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Ventral extra-striate cortical areas are required for optimal orientation averaging

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Abstract

We examined the ability of a previously well-studied patient with visual agnosia to compute the average orientation of elements in visual displays. In a structural MRI study, we show that the lesion is likely to involve a variety of ventral extra-striate areas, including V2, V3 and V4; however, the lesion does not extend dorsally. Subsequently we show that some ability to compute average orientation is spared, though there are limitations on the ability to scale the averaging process as a function of the numbers of elements. The results suggest that some aspects of orientation averaging can be accomplished in spared regions of V1 but flexible averaging requires ventral extra-striate cortex.

Keywords: Orientation; External noise; Internal noise; MRI; Lesion; Texture

1. Introduction

Study of human brain function after brain lesions can reveal much about the function of the intact brain. HJA suffered a stroke in 1981 which led to a large lesion in the ventral visual pathways. After the lesion, he became visually agnosic for objects and for scenes (topographical agnosia), prosopagnosic, alexic and achromatopsic, although he was able to remember and describe visual attributes of objects from long-term memory. His disorder was defined as integrative agnosia (Riddoch & Humphreys, 1987; Riddoch, Humphreys, Gannon, Blott, & Jones, 1999) since his object recognition deficit seems to derive from an inability to organise global forms from local features, especially when there are multiple objects in the scene (Giersch, Humphreys, Boucart, & Kovacs, 2000).

HJA's inability to combine image features is illustrated by his performance with silhouetted images of objects. Typically adding internal details to an image improves identification performance. HJA's performance on tasks involving silhouettes of objects (i.e. without internal details) is similar to (or even better than) his performance with line-drawn elements (Lawson & Humphreys, 1999; Riddoch et al., 1987). This suggests that for HJA, the internal detail is not combined properly with the global percept, but rather it can serve as a segmentation cue, leading to him over-segmenting and misidentify objects. His problems with integrating elements into coherent shapes are also demonstrated by the difficulty that HJA has in identifying overlapping figures. He may group parts that do not belong together whilst segmenting parts of the same objects (Giersch et al., 2000; Riddoch & Humphreys, 1987). Despite such perceptual problems, other visual processing abilities remain relatively preserved. For example, HJA's copying of objects is accurate (Riddoch & Humphreys, 1987), as is his ability to discriminate between squares and rectangles in the Efron shape-matching task (Humphreys, Riddoch, Quinlan, Price, & Donnelly, 1992). He is also able to discriminate simple shapes generated by grouping between collinear contours, to a level matching that found in control participants (Giersch et al., 2000).

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The data have been interpreted as indicating a deficit in intermediate visual processing, after initial coding of edge features (Humphreys & Riddoch, 2006).

1.1. The present study

Details of HJA's lesion were last reported in 1999 (Riddoch et al., 1999) and the aim of this paper is to provide up to date information on the extent of the lesion and to relate the lesion to one particular visual processing ability. To this end we report an up to date, detailed, structural MRI of the lesion. We then report data on psychophysical studies of orientation averaging. If he suffers a deficit in visual integration (Riddoch & Humphreys, 1987), does this extend to this low level task level, or does it only reside at a higher level, in which whole shapes must be organised and represented? The data suggest that HJA's lesion is confined to ventral visual cortex, including area V2 as well as V3 and V4. Despite this, some ability to average orientation information is preserved but without the ability to scale the averaging process to the number of displayed elements. Our results indicate that whilst some aspects of orientation averaging maybe conducted in V1, others require ventral extra-striate cortex.

1.2. HJA brief case history

HJA suffered a posterior cerebral artery stroke peri-operatively in 1981 when aged 61. The present studies took place from 2003 to 2006, when HJA was 83–86. HJA has remained medically stable, and maintained a similar level of cognitive performance, across the time period (see Riddoch et al., 1999). The stroke resulted in lesions in the occipital lobe, extending anteriorly towards the temporal lobe. An MRI scan in 1989 (see Riddoch et al., 1999 for an image from this scan) revealed that he has bilateral lesions of the inferior temporal gyrus, lateral occipital gyrus, the fusiform gyrus and the lingual gyrus. After his stroke, HJA experienced a dense visual agnosia, prosopagnosia, alexia without agraphia, achromatopsia and topographical impairments (Riddoch et al., 1999). He also has large scotoma in the upper visual field. Results of perimetry measurements show losses above the meridian although this does not seem to impair him in everyday life. Of relevance to the present study, HJA has poor visual recognition of objects and has been described as suffering from 'integrative agnosia' (Riddoch et al., 1987), suggesting that his recognition deficit is due to being unable to group local and global information to generate coherent object percepts. Apart from these impairments, HJA seems to suffer from no intellectual impairments and is a well practiced and patient participant in experiments.

2. Structural MRI

Images were acquired on a 3T whole body scanner (Varian Unity Inova, Palo Alto, CA) with a head insert coil (Magnex, Oxford, UK). 1 mm thick axial slices were acquired with resolution 1 mm × 1 mm. These anatomical images were segmented into grey and white matter using custom software (Teo, Sapiro, & Wandell, 1997). Segmented grey matter was then rendered to allow visualisation of the cortical surface.

Fig. 1 shows slices from the high resolution anatomical MRI. The lesion can be seen to cover large regions of the bilateral occipital and ventral cortex. These anatomical images complement those published previously (Riddoch et al., 1999) and confirm the lesion's location. Furthermore, these images are at a higher resolution than earlier studies and confirm the location and extent of the lesion 24 years after the original stroke. These higher resolution scans enable us to more precisely locate the edges of the lesion, for example, at least some of the inferior temporal sulcus has survived. Fig. 2 shows the same anatomical scan but on a rendered surface of the brain. Medial and lateral views are shown from right and left hemispheres. For comparison, the same areas of cortex are shown from a (young) control participant with retinotopic areas overlaid. Ideally we would have functionally defined retinotopic areas for HJA, however a combination of factors (such as his age and frailty, visual acuity, difficulties with fixation for long durations and low overall BOLD signal) have made this impossible so far. For the interested reader, however, we show the results of HJA viewing a rotating wedge stimulus, compared to the same control participant in Supplementary Figure 1. It is apparent from Fig. 2 that HJA lacks the brain tissue that typically contains the ventral visual areas. In the left hemisphere, both the ventral and dorsal sides of the calcarine sulcus appear to be intact, however the areas corresponding to ventral V2, V3 and V4 are missing. In the right hemisphere it appears that part of the calcarine sulcus is missing and also most of the ventral visual areas. The cortical tissue underlying the dorsal visual areas appears to be present in both hemispheres.

The lesion may include the most anterior part of V1 and the ventral portion of V2, consistent with HJA having a visual field deficit in part of upper visual field (as these brain areas tend to represent the upper visual field). The lesion extends across the collateral sulcus into the inferior temporal gyri, and may therefore also include the ventral portions of V3 and V4. HJA's lack of colour vision supports a deficit in V4 and/or V8 which is usually linked to colour perception (Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998), and his poor face and scene perception indicate that the lesion to the occiptotemporal gyrus probably also includes the parahippocampal 'place area' (Epstein & Kanwisher, 1998; Epstein et al., 1998) and the fusiform 'face area' (Kanwisher, McDermott, & Chun, 1997).

3. The mean orientation task

In the mean orientation task, observers indicate the mean, or average, orientation of an array of Gabor patches. Their performance on this task is measured when all the

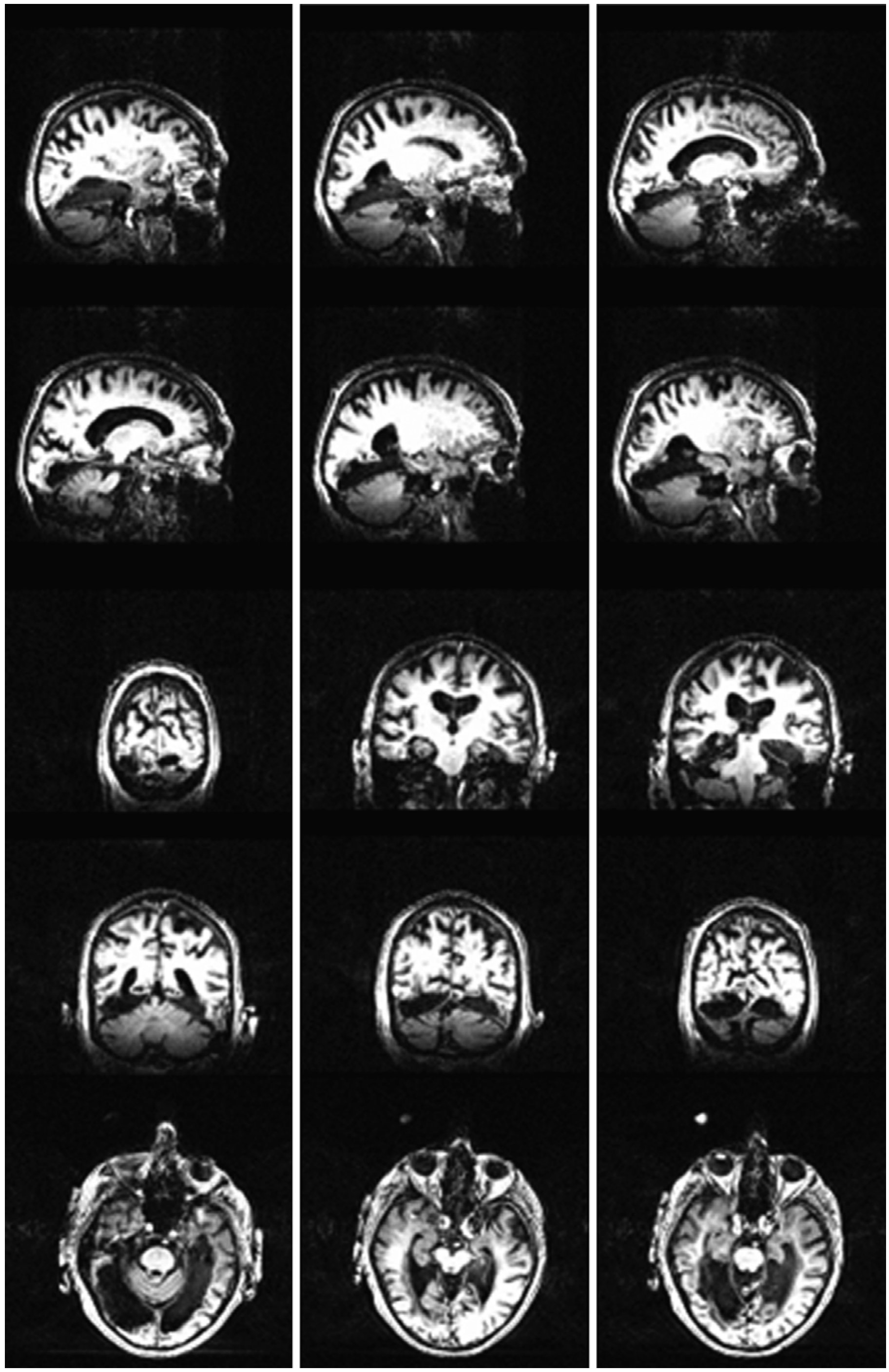

Fig. 1. Slices from high resolution anatomical scan of HJA.

Gabors in the array are collinear and then when the array contains increasing amounts of orientation noise (see Fig. 3 for an illustration). Performance is typically good when the elements are aligned and it deteriorates as the range of orientations in the array increases. The pattern of performance can be used to indicate the level of internal noise and the efficiency with which the visual system can combine (or average) the orientation information. For example if an observer can perfectly average over all the Gabors (and there are sufficient Gabors in the display) they should be equally able to estimate the average orientation of collinear and noisy displays.

In this experiment we use the mean orientation task to investigate how well HJA is able to combine information from across the display. To quantitatively assess his ability to do the task and compare it to previous results, we use an equivalent noise technique (Pelli, 1981; Pelli & Farell, 1999). This technique has previously been successfully used to quantify performance on this task in normal (Allen, Hess, Mansouri, & Dakin, 2003; Dakin, 1999) and clinical

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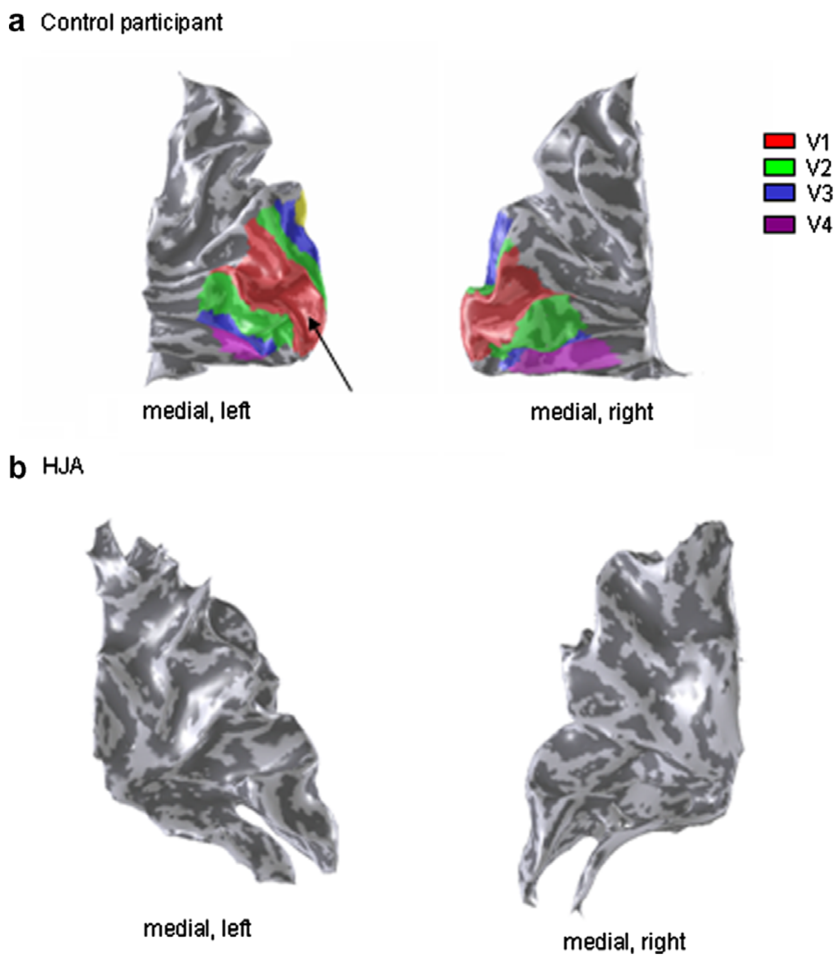

Fig. 2. Flattened cortical maps. (a) Retinotopic areas from an example intact brain (a) and HJA (b) for medial and lateral views of left and right hemispheres. Arrow indicates location of the calcarine sulcus (V1) and colour coding indicates activation consistent with the area named in the key.

(Mansouri, Allen, Hess, Dakin, & Ehrt, 2004) populations, as well as on other visual tasks (Ahumada & Watson, 1985; Barlow, 1956; Barlow, 1957; Lu & Dosher, 1998). The equivalent noise model assumes that when observers perform the task with noiseless stimuli, their performance is limited by their own internal noise. Internal noise, in this case, is used to include all, internal, sources of uncertainty in making the response including encoding errors, perceptual errors, motor errors etc. When noise is added to the stimulus, performance deteriorates when this external noise exceeds the internal noise. In the case of the mean orientation task, the stimulus is considered noiseless when the elements are collinear. External noise is added by increasing the variability of the orientations of the elements. At low levels of external noise, the average orientation can be adequately estimated by considering the orientation of only a few elements and performance is therefore limited by internal, rather than external, noise. At high levels of external noise (high levels of orientation variability) the effect of external noise is now greater than the effect of internal noise. The average orientation can only be accurately estimated by averaging over larger numbers of elements. Participants' ability to average orientation over multiple elements can be measured by how well they are able to judge mean orientation at high levels of orientation variability. For example, if they are able to average over a large number of samples they will be less affected by increasing amounts of external noise. For illustration, Fig. 4 shows examples of the equivalent noise model with different parameter estimates. In Fig. 4a, the estimates number of samples is held constant and the internal noise varies. This affects the asymptotic values at the low external noise values. In Fig. 4b, the internal noise is held constant but the number of samples is varied. This affects the slope (efficiency) at the higher external noise values.

Dakin (2001) systematically investigated participants' performance on the mean orientation task. Using arrays of Gabors, similar to those used here, he varied element density, the radius of the array and the number of Gabors presented, to investigate how these parameters affected performance in normal observers. Internal noise was found to be dependant on the density of elements, probably reflecting increasing internal noise when the display became crowded. The number of orientation samples used in the task was determined by the number of elements presented in the display. This indicates that the mechanism underlying this task

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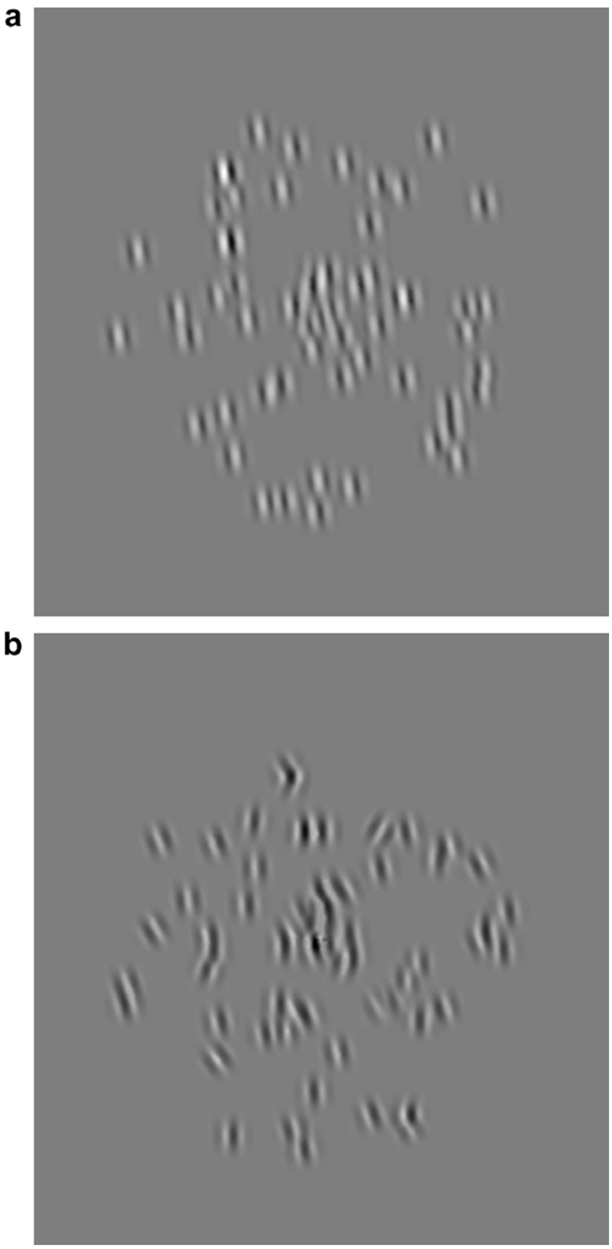

Fig. 3. Illustrations of stimuli in mean orientation experiment. (a) 64 Patches in an array of 12° with no orientation variance. (b) As a, except the distribution of orientations of the Gabors has variance of 12°.

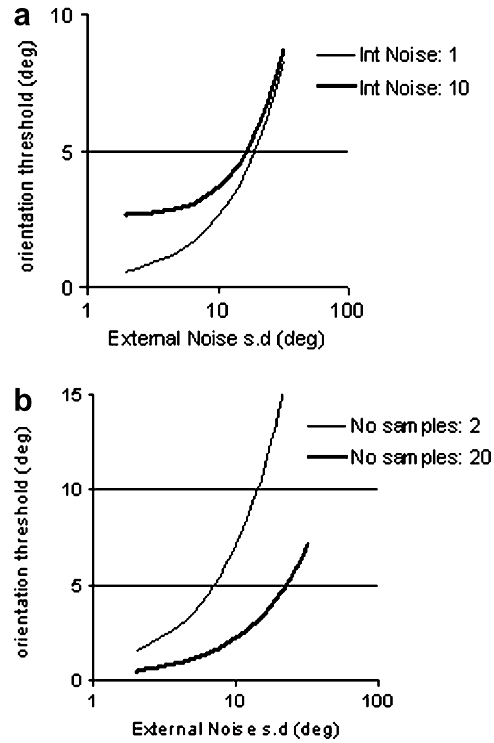

Fig. 4. Example model fits. (a) Effect of changing internal noise parameter when the number of samples is held constant. (b) Effect of changing number of samples when internal noise is held constant.

is not, as might be intuitively predicted, a simple, inflexible low level averaging device.

Mansouri, Hess, Allen, and Dakin (2005) presented the mean orientation array either dichoptically or in depth and with, or without, additional randomly oriented Gabors. Their results indicated that the mean orientation of the display was determined by a mechanism after the site of binocular combination but prior to disparity processing. This suggested that the mechanism might be somewhere in either late V1 or V2. The ability of observers to flexibly adapt the number of elements used to make their estimation (Dakin, 2001) suggests, however that there might be some further, additional processes that are involved in this task.

Since HJA's lesion may include much of V2, it is unclear whether he will be able to estimate mean orientation from an array of local items. HJA is impaired in tests where he is required to group multiple non-aligned local items to segment a target item (Humphreys et al., 1992), though he is able to link Gabor elements into simple shapes (Giersch et al., 2000). Furthermore, if HJA can estimate mean orientation, it is unclear whether he will be able to flexibly change his sampling strategy as non-lesioned observers are able to do, as the number of elements increases. This was tested here.

4. Methods

4.1. Participants

HJA and 2 age-matched control participants took part in this experiment. The control participants were approximately matched for general level of function and age.

4.2. Equipment

Stimuli were presented on a Mitsubishi Diamond Scan 50n monitor driven by an ATO Rage 128y graphics card. The screen had a mean luminance of 26 cd/m^2. The experimental programs were written on an Apple Macintosh G3 computer using the Matlab environment and the Psychophysics Toolbox and Video Toolbox packages (Brainard, 1997; Pelli, 1997). The monitor had a resolution of 1024 by 768 and a frame refresh rate of 85 Hz. One pixel on the screen was 0.27 mm^2. The screen was viewed binocularly at approximately 77 cm from the screen, although no

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restraints were used. The non-linear relationship between the voltage supplied to the display and the output luminance was corrected using a look-up table. Prior to the experiment, luminance values at the screen were measured using a photometer. These were used to create a look-up table to voltages which corrected for the non-linearities of the screen such that an equal voltage increment led to an equal luminance increment at the screen.

4.3. Stimuli

The stimuli were arrays of Gabor micro patterns (see Fig. 3). At a viewing distance of 77 cm, the spatial frequency of the modulation was 2 cycles/° and of the envelope was 4 cycles/°.

In the main experiment, on each trial 64 micro patterns were randomly positioned in a circular array (diameter 3°, 6° or 12°) within the stimulus area. The contrast values of overlapping elements were summed and grey levels falling outside the possible range of the screen were clipped at the maximum or minimum grey level appropriately. In other conditions, 4 or only 1 Gabor element were presented. These Gabors were also positioned randomly within the stimulus area.

The orientation of the modulation in each Gabor was selected from a Gaussian distribution with a mean equal to the cued orientation (i.e. 90°, upright plus or minus the cue generated by the adaptive probit estimation procedure, see below) and a variable bandwidth. The bandwidth standard deviation was varied from 0° (all elements aligned) to 24° (high orientation variability).

4.4. Procedure

The experiments measured the ability of participants to judge whether the mean orientation of the array of Gabors was to the left or right of vertical. Full training was given prior to the start of formal data collection. If only 1 Gabor was presented, participants reported the orientation of the single Gabor.

Participants made a single interval binary forced choice response. An array of Gabors was presented on the screen for 1000 ms. Two participants reported verbally if the mean orientation of the array was to the left or right of vertical. The response was recorded (with a key press) by the experimenter. One control participant indicated his response with a key press. No feedback was given. When participants then indicated that they were ready to proceed, the next trial was initiated. On each trial the experimenter encouraged the participant to make their best possible guess, however on those trials where the participant indicated that they completely missed the presentation, this trial was repeated later in the run.

Performance was measured as the mean orientation of the generating orientation distribution of the Gabor array was varied around vertical. APE, an adaptive method of constant stimuli was used to sample a range of mean orientations appropriate to the participants' performance (Watt & Andrews, 1981; Watt et al., 1981). A session consisted of up to 6 interleaved runs of 64 trials, one for each of the orientation bandwidths used. At least 3 runs were undertaken for each plotted data point. Data were pooled across runs with each stimulus configuration and orientation bandwidth and a bootstrapping procedure was used to fit a cumulative Gaussian function to the data. This procedure yielded estimates of the standard deviation and bias parameters of the fitting function. The term orientation threshold is used to refer to the standard deviation of the best fitting psychometric function. Estimates of the associated 95% confidence intervals were derived using a bootstrapping procedure on the pooled data.

The thresholds from the fitted function were fitted with an equivalent noise model to estimate the internal noise and number of information samples that they used for each task. The relationship between the participants' internal noise, the external noise (orientation variability) and the participant's efficiency (number of orientation samples used to perform the task) can be expressed as:

$$\sigma_{\mathrm{obs}} = \sqrt{(\sigma_{\mathrm{int}}^2 + \sigma_{\mathrm{ext}}^2/n)} \quad (1)$$

where σ_{obs} is the participants observed threshold performance, σ_{int} is the estimated standard deviation of participants internal noise, σ_{ext} is the standard deviation of the external noise (orientation distribution generating the Gabor array) and n is the number of samples estimated to be used by the participant (see Fig. 4 for examples). Separate estimates of both parameters were made for each condition (radius, density, number of Gabors) and 95% confidence intervals were estimated from 1000 bootstrap replication of the model fit.

5. Results

5.1. Presence of additional patches

Performance was compared when HJA judged the orientation of a single Gabor positioned randomly within a circular display area (diameter = 6°) and when there were 64 elements in this display area, see Fig. 5a. There was a small increase in the orientation required to discriminate an orientation difference from vertical but comparison of the 95% confidence intervals reveals that this is not significant. Orientation discrimination thresholds of 2° or 3° are similar to those found with normal observers in previous studies (Andriessen & Bouma, 1976).

5.2. Changing density of aligned items

The effect of increasing the diameter of the array was measured with Gabor arrays that had orientation bandwidth of 0 (i.e. elements were aligned). 64 Gabor pattern elements were presented in three different display areas, resulting in three different texture densities. As can be seen in Fig. 5b, there was little effect of decreasing the density on performance when all the Gabor elements were aligned. This is unsurprising since the task can be performed, in theory, by discriminating the orientation of 1 Gabor element.

5.3. Increasing bandwidth

Fig. 6 shows the mean orientation thresholds as the orientation bandwidth of the array increases. In all cases thresholds increase as the orientations in the array become more noisy, as found with normal observers in previous studies (Allen et al., 2003; Brainard, 1997; Dakin, 2001). The data were fitted by the internal noise model (see Section 4) and the parameters of the model for HJA, the 2 age-matched control participants plus the data from Dakin (2001) are shown in Tables 1 and 2.

Fig. 6a shows the results from when HJA judged the mean orientation of 64 elements in an area with a diameter of approximately 12° (solid diamonds) and 3° (solid triangles) with the data from the same conditions for the age-matched controls. Fig. 6b shows the results from when HJA judged the mean orientation of 4 elements over the larger (solid diamonds) and smaller (solid triangles) display areas plotted with the data from the age-matched controls. Estimated internal noise values for all the combinations of display size and numerosity (Table 1) are within the range

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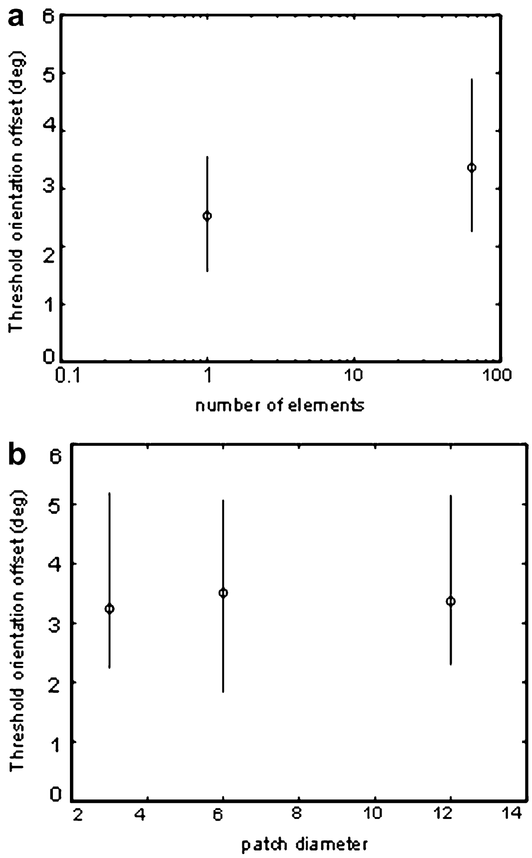

Fig. 5. (a) Orientation discrimination thresholds for HJA when the display contains 1 or 64 elements. (b) Orientation discrimination thresholds when 64 Gabors are presented in arrays with three different display diameters, and thus three different densities. Error bars are 95% confidence intervals.

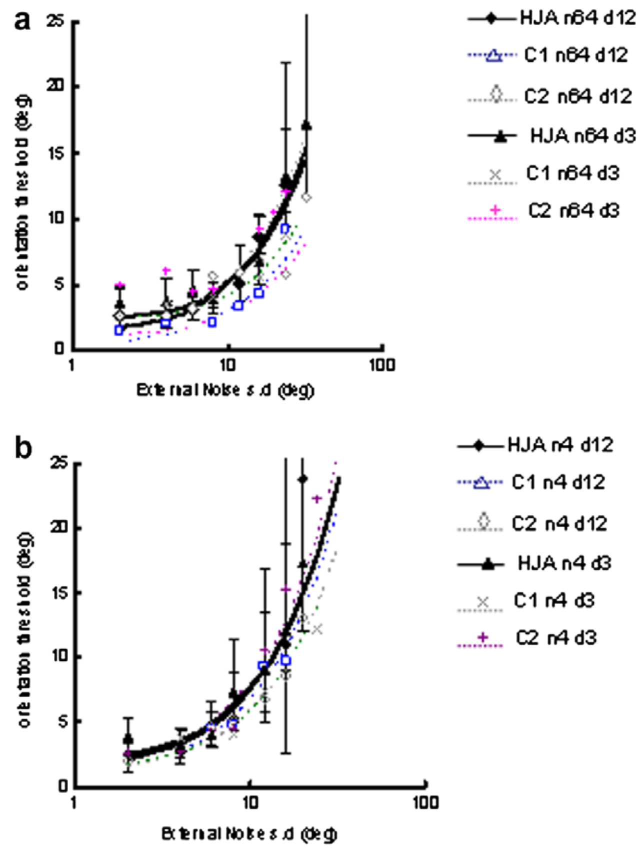

Fig. 6. Orientation required to discriminate the mean orientation of arrays of Gabors for HJA and age-matched controls. (a) Thresholds for when there were 64 Gabors (n64) presented in arrays with diameter 3 (d3) or 12°. (d12) (b) thresholds for when there were 4 Gabors (n4) presented in arrays with diameter of 3° or 12°. Error bars are 95% confidence intervals.

of the values found for the control participants and those found by Dakin (2001).

HJA's data, however, differ from the control participants when it comes to the estimated number of samples used (Table 2). With the lower number of elements, i.e. 4 elements in an area of 12° or 3° (n4d12, n4d3 respectively), we estimate that he uses a similar (but non significantly) lower number of samples to other observers. When a greater number of elements is presented, i.e. 64 elements in an area of 12° or 3° (n64d12, n64d3 respectively) he uses a lower number of samples than other observers and only a slightly larger number than when there were only 4 elements presented. Estimates for the number of samples used for other participants increased by a factor of 3 or 4 when the number of elements increased. For HJA, however, the increase is smaller, only doubling.

5.4. Visual field deficit control experiments

Since, HJA has an upper visual field deficit; it could be argued that his inability to scale the number of averaged elements is due to some of the elements being within the scotoma. We felt that this was unlikely since the number of samples used by non-lesioned participants (up to 12, see Table 2) is always well below the number of items on screen (i.e. 64). However, to rule this possibility out, we conducted two control experiments. In the first control experiment HJA repeated some data points but with a different fixation mark which brought all the Gabors into his intact visual field (as measured by perimetry). In the second control experiment an age-matched control repeated the experiment but with a mask across the top of the Gabor array to simulate HJA's scotoma. All methods were as before, except where stated below.

6. Method and results

For the first control experiment, a sticker was placed on the screen at the top of the presentation area for the array of Gabors. This was always visible and HJA was asked to fixate there before and during each trial. 64 Gabors were presented in the larger display area, exactly as before. The results are shown in Fig. 7a together with the data from HJA when there were 64 Gabors presented in the larger and smaller area for the first experiment. The orientation thresholds from the three levels of external orientation noise with the new fixation point (crosses) clearly lie

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Table 1
Internal noise estimates for HJA, age-matched controls and from previous studies

	n64d12	n64d3	n4d12	n4d3
Dakin (2001) average	3.80	7.07	Not tested	3.33
Age-matched control 1	0.10	2.96	1.02	1.68
Age-matched control 2	7.51	3.88	2.15	1.97
HJA	2.23 (1.4–2.7)	3.11 (2.1–3.6)	2.19 (1.1–2.7)	2.79 (2.0–3.0)

Each column shows a different condition, there were either 64 or 4 elements presented in arrays with diameters of 3° or 12°. Numbers in brackets indicate 95% confidence intervals for figures above.

Table 2
Estimated number of samples, otherwise as Table 1

	n64d12	n64d3	n4d12	n4d3
Dakin (2001) average	10.43	9.93	Not tested	2.80
Age-matched control 1	12.26	9.65	2.20	2.99
Age-matched control 2	9.50	15.90	3.04	1.58
HJA	4.71 (2.7–7.1)	4.41 (2.3–7.0)	1.86 (0.5–2.8)	1.82 (1.8–2.9)

on the same line as the other data. Of course, it is possible that HJA always fixated away from the centre of the array (although he denied this when asked) and this could explain why there is no difference between his results in the first experiment and here. Nevertheless, even when all the Gabors are definitely in the intact visual field, HJA does not appear to be able to improve his estimate of average orientation.

Since we were unable to record from the full range of external noise levels in the first control experiment, we conducted a second control experiment. 64 Gabors were presented in the larger display area but a mask was placed over the top part of the screen to simulate HJA's scotoma. This assumed that HJA took no compensatory measures for his scotoma. Results are shown in Fig. 7b. Data from the first experiment for HJA (diamonds) and Control 1 (triangles) are shown with the data from Control 1 with the mask (crosses). Performance with and without the mask is very similar. The estimated number of samples used when the mask was in place was 11.4, only slightly lower than found without the mask (12.3). Even though many of the Gabors were not visible to the participant, they still used far more orientation samples than HJA.

These results from these control experiments make it unlikely that the poor scaling shown by HJA is due to his visual field deficit.

7. Discussion

HJA's performance with single Gabors and with arrays of aligned Gabors is similar to that found with normal, younger, observers. It is unlikely, therefore, that HJA has a specific deficit for processing orientation or that the presence of the additional patches greatly suppresses the response of individual detector units. HJA does have a deficit, however, when it comes to using the full amount of information available in the display. When there are four patches visible, HJA uses slightly less information than normal observers (Table 2). When there are 64 patches, HJA seems to be even worse. Dakin (2001) found that, for normal young observers, the estimated number of samples remains approximately constant as element density increases but increases as the number of Gabor elements in the display increases. Normal observers, therefore, appear to scale their integration area according to the number of elements in the display (see also Allen et al., 2003; Dakin, 2001; Mansouri et al., 2004). We replicated this result with the two normal elderly participants here (Table 2). For HJA, however, the number of samples used by HJA is only slightly larger with 64 elements than with 4. HJA thus seems less able to scale the area from which information is integrated.

In the other part of this study, using anatomical MRI we have characterised the lesion suffered by HJA in greater detail than has been previously possible. This increased understanding allows us to characterise the underlying nature of his deficit more precisely than before. HJA's lesion begins at the edge of what would be ventral V1 and encompasses much of what is known as the ventral visual stream, including the locations of ventral V2, V3 and V4. The lateral occipital cortex, implicated in object processing and recognition is likely to be at least partially spared.

These results suggest that the mechanism underlying the flexible scaling of orientation sampling is not in V1. HJA does have a scotoma in his upper visual field, which might result from a small lesion of V1. This visual field deficit might be considered an explanation for HJA's poor performance. A proportion of the items might fall within the scotoma, meaning HJA cannot use them to estimate the average orientation, leading to a reduction in the estimated number of samples used. This is unlikely to explain poor scaling for several reasons. First, a large proportion of the patches, far in excess of the number even normal observers use for the task were visible to HJA. Second, our control experiment showed that his performance is the same even when the patches are explicitly moved into

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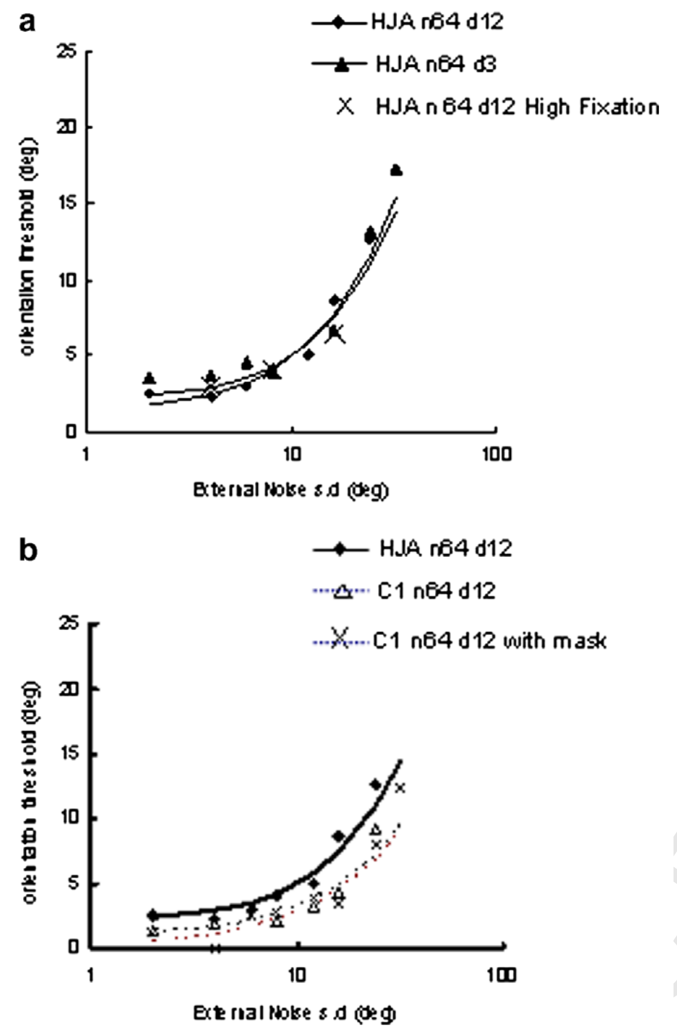

Fig. 7. Results of control experiment. (a) HJA's data from the two original conditions with 64 items in an area of 12° or 3° (diamonds and triangles respectively) plotted with results of the new control condition with 64 patches in 12° but HJA explicitly instructed to fixate at the top of the pattern. (b) Data from HJA and control from when there were 64 Gabors in a 12° area. Diamonds: original data from HJA, triangles original replication from age-matched control 1. Crosses show data from the same participant but with the top of the screen masked.

his intact visual field. Furthermore, simulating the scotoma in a non-lesioned participant did not cause any significant decline in performance. Third, although HJA may have relied more on the lower visual field and possibly moved fixation so that more patches were visible, he was still unable to improve his performance. This is consistent with additional, lesioned, areas being at least partially required for the flexible sampling.

We propose that the flexible scaling of orientation sampling requires both the dorsal and ventral visual processing streams. HJA is less able to scale the number of samples used than non-lesioned observers suggesting that some of the processes underlying this ability might normally lie in the lesioned areas. In HJA the dorsal visual pathway is present, but the ventral visual cortex is almost completely absent. Thus one can propose that HJA is able to use scaling from the dorsal visual pathway but not the ventral, leading to his partial scaling performance. Without the ventral visual stream, as in HJA, the visual system does not seem to be able to behave as flexibly as when both streams are present.

From our experiment, we are unable to determine whether the signal to flexibly scale the number of orientation samples derives from the missing ventral areas, or whether it derives from further 'upstream' and is a feedback signal that would travel through ventral V3, V2 etc. Furthermore, if one of the lesioned areas is responsible for flexible scaling it is unclear whether this would be the higher missing areas (e.g. V4) or the earlier areas (e.g. V2). It may be possible to elucidate this problem by presenting the Gabor arrays to only the superior or inferior hemifields and thus only the ventral or dorsal streams. Previous work using a different approach—interocular presentation has, however, indicated that the basic mechanism underlying orientation averaging is likely to be in V2 or earlier (Mansouri et al., 2005). This work confirms, therefore, that it is V2 that is responsible for this basic mechanism.

7.1. Relation to behavioural deficit

Despite his lesions and poor scaling performance, it is worth pointing out that HJA showed relatively good performance on some aspects of the orientation averaging tasks. For example, he performed at a level similar to control participants when asked to average orientation in aligned arrays of Gabors or with low levels of orientation noise. These data stand in contrast to prior results, where HJA has been shown to be very impaired at dealing with multiple edges (e.g., in parsing overlapping figures; Riddoch & Humphreys, 1987), and at organising edges into holistic objects (Giersch et al., 2000). It appears then that the process of integrating oriented elements, to compute their mean orientation, is distinct from (and prior to) processes involved in organising edges into shapes. We suggest that there are several processes of shape integration, which can serve different computational purposes, and which can dissociate following brain lesions. Our prior work indicates that organising edges into coherent shape representations may be critical for object recognition (impaired in HJA). Computing the mean orientation of a display, in contrast, may sub serve tasks such as texture perception. It is interesting that HJA's object recognition is overly-dependent on texture processes, when compared with normal participants (Chainay & Humphreys, 2001), and this may be reliant on the averaging process we document here. It should also be noted that the failure to scale the number of elements used in averaging, as the display size increased, may reflect a tendency for attention to remain locked at a local level, which is also characteristic of his object recognition (see Riddoch & Humphreys, 1987). It is not the case that HJA is unaware of increases in display size, as might be found in 'simultanagnosia',

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since his basic ability to count elements is preserved (Humphreys et al., 1992).

It is also interesting to examine the relations between HJA's processing of edge orientations and his brain lesion. Structural and functional imaging indicates that V1 and dorsal extra-striate cortex is relatively spared, and this matches previous behavioural results where HJA shows comparatively normal performance on a range of tests of early vision, including the Efron shape matching test, visual search for a single oriented item and copying tests (Humphreys et al., 1992; Riddoch & Humphreys, 1987).

8. Conclusions

The present data indicate that the ability to average orientation information can be partially spared following damage to ventral extra-striate cortex, though there are limits in scaling the process according to the numbers of elements present. Scaling orientation averaging, therefore, requires both ventral and dorsal extra-striate cortex.

9. Uncited references

Boucart and Humphreys (1992), Boutsen and Humphreys (2002).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2006.10.018.

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