normal or anomalous binocular vision and (iii) their squinting is inconstant – the patients naturally alternate between normal vision and squint at all viewing distances. Thus, both the fovea and the second sensitive zone of their squinting eye may be recruited for binocular vision. Then, the two regions may send simultaneous signals which, under suitable geometric conditions, give rise to a fused percept.

The two patients followed by Ramachandran et al. (1994a) and (1994b) had a different form of squint, “intermittent exotropia”. They used NRC during near fixation, and ARC when looking at distant objects. One patient, viewing two rivalrous patches with a single eye perceived a mosaic pattern “analogous to what one usually

observes in binocular rivalry” (Ramachandran, Cobb & Levi, 1994b). Monocular fusion was not observed, or at least not reported for this patient.

3.2. Lustre

When two corresponding regions in a stereoscopic stimulus disagree in their shade of grey, the stereoscopic interpretation is nevertheless carried out successfully, and the region with mismatched grey levels is perceived with lustre. Metallic or shimmering lustre is also experienced monocularly with flickering stimuli alternating at or above 16 Hz (Anstis, 2000). Our patients were tested with the stimulus of Fig. 1b, in which the corresponding central discs of Fig. 1a differed in their grey level and in which the protruding bars had different colours. They were asked to say which colours they perceived. Most patients (37/44) spontaneously reported the lustrous character of the fused central disc. Four other patients reported that the central disc alternated between dark grey and light grey. Lustre or grey level instability occurred only in conjunction with the fusion of two images. It was never perceived with a non-strabismic eye (22/22 negative responses).

Lustre was always observed in the disc region, but never on the monocular protruding bars. Depending on the subject, it could be perceived on the fixated image alone (21 cases), on the non-fixated image alone (19 cases), or on both images (20 cases). In one case the lustre effect alternated between the fixated and the non-fixated image.

3.3. Colour binding

We also examined how colours were treated in the fused image, using again the stimulus of Fig. 1b in which a downward bar in the left image is red and an upward bar in the right image is green. Out of 44 subjects, 16 were not able to form a fused image with both bars. Among the others, a fused image could be seen in the direction of the fixated image alone (five subjects, seven eyes), in the direction of the non-fixated image alone (12 subjects, 20 eyes), or in both directions (11 subjects, 17 eyes). Three among these 28 subjects perceived an inconstant fused image at an intermediate location between the fixated and the non-fixated images.

While in the fused percept the two bars were seen correctly aligned, their colours were not always correct. The true colour of the foveal bar often applied, in the perceived fused image, to both the foveal and the extrafoveal bars (12 subjects, 17 eyes). Such errors on the extrafoveal bars occurred when the fused percept was on the foveal side (that of the fixated image). The opposite substitution error (a foveal bar seen in the colour of the extrafoveal bar) was observed in a single case. It occurred when a fused percept was on the extrafoveal side (that of the non-fixated image).

Such colour attribution errors are, we think, an illustration of the more general binding problem (see, e.g., Treisman, 1996). Fusion would work here essentially on achromatic signals. Colour and shape would be processed in separate pathways and colour would subsequently be assigned to parts of the fused image. Note that colour misbinding has already been observed in situations of binocular rivalry (e.g., Carney, Shadlen, & Switkes, 1987) or in situations of conflict between colour and motion signals (Smith, Levi, Harwerth, & White, 1982).

3.4. Depth perception

We established in the preceding sections, that two projections from one eye could be associated into a single fused image. We now examine the fate of truly stereoscopic stimuli. A set of 13 stereograms together with a number of variants, probing various aspects of stereoscopic processing were prepared (Fig. 2) and

presented to 30 subjects (43 strabismic eyes). Six subjects were tested on a subset of six stereo pairs (Fig. 2a–f), as well as the six pairs generated by exchanging the left and the right images (thereafter designated as “inverted variants”). Twenty four subjects were tested on 13 stereo pairs (Fig. 2a–m) and their inverted variants. For every subject, each eye, whether strabismic or not, was tested while fixating the left or the right image of the stereo pairs. For each stimulus of Fig. 2, the number of subjects having experienced a depth perception with either this stimulus or its inverted variant is indicated in Fig. 2, under the stimulus.

The total number of tests before treatment was 2784. For each eye and each stimulus, we asked the subjects to fixate one of the images, then the other. All tests with the non strabismic eyes (828 tests) failed to elicit any depth perception. All tests with strabismic eyes in the unfavourable geometric condition (a convergent squinting eye fixating the image on its side, or a divergent squinting eye fixating the image on the other side) failed to elicit any depth perception (978 tests). With strabismic eyes in the favourable geometric conditions, shown in Fig. 3 (978 tests) depth was perceived for some images but not for others. Note in Fig. 3 that one image projects on the fovea, while the other image projects on its nasal side for a convergent squinting eye, or its temporal side for a divergent squinting eye.

When depth was perceived (417 cases), it could be perceived on the fixated image alone (282 cases), on the non-fixated images alone (47 cases) or on both the fixated and the non-fixated images

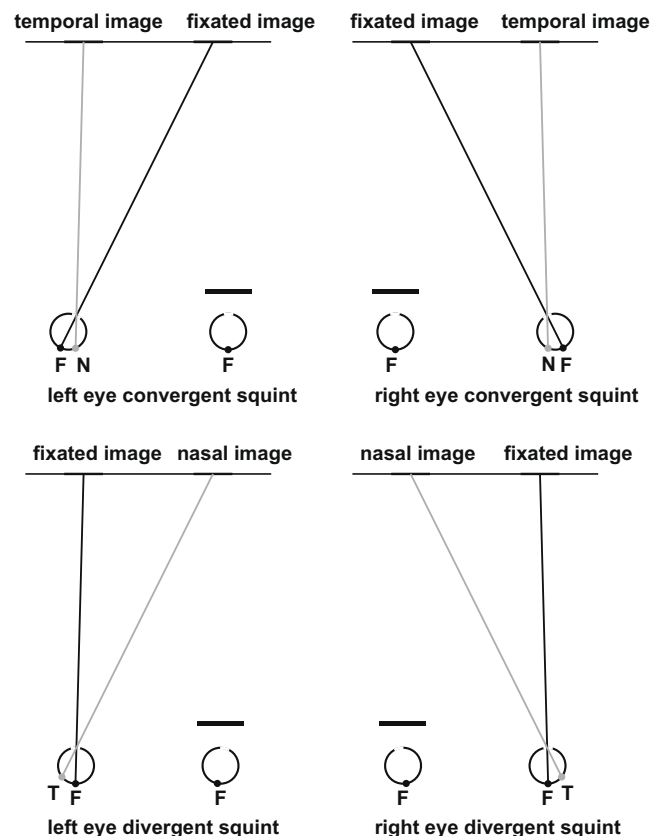


Fig. 3. The four viewing conditions which produce paradoxical fusion, lustre and depth perception. The effects are observed in the deviating eye condition for cross-eyed squinters, and the non-deviating eye condition for divergent squinters. Note that the temporal and nasal parts of the stimuli, respectively, project on the nasal (N) and temporal (T) regions of the retina. F designates the fovea. The occluded eye is represented here with an inward or outward deviation which occurs naturally to maintain the standard strabismic deviation angle normally present between the two eyes.

(88 cases). In the latter case, depth was always in the same direction for the fixated and the non-fixated images. In what follows, we will lump together the positive depth responses reported for the fixated and the non-fixated images, and give the results for this pool of 417 positive depth responses.

For subjects with two strabismic eyes, a stimulus elicited depth in the same direction for the two eyes (133/133 cases). The most favourable stimuli for depth perception were the disc of Fig. 2e and the hemisphere of Fig. 2f (depth reported by 30/30 subjects). Note that only 15 subjects in this set could fuse the nonius stimuli of Fig. 1. The most unfavourable stimuli were the camouflaged vertical or horizontal rectangles (Fig. 2l and m), which elicited depth responses in only two out of 24 subjects, while their uncamouflaged counterparts (Fig. 2j and k) elicited depth responses in 23 out of 24 subjects.

Stereograms 2l and 2m represent overhanging surfaces and thus contain flanking monocular regions. Such regions are expected, in some cases, to facilitate depth interpretation (Gillam & Borsting, 1988) because they help define the lateral boundaries of overhanging surfaces. If our images are presented to the subjects as 1.5 cm wide squares placed at 40 cm distance, the angle subtended by the monocular regions is about 6 min of arc. The disparities thus generated are clearly above threshold for normal subjects (McKee, 1983) but could be too small here.

Depth was often perceived in camouflaged stereograms representing continuous surfaces (Fig. 2f–i). They could be perceived as convex (99 cases) or concave (10 cases). However, the shapes of the cylinders (Fig. 2h and i) were generally not defined to the point of distinguishing them from protruding or recessing domes. None of the subjects detected the double curvature in the stimulus of Fig. 2g.

The stereograms of Fig. 2a and c represent slanted bars. They were seen in depth by 14 and 17 subjects out of 30, respectively, while the non-slanted counterparts (Fig. 2b and d) were seen in depth by 26 and 28 subjects, respectively. Yet, the presence of surrounding arcs creates a reference frame which, in principle, should have facilitated the detection of slant in Fig. 2a and c (see, e.g., Gillam, Chambers, & Russo, 1988; van Ee & Erkelens, 1996). When the slanted stimuli were seen in depth, they were usually seen as protruding or recessing frontoparallel bars. The slanted aspect was reported by only seven subjects and, even with them, non systematically. Note that in normal stereoscopic vision as well, and at least for some classes of stimuli, slanted surfaces appears harder to detect than curved ones (Rogers and Cagenello, 1989; Devisme, Drobe, Monot, & Droulez, 2008) or frontoparallel ones (Mamassian, 2008).

Depth rarely changed when exchanging the left and the right images. In most cases, the subjects reported the presence of depth in one arrangement, and no depth at all for the other arrangement. Only five out of the 30 subjects reported depth for both variants of the stimuli. With the stimuli as shown in Fig. 2, excluding the slanted stimuli 2a and 2c, there was a tendency to see the figures as protruding (262 “near” answers versus 20 “far” answers). The bias was not observed with the inverted variants (39 “near” versus 44 “far” answers).

The optimal angle for perceiving the lustre or depth effects varies slightly with the presentation distance. It corresponds, within $\pm 2^\circ$, to the strabismic deviation angle, as determined on the synoptophore (see Fig. 4 in the Supplementary material). There is an inward bias, the binarimeter angle being slightly smaller than the synoptophore angle (mean signed difference: -0.68° , median: -0.21° , standard deviation, 2.1°). The mean absolute difference was 1.42° and the median was 0.79° , for a standard deviation of 1.71° . The boundaries of the lustre, colour binding and depth effects were estimated in every case, by varying the separation between the two images, and determining when the patients ceased to experience the effects. A few patients experienced the ef-

fects over a 4-degree range. The mean amplitude was 2.2° , the median was 0.77° and the standard deviation was 1.1° .

3.5. The effect of treatment

All 44 patients in this study followed an orthoptic treatment on a synoptophore during 20–30 min, 5 days a week, for 2–3 weeks. If necessary, the treatment was repeated after a 1–2 months interval. In this treatment, images were presented under the NRC condition, alternately to each eye at a 2 Hz frequency, in order to promote foveal capture by both eyes. The alternation frequency was then raised progressively up to 8 Hz. If the patient was able to fuse the two foveal images at the 8 Hz frequency, we switched to a simultaneous presentation of the two images, and gradually lowered the display frequency from 8 to 2 Hz. As a result of this treatment, (i) the position of the non-strabismic eyes became more stable in all the patients, (ii) 41 out of 44 patients had stable NRC, 25 patients had normal binocular vision according to Worth's test and (iii) 17 patients had positive responses to the Titmus fly and the Lang's stereo tests.

After treatment, most subjects rapidly lost most of their paradoxical effects of fusion and depth perception. 20 out of 37 subjects lost the lustre effect with a single eye; the flicker effects previously reported by four subjects disappeared, 18 out of 28 subjects lost the fusion of the protruding bars with a single eye. 21 subjects were tested again on the stereoscopic stimuli of Fig. 2. There was some residual depth perception, less vivid than before, and for a smaller subset of images (on average, 7.9 images elicited depth before treatment, 2.4 elicited depth after treatment). Depth was then perceived mostly on the fixated image alone (94 out of 104 cases).

4. Discussion

We have documented a new phenomenon in which the diplopic images originating from a squinting eye, with the other eye occluded, give rise in about 8% of strabismic patients to phenomena of fusion, lustre, colour misbinding and, even more surprisingly, depth interpretation. These patients share the characteristic of being inconstant squinters. A favourable but not necessary condition (17/44 patients) is to have both normal (NRC) and anomalous (ARC) binocular vision.

Monocular fusion of two images differing in their grey levels often gave rise to lustre effects, and monocular fusion of stereoscopic couples occasionally gave rise to depth perception. We propose that these monocular effects which mimic binocular effects occur when the signals sent by the two sensitive zones of one retina are processed by brain areas normally dedicated to the processing of stereoscopic information.

Let us consider that at some early stage of normal stereoscopic processing, the two brain hemispheres are working in parallel, and each hemisphere receives input from both eyes.

Then some depth information might be extracted independently in each hemisphere, and more depth information might be obtained by comparing the information in the two hemispheres. In the situation of monocular fusion, we expect that the foveal region of the active eye would send, as usual, redundant output to the two hemispheres, but that the second sensitive zone would send its output to a single hemisphere. Furthermore, this output would be poor in parvocellular connections. With divergent squinters, the sensitive zone is in the temporal region of the retina, so it is expected to send output to the ipsilateral hemisphere. In the case of convergent squinters, the second sensitive zone is on the nasal side of the retina, and it is therefore expected to send its output to the contralateral hemisphere. In both cases, the brain would work with three representations instead of four. In addition, while

in normal stereoscopic viewing the eyes move in a coordinated fashion and focus on corresponding regions of the images, there is no such latitude in monocular fusion, because the distance between the fovea and the other sensitive zone is fixed.

Therefore, part of the information which is usually available for stereopsis is missing in our case, explaining perhaps the difficulty encountered with slanted stimuli (Fig. 2a and c) or with overhanging surfaces (Fig. 2m and l). From what we know of normal stereoscopic vision, a few other effects seem harder to explain, (i) we found no significant difference between convergent and divergent squinters, (ii) there was a tendency to see the shapes as protruding (332 “near” versus 66 “far” responses, all stimuli being taken into account here in both their standard and their inverted variants) and (iii) depth was more often seen with the stereo pairs as shown in Fig. 2 than with the inverted variants (232 positive responses for the variants of Fig. 2 alone, seven responses for the inverted variants alone, 89 responses for both variants).

Actually, there are subtle geometric constraints in the monocular fusion tests which may, in part, explain the strange asymmetries between near and far responses on the one hand, and the relative ease of seeing depth in standard versus inverted stimuli on the other hand. In normal stereoscopic vision, under natural viewing conditions, the position in 3d space of the point on which the two eyes are focused is near the intersection of the visual rays from the two foveas to that point. In monocular fusion, the visual rays from the two sensitive zones of a same eye to the target images intersect on the pupil of the eye, hence the represented surface should appear very close independently of the viewing conditions! This is one among various reasons why the brain might initiate the stereoscopic matching process with a bias regarding the ‘near’ or ‘far’ character of the surface to be reconstructed.

Let us recall here a curious phenomenon, occasionally encountered when performing stereoscopic tests. People with rather good stereoscopic aptitudes, looking at a camouflaged stereogram through a stereoscope, may occasionally see the correct shape, but inverted in depth. This was noted for instance in Ninio and Herlin (1988). This phenomenon suggests that – at least in these cases – the matching process may be carried out on the basis of an erroneous assumption regarding which representation comes from which eye (this is the eye-of-origin or utricular issue, reviewed in Howard and Rogers (2002), chap. 17. To put it more concisely, the brain uses a “depth sign” to convert inward or outward disparities into near or far positions in depth. The depth sign should be unambiguous when the eye-of-origin information is available. Otherwise, the brain may use various clues to determine what the appropriate depth sign is, in particular the vergence signals, which are of no use in our case.

In normal stereopsis, when the stimuli of Fig. 2 (except the slanted stimuli 2a and 2c) are viewed under the uncrossed-eye condition, they are seen as protruding surfaces. Note the inward character of the disparities in this case. When the same stimuli are viewed under the crossed-eye condition, there is depth reversal. However, in the case of monocular fusion, the two images are captured by the same eye and form an arrangement on the retina which matches the objective arrangement of the stimulus. This

consideration could explain why there is no depth sign difference between convergent and divergent squinters.

Beyond the paradoxical character of depth perception after monocular fusion with a single eye, important questions are raised about normal stereoscopic mechanisms, such as the relative contributions of the two cerebral hemi fields to the complete 3d representation, the utricular issue and the related depth sign issue, or the resources required in the computation of slant versus curvature, or of camouflaged continuous shapes versus discontinuous ones.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2008.12.018.

References

- Anstis, S. M. (2000). Monocular lustre from flicker. *Vision Research*, 40, 2551–2556.
- Bielschowsky, A. (1898). Über monokulare Diplopia ohne physikalische Grundlage nebst Bemerkungen über das Sehen Schlienlender. *Albrecht v. Graefes Archiv für Ophthalmologie*, 46, 143–148.
- Carney, T., Shadlen, M., & Switkes, E. (1987). Uncrossed-eye processing of motion and colour information. *Nature*, 328, 647–649.
- Devisme, C., Drobe, B., Monot, A., & Droulez, J. (2008). Stereoscopic depth perception in peripheral field and global processing of horizontal disparity gradient pattern. *Vision Research*, 48, 753–764.
- Gillam, B., & Borsting, E. (1988). The role of monocular regions in stereoscopic displays. *Perception*, 17, 603–608.
- Gillam, B., Chambers, D., & Russo, T. (1988). Postfusional latency in slant perception and the primitives of stereopsis. *Journal of Experimental Psychology: Human Perception and Performance*, 14, 163–175.
- Howard, I. P. (2002). *Seeing in depth. Volume 1 Basic mechanisms*. I. Thornhill. Ontario, Canada: Porteous.
- Howard, I. P., & Rogers, B. (2002). *Seeing in depth. Volume 2 Depth perception*. I. Thornhill. Ontario, Canada: Porteous.
- Mamassian, P. (2008). Dramatic insensitivity for surface orientation from binocular disparities. *Perception* 37 (Suppl. 124).
- McKee, S. P. (1983). The spatial requirement for fine stereoacuity. *Vision Research*, 23, 191–198.
- Ninio, J. (2007). The science and craft of autostereograms. *Spatial Vision*, 21, 185–200.
- Ninio, J., & Herlin, I. (1988). Speed and accuracy of 3D interpretation of linear stereograms. *Vision Research*, 28, 1223–1233.
- Ramachandran, V. S., Cobb, S., & Levi, L. (1994a). The neural locus of binocular rivalry and monocular diplopia in intermittent exotropes. *NeuroReport*, 9, 1141–1144.
- Ramachandran, V. S., Cobb, S., & Levi, L. (1994b). Monocular double vision in strabismus. *NeuroReport*, 5, 1418.
- Rogers, B., & Cagenello, R. (1989). Disparity curvature and the perception of three-dimensional surfaces. *Nature*, 339, 135–137.
- Rychkova, S. I. & Malyshev, V. (2007) Paradoxical fusion of two images with a squinting eye. *Perception* 36 (Suppl. 71).
- Siriteanu, R. (1982). Binocular vision in strabismic humans with alternating fixation. *Vision Research*, 22, 889–896.
- Smith, E. L., Levi, D. M., Harwerth, R. S., & White, J. M. (1982). Color vision is altered during the suppression phase of binocular rivalry. *Science*, 218, 802–804.
- Treisman, A. (1996). The binding problem. *Current Opinion in Neurobiology*, 6, 171–178.
- van Ee, R., & Erkelens, C. J. (1996). Temporal aspects of binocular slant perception. *Vision Research*, 36, 43–51.