



Stereoscopic Vision in the Absence of the Lateral Occipital Cortex

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Abstract

Both dorsal and ventral cortical visual streams contain neurons sensitive to binocular disparities, but the two streams support different aspects of stereoscopic vision. Here we investigate stereopsis in the neurological patient D.F., whose specifically lateral occipital cortex, has been damaged bilaterally, causing profound visual form agnosia. Despite damage to cortical visual areas, we report that DF's stereo vision is strikingly unimpaired. She is better than most at using binocular disparity to judge whether an isolated object appears near or far, and to resolve ambiguous motion. DF is, however, poor at using relative disparity between features at different locations across the visual field from a difficulty in identifying the surface boundaries where relative disparity is available. We suggest that the ventral stream may play a critical role in enabling healthy observers to extract fine depth information from relative disparity between surface or between surfaces located in different parts of the visual field.

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Introduction

Humans use the different viewpoints provided by their two eyes to produce a vivid percept of the world in depth. A key aspect of stereoscopic perception is that we are far better at judging the relative disparity between two features than the absolute depth of an isolated feature [1]. For example, in Figure 1A, the eyes are directed at point *a*, so the retinal image of point *b* falls further from the fovea in the right eye than in the left. This difference between the retinal images of point *b* is called absolute disparity. If the absolute disparity is large enough, we will perceive *b* as closer to us than the fixation point, even if *b* is actually further away. However, our sensitivity to the depth of *b* is greatly enhanced if points *a* and *b* are simultaneously visible. In such a case, we can directly compare the *relative disparity* between the two points. In a complex scene, one can distinguish many different relative disparities [2]: e.g. relative disparity within a surface (Figure 1B), between adjacent surfaces (Figure 1C) or between surfaces viewed transparently (Figure 1D).

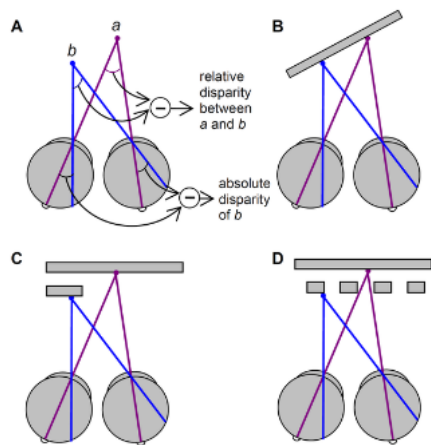


Figure 1. Different stimulus configurations that give rise to relative disparity.

A: Relative disparity between two points. Absolute disparity of an object = difference in its angular distance from the two eyes. Here the eyes are looking at point *a*, so *a* has zero absolute disparity but *b* has a non-zero value. The relative disparity of the two points is equal to the difference in their absolute disparities (equivalent to difference in angles at each point, as shown). **B:** Relative disparity between different points on a surface. **C:** Relative disparity between two points, one of which occludes the other. **D:** Relative disparity between transparently-visible surfaces, as can occur when one opaque surface or structure, such as a picket-fence or tree, partially occludes a more distant surface. <http://dx.doi.org/10.1371/journal.pone.0012608.g001>

The cortical pathways underlying our sensitivity to these various forms of relative disparity are unclear. Area V1 is tuned to adjacent-surface relative disparity [3]–[5], and the proportion of such neurons increases along the ventral stream. However, dorsal areas V3A and the caudal intraparietal sulcus CIPS are also strongly activated by adjacent-surface relative disparity [9]. Human fMRI reveals no difference in the response of V1 and V2 to the relative disparity between the ventral stream responds to both absolute and transparent-surface relative disparity while dorsal areas respond to absolute disparity [10].

One particular stimulus that has revealed intriguing differences between the ventral and dorsal streams is the random-dot stereogram, in which the colours of black and white dots are switched over in one eye with respect to the other. This stimulus does not correspond to any real physical surface, so a system designed to detect the depths of real surfaces should not respond to it [11], and in accordance with this expectation, neither humans nor monkeys can discriminate depth [12]–[15]. A naïve disparity detector based on cross-correlating the two eyes' images will respond, but with a sign inversion. This signature sign-inversion is found in V1 [14], in many neurons in MT [17], in disparity filters deduced from MT [18], and in rapid vergence corrections with anti-correlated stimuli [19].

Beyond V1, it has been suggested that ventral and dorsal streams may differ in their responses to anti-correlated stimuli. Areas MST [20] and MT [17] contain many neurons which are tuned to disparity in anti-correlated stimuli, whereas in areas V4 [21] and IT [22], most neurons are not tuned to anti-correlated disparity. In fMRI, Bridge & Parker [23] found differences in activation between correlated vs anti-correlated stimuli alternating in depth are found in areas MIP and MIP. [24] performed a multi-voxel pattern analysis to estimate how much information the BOLD signal in different areas carries about the sign of disparity in correlated and anti-correlated stimuli. They found that, in ventral areas V3v and V4, the BOLD signal could be read out with about the same accuracy for both correlated and anti-correlated stimuli, whereas in LO areas examined, much greater accuracy was obtained for correlated stimuli. Thus, all these different studies agree that the strongest and most reliable differences between correlated and anti-correlated stimuli are found in the ventral stream.

These neurophysiological and imaging studies can only reveal correlations between brain activity and behavior. Lesions provide one of the few available ways of testing for causal relationships between brain circuitry and behavior. Here we present the first neuropsychological study to investigate the cortical processing of relative disparity. In a patient who suffered carbon monoxide poisoning, which generated bilateral damage to the lateral occipital cortex, an impairment of the ventral stream [25], [26]. As a result, DF has profound visual form agnosia. Although she has partial visual form agnosia, she is unable to recognize objects by shape, or even to report correctly whether a line or grating is vertical [25]–[27].

The initial description of DF (Milner et al. 1991) reported that she retains stereo vision (though unable to identify objects present in depth, and with lower acuity than controls). Beyond that, however, there has been little systematic study of her perception. Here, we present a detailed examination of DF's stereoscopic vision, including all three forms of relative disparity identified in Figure 1.

Methods

Experimental stimuli

This paper describes a sequence of experiments, designed to probe different aspects of DF's stereo vision, ca occasions over a period of some 15 months. As we learnt more about DF's abilities, we adapted the stimuli ac introduced new stimuli to exclude various interpretations. The experiments will be described in detail as each i are summarized in Figure 2, with each stimulus given a numerical identifier. The duration of each stimulus is al 2. Experiments performed at long (500ms or free viewing) and short (160ms or 200ms) durations are indicated in Figure 2. Some experiments were performed with anti-correlated stimuli. These are stimuli in which the cont eye's image is inverted, so that black pixels are replaced with white and vice-versa. These are indicated by the stimulus identifier. Figure 3 provides a timeline showing when DF was tested on each stimulus.

Experiment	Exp code	Description of stimulus	Stimulus duration	Stimulus Orientation	Stimulus Size
1. Relative disparity between adjacent surfaces (Figure 1)	1.1	Target disk. Two half-disk arrangements of a target disk, with or without a surrounding reference surface in the plane of the screen. Target and reference surfaces were both defined with stereo black and white dot patterns scattered on a gray background. The left reference target and reference stimuli were 1000 dots (1000x1000) and 1200 dots (1200x1200) respectively.	Figure 2, 2A, 2B, 2C	Figure 2D, 2E	Figure 2F, 2G, 2H
	1.2	Target disk. Two half-disk arrangements of a target disk, with or without a surrounding reference surface in the plane of the screen. Target and reference surfaces were both defined with stereo black and white dot patterns scattered on a gray background. The left reference target and reference stimuli were 1000 dots (1000x1000) and 1200 dots (1200x1200) respectively.	Figure 2D, 2E	Figure 2D, 2E	Figure 2F, 2G, 2H
	1.3	Target disk. Two half-disk arrangements of a target disk, with or without a surrounding reference surface in the plane of the screen. Target and reference surfaces were both defined with stereo black and white dot patterns scattered on a gray background. The left reference target and reference stimuli were 1000 dots (1000x1000) and 1200 dots (1200x1200) respectively.	Figure 2D, 2E	Figure 2D, 2E	Figure 2F, 2G, 2H
2. Relative disparity across a single surface (Figure 1B)	2.1	Disparity-defined plane. Full-screen condition. The participant is the two open eyes subjected to the same magnification, no magnification specified at a fixed distance. The task was to indicate whether the left or right side was closer. Stimulus duration 100ms.	Figure 10A, 10B, 10C	Figure 10D, 10E, 10F	Figure 10G, 10H, 10I, 10J
	2.2	Disparity-defined plane. Edge condition. As 2.1, but the magnification was only applied to the visible part of the screen.	Figure 10A, 10B, 10C	Figure 10D, 10E, 10F	Figure 10G, 10H, 10I, 10J
3. Relative disparity between dissimilar surfaces (Figure 1D)	3.1	Rotating cylinder. The task was to identify the direction of rotation of a vertically oriented cylinder. Stimulus duration was until the subject responded.	Figure 12A, 12B, 12C	Figure 12D, 12E, 12F	Figure 12G, 12H, 12I, 12J
	3.2	Rotating disk. Two half-disk arrangements of an outer ring of random dots, either static, moving randomly, or moving unipolarly in opposite directions. Stimulus duration 200ms.	Figure 12A, 12B, 12C	Figure 12D, 12E, 12F	Figure 12G, 12H, 12I, 12J
	3.3	Dot in the plane. Random dot depicted either a single plane of dots moving with uniform velocity, or two planes moving non-parallel in opposite directions. The task was to identify the number of planes. Stimulus duration until the subject responded.	Figure 12A, 12B, 12C	Figure 12D, 12E, 12F	Figure 12G, 12H, 12I, 12J

Figure 2. Reference list of experiments.

The experiments are grouped together according to the type of relative disparity investigated, and each stimulus given a numerical identifier. For experiments which were performed at different stimulus durations, the suffix L indicates long duration (either 500ms or until the subject responded) and S indicates short duration (stimulus on-screen for 160ms or 200ms). Figure 3 shows when DF was tested on each stimulus. <http://dx.doi.org/10.1371/journal.pone.0012608.g002>



Figure 3. Timeline of experiments performed by DF.

See Figure 2 for experiment codes. For experiments done at both short and long durations, the duration is indicated by suffix S or L. The suffix A indicates the anti-correlated version of the stimulus. <http://dx.doi.org/10.1371/journal.pone.0012608.g003>

For each stimulus, we initially explained the task to the participant by presenting a few examples in which we could see a response. During data collection, no feedback on individual trials was provided to participants.

Subjects

Patient DF was aged 53–55 at the times of testing. DF's brain damage has been assessed by structural and functional MRI measurements [25], [26]. The principal lesions in visual cortex lie bilaterally in the lateral occipital region, specifically in the lateral occipital sulcus, although there is diffuse damage elsewhere, as is typical following carbon monoxide poisoning. The lateral occipital sulcus was compromised on structural scans and is not activated functionally during scans that show a greater activation than scrambled, visual objects in control subjects [26].

We compared DF's performance with that of 7 controls: 2 authors (JR, female, aged 35 years at the time of testing) and 5 volunteers without previous psychophysical experience, of similar age to DF: three females, F1 (53), F2 (54), and F3 (55), two males, M1 (60), M2 (63). DF wore prescription spectacles suitable for the viewing distance of 90cm, and had normal visual acuity. Psychophysical experiments were carried out at Durham, Oxford and Newcastle Universities. All experiments were conducted with the understanding and written consent of each subject, and the study complies with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Psychophysics research was approved by internal ethics committees at each of the three sites where experiments were conducted.

Equipment

All experiments were programmed using *Matlab* (The Mathworks, Natick, MA) with the Psychophysics Toolbox running on a PC. Stereo images were presented in red/blue anaglyph. Except for Experiment 1.3, stimuli were presented on a 20" screen LCD monitor, 1280x1024 pixels and 37.5x30cm, viewed at 90cm in normal ambient lighting. 1 pixel subtended 23.5° horizontally and 18.9° vertically. In Experiment 1.3 only, stimuli were presented on a 20" screen LCD monitor, 1280x1024 pixels and 30x24cm, viewed at 53cm in a dark room. All our experiments used random-dot patterns to enable the binocular disparity depth cue to be isolated from other cues which signal depth in natural viewing, such as occlusion, size, texture etc [30]. The random-dot patterns consisted of equal numbers of black and white dots with the same mean luminance. The dots were either 7 or 9 arcmin across. Their density was such that if none

overlapped, they would have occupied 30% of the stimulus area. Anti-aliasing was used to produce sub-pixel c between stimuli, observers converged their eyes on a fixation cross in the plane of the computer screen. Nonius used, since this would add to the complexity of the tasks DF was being asked to carry out, and since it seemed patient with visual form agnosia would be able to monitor vergence using Nonius lines.

Data analysis

Psychometric functions were fitted with a cumulative Gaussian scaled to run from 0.5% to 99.5%, i.e. allowing

$$\frac{1}{2} + \frac{(1-l)}{2} \operatorname{erf}\left(\frac{x-\mu}{\sigma\sqrt{2}}\right)$$

where $l=0.01$ is the lapse rate, μ is the point of subjective equivalence, σ is the threshold, and x is the metam disparity or magnification. The fitted threshold was not significantly affected by the precise value of the lapse rate; lapse rate altogether produced artefactually large thresholds for a few psychometric functions (see Supporting and [31]). Parameters were adjusted, using MATLAB's FMINSEARCH function, to maximize the likelihood.

In both the main paper and the Supporting Information, error bars show the 95% confidence intervals. For psych were calculated using the score confidence interval for simple binomial statistics [32]. Other error bars were of resampling [33]. First, a new set of simulated psychophysical data was generated from the original cumulative. Each set of simulated data was then analysed in exactly the same way as the original data-set, in order to provide estimate of the quantity of interest (e.g. threshold, regression gradient). This process was repeated 10,000 times. 97.5 percentiles were taken as the end-points of the 95% confidence interval on the original quantity.

To assess whether DF's performance differed significantly from those of controls, we used the techniques developed by Garthwaite [35], [36] for the analysis of neuropsychological data with single cases, and implemented in their code SINGLIM.EXE and SINGSLOPE.EXE (available online at <http://www.abdn.ac.uk/~psy086/dept/SingleCaseMethodsComputerPrograms.HTM>).

Results

Experiment 1: Sensitivity to absolute and relative disparity between frontoparallel surfaces

Experiment 1.1: Depth discrimination of a target disk.

In Experiment 1.1, observers viewed a random-dot stereogram that depicted a disparate disk, 5.6° in diameter reference surface in the plane of the screen (Figure 4Ai). They reported whether the disk appeared in front of or behind the reference surface. This stimulus presents both absolute and relative disparity to the observer: the absolute disparity of the central disk and the zero-disparity adopted by the subjects (typically the fixation cross displayed initially), and the relative disparity between the central disk and the zero-disparity surround. Next, the experiment was repeated with a featureless, annular gap between the disk and the reference surface (Figure 4Aii), and finally, if the subject was still able to do the task, the disk was presented against a featureless gray background with only the edges of the display screen available as a reference for relative depth (Figure 4Aiii). The stimulus presents the same absolute disparity as the first, but the information about relative disparity is greatly reduced, which enables us to quantify the additional sensitivity contributed by adjacent-surface relative disparity.

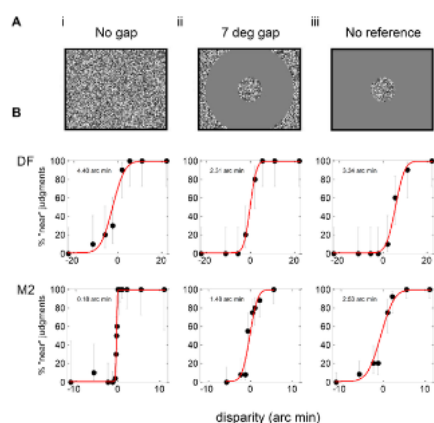


Figure 4. Experiment 1.1L: Front/back discrimination on a target disk.

A: Stimuli: (i) Central disparate disk is contiguous with a zero-disparity random-dot reference surface; (ii) central disk separated from reference surface by annulus of width 7°; (iii) no reference surface. In each case, the central disk has a diameter of 5.6°. **B:** Psychometric functions for patient DF and age-matched control M2, showing percentage “far” judgments as a function of target disparity, for long stimulus presentations. See Supporting Information File S1 for full data. <http://dx.doi.org/10.1371/journal.pone.0012608.g004>

Figure 4B shows psychometric functions for patient DF and for a typical control subject M2, for a stimulus duration of 160ms. DF's thresholds are higher than M2's and, critically, they are essentially similar for all 3 gaps, whereas M2's thresholds increase in an exponential order of magnitude as gap size increases. This is shown in Figure 5A, where thresholds are plotted on a log scale (the "no reference" condition is plotted as a gap of 12.5°, which is the smallest gap that completely removes the reference surface from view, even in the diagonal corner of the screen).

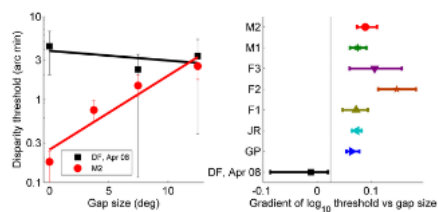


Figure 5. Results of Experiment 1.1L, long stimulus duration.

A: Threshold as function of gap size for DF (black squares, gray diamonds) and M2 (red circles), together with regression lines for log threshold as a linear function of gap size. **B:** Regression gradients (\log_{10} arcmin/deg) for DF (black squares) and 7 controls (colored symbols). For the regressions, the "no reference" condition was taken to be equal to a gap of 12.5°, the smallest annulus width that completely removes the reference surface from view, even in the diagonal corner of the screen. In both panels, the error-bars are 95% confidence intervals generated by bootstrap resampling. The line in panel B demonstrates that the 95% confidence interval for DF's gradient does not overlap the 95% confidence interval of any of the 7 controls. See Supporting Information File S1 for full data. <http://dx.doi.org/10.1371/journal.pone.0012608.g005>

To quantify this across subjects, we calculated the gradient of a regression line fitted to $\log_{10}(\text{threshold})$ as a function of gap size. Figure 5B shows this for DF and 7 controls. For each of the 7 controls individually, this gradient was significant. On average, there was a doubling of threshold for every 3° increase in gap size. In contrast, DF's gradient was different from zero.

To assess whether DF's gradient differed significantly from the population of controls, we used the modified inc test method [35] for comparing the slope of a patient's regression line with those of a sample of controls. For the 7 gradients in Figure 5B, just 0.9% of the healthy population are expected to have a gradient lower than DF.

DF shows no impairment on an absolute disparity task.

On the absolute disparity task (Figure 4Aiii), DF performed as well as the controls. This is a demanding task, as age- and gender-matched controls (F2 and F3) could not perform it at all, at any disparity. We emphasize that these controls lacked stereo vision, since they had no difficulty with the zero-gap condition, recording threshold in arc min respectively (Supporting Information File S2). Rather, it reflects the well-known difficulty of basing performance on absolute disparity alone [1], [2], [37].

We tested whether DF's threshold on the absolute disparity condition differed significantly from those of controls. There was no significant difference, even under the conservative assumption that participants F2 and F3 are assigned the worse of DF's two thresholds, 8.44 arc min (whereas in fact they could not perform the task at all even at 22 arc min).

In estimating the distance to a target, DF places great weight on binocular vergence information [39]. In theory, the absolute disparity task can be performed by fixating first on the central target and then on the edge of the screen, monitoring vergence. To rule out this strategy, we repeated Experiment 1.1 with a stimulus duration of 160ms, and obtained similar results (Figure 6). Once again, DF showed similar performance to controls on the absolute-disparity condition. DF performed better than 4/6 controls (DF's threshold 5.1 arc min; Controls GP 2.1, M2 3.6, JR 10.7 and F1, F2, F3 the task; see Supporting Information File S2). However, whereas controls found the task substantially easier when a reference surface was introduced, DF once again showed no significant improvement.

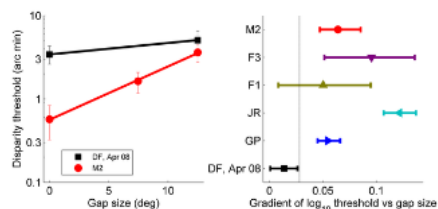


Figure 6. Results of Experiment 1.1S, 160ms stimulus duration.

As Figure 5, but for stimulus durations too short to allow eye movements. See Supporting Information File S1 for full data.

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In summary, then, DF is not impaired on this very demanding short-duration, absolute-disparity task, despite her damage to visual cortical areas. Rather, she appears to have a specific difficulty in using the relative disparity information reference surface to improve her sensitivity.

Experiment 1.2: perceiving disparity away from the fovea.

In Experiment 1.1, the boundary at which relative disparity is available is around the edge of the central target eccentricity of 2.8° . Thus, perhaps the simplest explanation for DF's failure to benefit from the relative disparity reference surface would be that DF can perceive disparity only in the center of her visual field. DF does have a threshold beyond 30° eccentricity [25] but this is too far from the fovea to be relevant here.

In Experiment 1.2, we asked DF to discriminate the depth sign of an annulus of random dots presented for 160 ms with an inner radius of 2.8° . The center of the annulus was blank gray. DF had some difficulty in learning to perform this short-duration, non-foveal absolute-disparity task, but, as Figure 7E shows, after some practice she was able to reach a threshold of 11 arc min. This demonstrates that DF does have stereo vision at the eccentricity of the reference surface used in Experiment 1.1, ruling out this potential explanation for her poor performance on the no-gap condition.

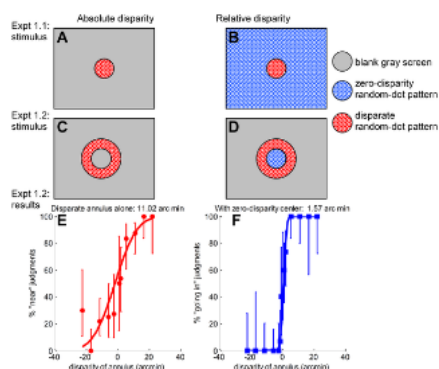


Figure 7. Results of Experiment 1.2, the annulus task.

A: "no reference" condition of Expt 1.1; C: Annulus stimulus with blank center. Both these stimuli require an absolute disparity judgment. B: "no gap" condition of Expt 1.1; D: Annulus stimulus when the center is filled with zero-disparity stimuli contain relative disparity information between abutting surfaces. EF: Psychometric functions for absolute (E) and relative (F) disparity stimuli in C (E) and D (F). The percentage of these judgments are plotted as a function of the disparity of the annulus. Errorbars show 95% confidence intervals based on simple binomial statistics.

<http://dx.doi.org/10.1371/journal.pone.0012608.g007>

DF shows a weak learning effect with relative disparity.

With a repeat of Experiment 1.2 with zero-disparity dots filling the center of the annulus (Figure 7D), DF was able to perform the task, but her threshold dropped by an order of magnitude, from 11 arc min to 1.6 arc min. It appears that DF benefits from the relative disparity information at this boundary.

We therefore next asked DF to perform the target disk task again, Experiment 1.1S (Figure 4A). DF's performance in the reference condition was unchanged, but she now showed an improvement as the reference surface was introduced within the same range as controls. Figure 8 summarises all the results obtained on Experiment 1.1 for all subjects in different sessions, for both long (A) and short (B) durations. The black squares show DF's fitted regression gradients in the reference condition, the gray diamond also shows the very similar value obtained in a brief pilot session with DF in Jan 08. The white diamonds show DF's gradient measured in Sep 08, immediately after Experiment 1.2 (see Supporting Information File 1 for psychometric functions and fitted thresholds). This gradient falls within the 95% confidence interval of 4/5 controls, in contrast to the results obtained previously.

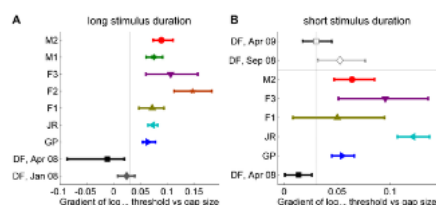


Figure 8. Experiment 1.1, fitted regression gradients from all control subjects and from DF in different testing sessions.

AB: Gradients of the regression lines are shown for the different subjects/sessions, for long (A) and short (1 durations). DF's data are shown in black/gray. Filled symbols show results from 3 sessions before she was t annulus task (Experiment 1.2, Figure 7, tested in Sep 08); empty symbols show results from 2 sessions car Control data are shown with colored symbols. The vertical dashed lines mark the separation between DF's April 2008 and those of controls. The horizontal dashed line in **B** separates DF's results after testing with E those obtained before.

<http://dx.doi.org/10.1371/journal.pone.0012608.g008>

This training effect did not persist completely. In Apr 09, DF performed Experiment 1.1S for a fifth time, with the the white square in Figure 8B (see also Supporting Information File S2). It is difficult to say with confidence wh training in Sep 08 persisted unchanged. Our best estimate is that the training continued to have some effect, b over the intervening six months. However, as we shall demonstrate, this training effect was specific to the exa which training was carried out.

Experiment 1.3: top/bottom surfaces.

To assess whether the improvement apparently produced by Experiment 1.2 would generalize to a different an surfaces, in March 2009 we tested DF on the stimulus depicted in Figure 9A. Here, random dots depicted a ne half of the screen and a far surface on the bottom half (or vice versa). The task was to say whether the top or t nearer. The surfaces either directly abutted on another, or were separated by a blank region. In Figure 9B, DF' independent of the size of the gap between the surfaces (gradient not significantly different from zero), whera became much better as the gap size reduced (individual gradients significantly positive for both control subject resampling; full data provided in Supporting Information File S3). Thus, despite the ephemeral training effects t the relative disparity between adjacent surfaces, she has a significant impairment compared to the ease with v effortlessly, automatically exploit this information.

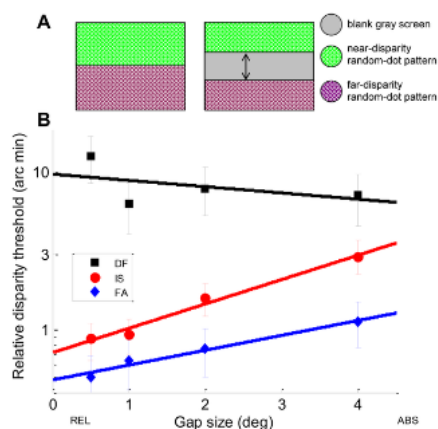


Figure 9. Experiment 1.3: top/bottom closer.

Controls perform worse as gap size increases, whereas DF is unaffected. **A**: sketch of stimulus geometry. T surfaces always had equal and opposite disparity relative to the fixation point; the task is to say which is clo relative disparity between the top and bottom surfaces to obtain the relative disparity threshold for 4 differ separating the two surfaces. The “surfaces” were depicted with black and white random dots on a uniform g the gap region was the same uniform gray. **B**: Thresholds as a function of gap size for patient DF (black sq controls (red dots, blue diamonds). See Supporting Information File S3 for full data.

<http://dx.doi.org/10.1371/journal.pone.0012608.g009>

Experiment 2: Sensitivity to slant defined by disparity

In Experiment 2, we examined DF's sensitivity to changes in disparity across a surface (Figure 1B). Subjects v discriminate the sign of slant defined by binocular disparity, i.e. to report which side of a slanted surface appea compared stimuli with and without relative disparity at surface boundaries. On the full-screen task (Experiment whole screen depicted a slanted surface, as if the surface of the monitor had been rotated about a vertical axis (Experiment 2.2, Figure 10B), the slanted region was confined to a horizontal strip running across the whole sc from fixation; the strips at the top and bottom of the screen had zero disparity. Thus, on the full-screen task, ad relative-disparity information was available only at the edges of the screen, at least 9.5° from the fixation cross eccentricities, this information was of little benefit unless the stimulus was displayed for long enough to enable saccade to the edge of the monitor. For stimulus presentations of 160ms, the full-screen stimulus effectively cc surface relative disparity information. The strip task, on the other hand, contained adjacent-surface relative-dis within 4.8° of the fovea. Many studies have shown that slant perception in control observers is greatly enhance boundaries [40], [41].

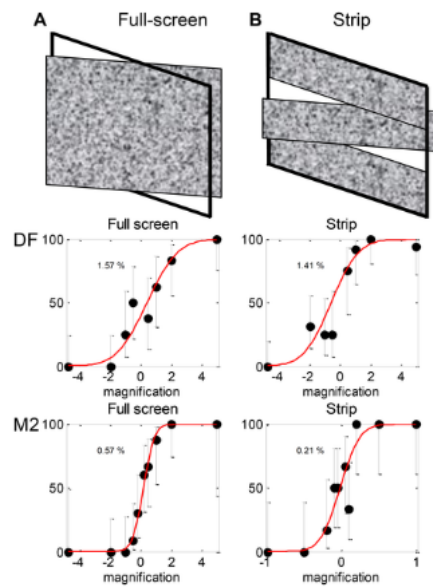


Figure 10. Experiment 2: Disparity-defined slant.

A random-dot pattern is magnified horizontally in one eye so as to depict a surface slanted about a vertical axis. **A**: Experiment 2.1, whole display is slanted. **B**: Experiment 2.2, only central strip is slanted. **C**: Psychometric function curves for patient DF (test session April 2009) and age-matched control M2, for stimulus duration 160ms. The x-axis range for M2, strip condition. See Supporting Information File S3 for full data. <http://dx.doi.org/10.1371/journal.pone.0012608.g010>

Figure 11A compares thresholds recorded on the two tasks: full-screen (red bars) and strip (blue), both for stimulus duration 160ms. On the full-screen task, DF's threshold is worse than most control observers', though better than authentic control subjects all show substantial significant improvements in the strip condition, whereas DF did not. This is shown in Figure 11B, which plots the ratio of thresholds on the full-screen condition to that on the strip condition. For each of the six subjects tested at 160ms, the threshold on the full-screen task was five times greater than that on the strip task (geometric mean ratio is 5.0). In contrast, DF's thresholds on the two tasks did not differ significantly from each other. This is further evidence of DF's inability to benefit from relative disparity information at surface boundaries.

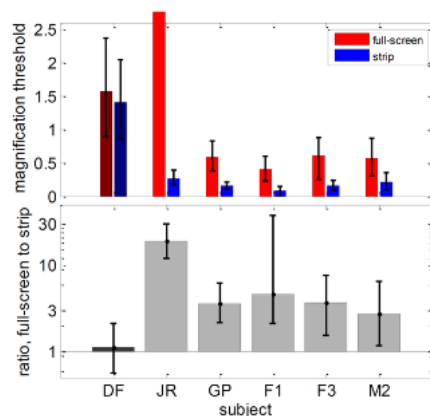


Figure 11. Results of Experiment 2: Disparity-defined slant.

A: Magnification thresholds for DF and 5 controls on Experiment 2, in the full-screen condition (red, 2.1, Figure 7A) and strip condition (blue, 2.2, Figure 7B), stimulus duration 160ms. Subject JR's threshold on the full-screen task is significantly better than that on the strip task. **B**: Ratio of magnification threshold obtained in the full-screen task to threshold obtained in the strip task. In both panels, error bars show 95% confidence intervals. See Supporting Information File S3 for full data. <http://dx.doi.org/10.1371/journal.pone.0012608.g011>

Experiment 3: Dynamic depth stimuli

Experiment 3.1: The rotating-cylinder stimulus.

In Experiment 3, we examined DF's ability to use a different form of relative disparity, that between transparent (Figure 1D). First we used the "transparent rotating cylinder" task (Experiment 3.1, Figure 12A). Here, dots move with a sinusoidal velocity profile depict a transparent rotating cylinder, and subjects are asked whether the front left or right. This stimulus has two advantages: first, normal human subjects have very low thresholds when use disparity to discriminate front and back surfaces; second, the neurophysiological evidence points strongly to dorsal involvement in this task [17], [42]–[45], so one might expect DF to be less impaired here than in Experiment 1.

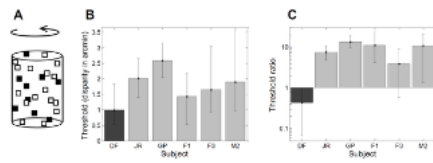


Figure 12. Experiment 3.1: Rotating cylinder.

A: sketch of the stimulus. Black and white squares move sinusoidally back and forth across a gray background impression of a glass cylinder covered in dots rotating about its own axis. The cylinder was 5.8° wide \times 9.2° high and completed one rotation every 5s, corresponding to an average dot velocity of $2.6^\circ/s$. **B:** Disparity thresholds for control subjects, i.e. the relative disparity between the front and back surfaces of the cylinder at which performance was at chance. **C:** Disparity thresholds on the rotating cylinder task expressed as a fraction of smallest threshold obtained on a standard discrimination task. See Supporting Information File S3 for full data.

<http://dx.doi.org/10.1371/journal.pone.0012608.g012>

Indeed, DF could easily perform this task, discriminating front and back surfaces on the basis of disparities of just 1.5° . This is better than any of our controls (Figure 12B), although the large confidence intervals mean we cannot be sure the difference is significant. DF's threshold on the rotating cylinder task is also twice as good as her performance on a standard discrimination task in Experiment 1 (Figure 12C), whereas all control subjects were between 3 and 10 times worse on the cylinder task. The rotating cylinder stimulus elicits strong activity in dorsal cortical area MT. Potentially, therefore, relying on dorsal areas for visual processing may mean she has learnt to use this information more efficiently than most observers.

Experiment 3.2: Relative disparity between transparent surfaces.

DF's good performance on Experiment 3.1 might reflect a generally better ability to use absolute disparity in motion than a genuine ability to use the relative disparity between transparent moving surfaces. To address this, we compared absolute disparity thresholds for an isolated random-dot plane when the dots were static (Figure 13A) versus when they moved at a constant velocity of 2.7° either leftwards or rightwards (Figure 13B). DF's threshold was the same whether the dots were static or moving. However, her threshold improved greatly when we added a second, transparent plane of dots with opposite direction of motion (Figure 13C; Figure 14B). The fact that DF was able to benefit from the relative disparity between two transparent planes suggests that it was the relative disparity, not the motion *per se*, which enabled her excellent performance on the rotating cylinder task. That is, DF can instantly and reliably use relative disparity information between moving transparent surfaces, in contrast to the difficulty she experiences in learning to use the relative disparity between spatially separate surfaces.

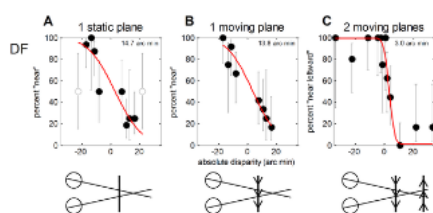


Figure 13. Experiment 3.2: front/back discrimination with static vs moving dots.

The stimulus was a patch of light and dark dots 4.5° wide \times 2.2° high on a gray background. In (A), the dots were in the same depth plane, with absolute disparity indicated on the horizontal axis. The red line shows a cumulative distribution function fitted to the black dots (white dots represent data not used for fitting); the number in the upper right is the fit parameter, the standard deviation of the fitted Gaussian. (B) as (A), except the dots were moving either left or right, with a constant velocity of $2.7^\circ/s$. In (A) and (B), the task was to report whether the plane appeared in front of or behind the screen. (C) there was a second plane of dots with the opposite direction of motion, and opposite disparity. The two planes transparently past one another; the total dot density was thus twice as great in (C) as in (A) and (B). The task was to report the direction of motion of the front plane. For comparison with A and B, the horizontal axis in C, and the vertical axis, shows the absolute disparity of the leftward-moving plane. The relative disparity between the two planes was 1.5° .

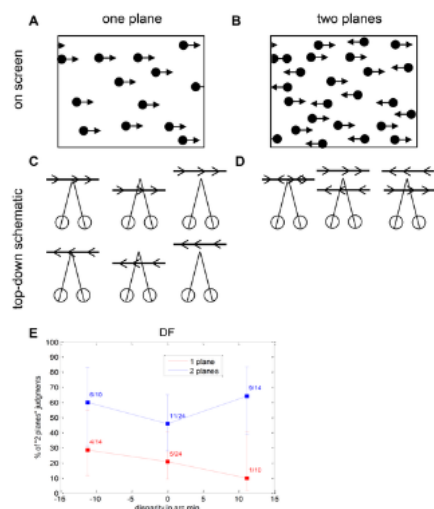


Figure 14. Experiment 3.3: One (A/C) vs two (B/D) planes, defined by moving dots.

Each plane was defined by dots moving with the same speed and direction, either left or right. Each plane had either 0 or ± 11.2 arc min; in the two-plane stimulus with non-zero disparity, the planes had opposite disparity between the two planes was either 0 or 22.4 arc min. A/B shows a schematic of an example stimulus. C/D shows a top-down view of the simulated planes, for each possible stimulus configuration of each type. The number of dots on each plane was constant, i.e. the total number of dots visible was twice as great in the two-plane stimulus. The task was to discriminate the one-plane stimuli (A/C) from the two-plane (B/D); this could be done either by the number of directions of motion present (one vs two), or using the density cue. <http://dx.doi.org/10.1371/journal.pone.0012608.g014>

Experiment 3.3: Perceiving transparent surfaces.

Curiously, despite this good performance, it transpired that DF in fact only ever perceived one direction of motion with two transparent planes of dots moving in opposite directions. When asked to discriminate such stimuli from where all the dots moved with the same velocity (Figure 14), she was able to guess slightly above chance (64% after practice, while she always reported phenomenal percepts of single-direction motion). For any normally sighted observer the difference between one or two planes is obvious: one immediately perceives either one or two directions of motion. DF could still use information about transparent planes defined by motion and/or disparity to improve her depth thresholds – as well as or better than any of the control subjects we examined – despite being unable to perceive consciously.

Anti-correlated random-dot patterns

We tested DF on anti-correlated versions of the target-disk stimulus of Experiment 1.1 (Figure 4Ai), and the rotating cylinder stimulus of Experiment 3.1 (Figure 12A), using disparities with which she had performed near-perfectly for correlated stimuli. Specifically, on Experiment 1.1L with disparity ± 22 arc min, she performed at chance, just like control observers. Specifically, on Experiment 1.1L with disparity ± 22 arc min, she correctly identified the target on 59/60 trials when the stimulus was correlated, and on 20/40 trials when it was anti-correlated. On Experiment 3.1 with a relative disparity of 45 arc min between the front and back surfaces of the cylinder, DF answered correctly on 30/30 trials when the stimulus was correlated, and on 8/16 trials when it was anti-correlated. Thus, neither DF nor controls can perceive the sign of depth in anti-correlated stimuli, despite the fact that activity in many cortical areas contains the necessary information [14], [17].

Discussion

DF performs normally on many stereo tasks

Given the extensive damage to several areas of DF's visual cortex, perhaps the most surprising finding of the study is that she is impaired on stereoscopic vision. Previous investigations have established that DF has functional stereoscopic vision, although she was reported to have poorer stereoacuity than controls. Our results show that DF's poorer stereoacuity in previous studies reflected the task (a standard clinical test of the relative disparity between two surfaces), rather than a general deficit. On discriminating depth in isolated stimuli, or judging the relative depth between transparent planes, DF performed like controls. For example, on Experiment 1.1, 3 out of 5 age-matched controls with normal stereo vision could not identify the depth sign of a briefly-presented isolated target for any disparity, while author JR, an experienced stereo observer younger than DF, could not match her threshold. On the rotating cylinder task, DF outperformed all of the controls. Thus, the particular impairments that we have been able to record certainly do not reflect a general loss of stereoacuity or difficulty in achieving stereoscopic fusion.

DF is impaired in using relative disparity between different visual-field locations

The major impairment is DF's ability to exploit relative disparity between nearby surfaces. Thus, in Experiment performance drops dramatically below that of controls when the comparison surfaces are close together, because to judge the relative disparity between surfaces more accurately than the absolute disparity of either one alone defined slant task, the performance of controls improves when the slant is confined to a central strip (Experiment they benefit from the relative-disparity information available at the strip's boundary. In contrast, DF shows no such Thus, three different stimulus geometries all indicate that DF has difficulties in using relative disparity at surface

The results of Experiment 1 are consistent with previous suggestions that the dorsal stream predominantly handles stereopsis, e.g. absolute disparity signals representing objects' locations in 3D space, whereas the ventral stream handles stereopsis, including relative disparity between adjacent surfaces [2], [47], [48].

The firing of dorsal stream neurons contains information about fine disparities in the visual scene, but whether it contributes to perception depends critically both on the stimulus configuration and on training [44], [45], [47]–[49]. Over the 20 years since her lesion, DF has learnt to make particularly good use of the fine-disparity information and other dorsal areas. Since the rotating cylinder stimulus is especially effective in stimulating V5/MT neurons, the demands use of this information may actually benefit DF.

Possible interpretations

Given that DF's major cortical lesion is to the lateral occipital area LO, we suggest that this brain area may be responsible for the ultra-fine sensitivity that control subjects automatically display on these tasks. DF's spared ability to use the information between transparent surfaces in this way is consistent with imaging and neurophysiological evidence suggesting that stereopsis depends upon dorsal areas such as MT [42], [50], [51], perhaps because such disparity/motion parallax information is particularly important for guiding movements. There is in fact independent evidence that DF can exploit motion parallax, a form of disparity information, when reaching to grasp slanted objects [52], [53].

This then raises the question of how precisely area LO enables controls to exploit relative disparity information at surface boundaries. Human imaging studies suggest that LO is involved in the processing of stereo-defined shape, including boundaries [54]–[57]. However, DF's ability to use relative disparity information after appropriate training suggests that she has simply lost the neuronal tissue which computes relative disparity at surface boundaries, not the ability to exploit the principle. Rather, it may be that her lesion makes it difficult for her to identify the appropriate neuronal signals for a disparity task. For example, DF may have difficulty identifying disparity boundaries between surfaces. Her good performance on transparent stimuli may reflect the fact that these offer the same relative disparity information widely throughout the scene.

One possibility to consider is that DF's underlying deficit is in perceiving, or attending to, both surfaces simultaneously. Her subjective reports certainly indicate that, while aware of performing more accurately in trial blocks when gap sizes were small, she had no explicit perceptual awareness that the reference surround had moved closer. But it has been apparent from her performance that DF's perception and behaviour can be strongly influenced by stimuli that she cannot consciously discriminate [58]. We have internal evidence of this within the present study, in that DF was surprisingly unable to perceive superimposed planes defined by motion and/or disparity – she invariably saw motion in only one direction. Yet she was still able to use relative disparity between two such planes to improve her depth discrimination thresholds – as well as or better than on control trials. This demonstrates that DF's difficulty in using relative disparity information between adjacent surfaces is logical rather than surprising. In any case, there is also clear independent evidence in other contexts that DF can combine visual information from the peripheral visual field with central (target) information to perform a task, for example in order to avoid obstacles during reaching [59].

Conclusions

We have conducted a detailed, quantitative examination of stereo vision in patient DF, who has visual agnosia due to damage to predominantly ventral areas. On many stereo tasks, DF performs as well as controls. However, our results show a specific difficulty, namely in the use of relative disparity between spatially separate locations (Figure 1C). This suggests that ventral stream areas may usually be key in achieving the enhanced stereo vision that characterizes normal perception on these tasks.

Supporting Information

File S1.

Note on fitting psychometric functions.
doi:10.1371/journal.pone.0012608.s001
(0.20 MB PDF)

File S2.

Psychophysics data from Expt 1.1.
doi:10.1371/journal.pone.0012608.s002
(0.45 MB PDF)

File S3.

Psychophysics data from Expts 1.3, 2 and 3.1.

doi:10.1371/journal.pone.0012608.s003
(0.32 MB PDF)

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Author Contributions

Conceived and designed the experiments: JCAR AJP. Performed the experiments: JCAR GPP ISP AJP. Analy: ISP. Wrote the paper: JCAR ADM AJP.

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