Functional size of human visual area V1: A neural correlate of top–down attention

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ABSTRACT

Heavy demands are placed on the brain's attentional capacity when selecting a target item in a cluttered visual scene, or when reading. It is widely accepted that such attentional selection is mediated by top–down signals from higher cortical areas to early visual areas such as the primary visual cortex (V1). Further, it has also been reported that there is considerable variation in the surface area of V1. This variation may impact on either the number or specificity of attentional feedback signals and, thereby, the efficiency of attentional mechanisms. In this study, we investigated whether individual differences between humans performing attention-demanding tasks can be related to the functional area of V1. We found that those with a larger representation in V1 of the central 12° of the visual field as measured using BOLD signals from fMRI were able to perform a serial search task at a faster rate. In line with recent suggestions of the vital role of visuo-spatial attention in reading, the speed of reading showed a strong positive correlation with the speed of visual search, although it showed little correlation with the size of V1. The results support the idea that the functional size of the primary visual cortex is an important determinant of the efficiency of selective spatial attention for simple tasks, and that the attentional processing required for complex tasks like reading are to a large extent determined by other brain areas and inter-areal connections.

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Introduction

Searching for an item — such as a face in a crowd or a book on a cluttered desk – is attention-demanding, with an increase in the overall number of items usually leading to longer search times (Nakayama and Silverman, 1986; Treisman and Gelade, 1980). One common interpretation of this phenomenon is that a top–down spotlight of attention highlights one object location after another and the different attributes of each object such as colour, form, etc. are bound together finally by virtue of a temporal coincidence in the processing of these attributes (Treisman and Gelade, 1980). It has been postulated that the neuronal basis of such selective attention is a feedback from the dorsal parietal regions to the primary visual cortex (V1) that gates the information that enters the ventral temporal regions for object recognition (Bullier, 2001; Vidyasagar, 1999; Vidyasagar and Pammer, 2010). There is considerable evidence both for a top–down role of the posterior parietal cortex in directing attention in early visual areas (Saalmann et al., 2007) and for attentional modulation of area V1 from macaque electrophysiological (McAdams and Reid, 2005; Vidyasagar, 1998) and human neuroimaging (Brefczynski and DeYoe, 1999; Gandhi et al., 1999)

studies. It is thus plausible that a larger V1 may permit more efficient top–down processes such as increased selective attention by allowing more feedback connections and/or allowing connections to more effectively target the relevant processing regions when the spatial representations in V1 are magnified.

The surface area of retinotopically defined V1 shows nearly a 3-fold variation between humans, which is independent of any variations in overall brain size (Andrews et al., 1997; Dougherty et al., 2003). Recent studies have reported that this variation can explain individual differences in the magnitude of some visual illusions (Schwarzkopf and Rees, 2013; Schwarzkopf et al., 2011). This was interpreted by the authors as reflecting the role of lateral connections in V1 in the perception of relative object size. Here, we hypothesise that the extent of activated V1 may also reflect the operation of top–down feedback signals from higher areas on to V1 when performing certain cognitive functions. We investigated two such functions — *attentional efficiency* in a simple visual search task (Wolfe, 1993), and *reading fluency* in a specialised reading test.

Reading is a rather complex cognitive function that requires attention (Facoetti et al., 2006, 2010; Vidyasagar and Pammer, 1999). As it involves a large number of areas and pathways in the brain (Dehaene et al., 2010; Pugh, 2006; Shaywitz and Shaywitz, 2008) there is considerable controversy over whether the basis for reading impairments such

as dyslexia lies in visual or phonological processing (Goswami, 2011; Stein and Walsh, 1997; Vidyasagar and Pammer, 2010). Recently it has also been suggested that phonological impairments may be due to underlying visual attention deficits (Facoetti et al., 2010; Franceschini et al., 2012; Vidyasagar and Pammer, 2010; Vidyasagar, 2012).

Here, we determined whether the functional size of V1 could predict individual attentional efficiency in a simple search task and fluency in a complex reading task.

Materials and methods

Participants

Twenty-one participants (including the authors AV and SK) aged between 20 and 42 years (mean = 27 years, sd = 6.7 years, 7 males) took part in this experiment. Participants in this age range show relatively stable visual search performance (Hommel et al., 2004). All participants had minimum visual acuity of 6/6 (uncorrected or corrected with contact lenses), normal colour vision (Ishihara test) and fulfilled the prescribed MRI-safety criteria. Experiments were approved by the respective institutional Ethics Committees (The University of Melbourne and Monash University) and all participants provided written informed consents.

fMRI set-up

Imaging was done in a Siemens 3 T Skyra MRI scanner with a 32-channel receiver head coil. Functional MRI was performed using a gradient-echo planar imaging sequence with the following parameters: repetition time (TR) = 1500 ms, echo time (TE) = 35 ms, in-plane voxel dimensions = 1.76×1.76 mm with fifteen 3 mm thick coronal oblique slices aligned orthogonal to the calcarine sulcus starting posteriorly from the occipital pole. Parallel reconstruction was performed using the GRAPPA algorithm with speed factor 2. We collected four functional scans and one T2-weighted anatomical scan with identical voxel dimensions and slice locations to the functional MRI scans for co-registration purposes. Two 3D T1-weighted MPRAGE scans (averaged offline to improve SNR) were performed with the following parameters: TR = 1900 ms, TE = 2.43 ms, Inversion time (TI) = 900 ms, voxel dimensions = $1 \times 1 \times 1$ mm.

fMRI procedure

Retinotopic mapping was performed using standardised population receptive field mapping (pRF) techniques and stimuli (Dumoulin and Wandell, 2008). Chequered drifting bar stimuli (2 motion directions for each bar orientation of 0°, 45°, 90° and 135° from the vertical) were generated using mrVista (http://white.stanford.edu) software. An LCD projector (maximum flux = 1500 lumens; resolution = 1024 × 768; 60 Hz) was used to project the stimuli onto a screen at the rear end of the scanner. The stimulus was 155 cm from the participant's eyes and subtended a maximum of 12° (diameter) visual angle.

fMRI data analysis

The structural T1 weighted images were averaged and analysed using Freesurfer (v5.1.0) to re-construct the grey and white matter surfaces according to the standard processing pipeline (Dale et al., 1999). The segmented white matter mask was manually edited to remove any topological inaccuracies in the white matter surface. Subsequent analyses were performed using the mrVista MATLAB toolboxes. Grey matter was grown from the segmented white matter to form a 3–4 mm layer covering the white matter surface. To improve sensitivity, only voxels within this identified grey matter were analysed. The grey matter surface closest to the white matter boundary was rendered in 3D to form an inflated representation of the brain. The functional time

series was then analysed. An offline motion correction algorithm was applied between scans in each session as well as within individual scans. The pre-processed scans were averaged across imaging sessions to improve signal-to-noise ratio and the pRF modelling procedure (Dumoulin and Wandell, 2008) was performed. Only those voxels for which the model estimate explained at least 10% of the variance in that voxel's time series were mapped. The resulting pRFs were projected onto the inflated brain surface to allow for optimal definition of V1 boundaries. The V1 boundaries were identified manually by tracing the phase reversals between regions V1 and V2. These boundaries were also viewed on flattened representations to ensure accuracy. The surface area was then calculated using automated algorithms provided in mrVista.

Behavioural visual search task

Classic visual search paradigms (Li et al., 2007) were employed to measure attentional slope, a measure of attentional efficiency. Participants were presented with a conjunction search display (Eizo Flexscan F980 monitor, viewing distance = 135 cm, angular subtense = 12°) that had a variable number (set-size) of white (x = 0.3, y = 0.3, luminance = 25 cd/m²) distracter items — large vertical bars (0.98° × 0.24°) and small horizontal bars (0.12° × 0.50°) against a grey background (x = 0.3, y = 0.3, luminance = 18 cd/m²). In each trial, a target – a small vertical white bar – was either present or absent (see Fig. 1A). The observers' task was to make a rapid judgement as to whether the target was present or absent by pressing an appropriate button. The time taken for this decision (i.e., reaction time for correct trials) was then graphed as a function of set-size (Fig. 1C). The slope of this function (the search slope) determined the search rate (ms/item). Participants also performed a feature search task, where there was only one type of distracter – small horizontal bars (0.12° × 0.50°) – and the goal was to again find the small vertical target (Fig. 1B).

On each trial, 16, 80 or 144 items were presented at randomly determined, but non-overlapping, locations on the screen. There were 96 trials for each of the three set sizes tested, with a 2 s inter-trial interval. The target was present in half the trials. The order of presentation for each set size was randomly interleaved. Only the data for correct responses was analysed. All participants performed at least at 75% accuracy. Consistent with previous literature (Wolfe, 1993), conjunction
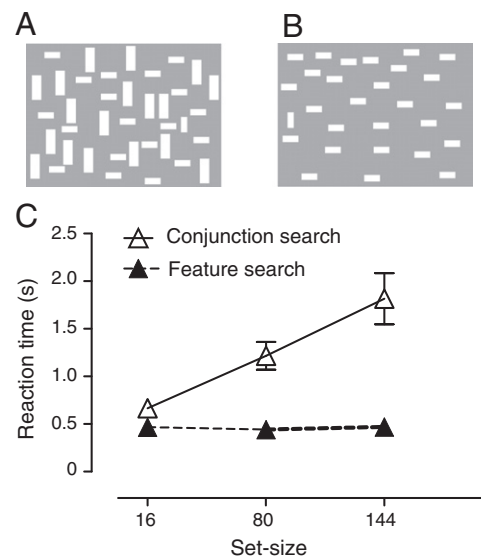

Fig. 1. Visual search task design. A) Conjunction search display. B) Feature search display. C) Search slopes in conjunction and feature search tasks for one of the participants. The target was a small vertical bar. The difference between these slopes is referred to as the *attentional slope*, and was the behavioural metric used for quantifying magnitude of attention or attentional efficiency in our participants.

searches in target-present trials that required top–down attention had a nearly linearly increasing search rate (~5 to 20 ms/item), while feature search tasks, where no top–down attention was required, had flat search rates (~0 ms/item). The difference in search efficiencies between the two tasks was referred to as the attentional efficiency (attentional slope) for each participant.

Reading fluency

All participants underwent the reading component of the Wechsler Individual Achievement Test Second Edition (WIAT-II-Australian; Pearson PsychCorp, 2007), which is used to assess the academic achievement of children, adolescents, college students and adults, aged 4 through 85. This reading test called for testing of the following components — Word Reading, Reading Comprehension and Pseudo-Word Decoding tests. As a sub-measure of reading comprehension, reading speeds (average time, in seconds, required to read five standardised comprehension passages at their self-determined pace) were also recorded. As reported in the test manual, the WIAT-II test has internal reliability coefficients ranging from 0.80 to 0.98 for the sub-tests. It also has an inter-scorer agreement of 0.94–0.98 across all ages. The test was administered by the same scorer for all participants.

Results

Area V1 was mapped in 21 participants using a visual stimulation and mapping technique of the central 6° (radius) around fixation. Three independent *raters* (one completely naive to the aims of the study) delineated the boundaries between V1 and V2. Bland–Altman analysis (Bland and Altman, 1986) verified the reproducibility of these manual delineations. Paired *t*-tests showed no significant differences between the surface areas of left and right V1 (mean difference = 80.8 mm², 95% CI = −108.7 to 270.3 mm², $p = 0.4$). Additionally, no significant correlations were obtained between the size of retinotopically mapped V1s and anatomically defined V1s (area around calcarine sulcus) (left − R = −0.3, $p = 0.15$; right − R = −0.02, $p = 0.9$) or the overall brain white matter, both calculated using Freesurfer (v 5.1.0) software (left − R = 0.09, $p = 0.7$; right − R = 0.06, $p = 0.8$). However, there was a considerable degree of variation in the functional size of V1. This variation was not gender based as revealed by an ANCOVA showing that when controlling for age, gender did not have an effect on V1 size (F(1,18) = 0.186, $p = 0.67$). Fig. 2A shows the visual field maps from one participant and Fig. 2B shows maps from three subjects demonstrating small, average and large V1s that are representative of the V1 extent for the cohort of subjects.

Individual attentional efficiency was quantified from the target-present trials using the visual search paradigm (Fig. 1 and Materials and methods). In order to quantify reading fluency, we used two measures, namely overall reading score and reading time for each participant (excluding the author administering the test). These two reading measures did not correlate with each other (Pearson's R = −0.31, 95% CI = −0.7 to 0.1, $p = 0.17$) and hence their relationship with attention was examined independently. A positive linear correlation was seen (Fig. 3A) between attention and reading time (R = 0.67, CI = 0.3 to 0.9, $p = 0.0013$) suggesting that people with better visual search efficiencies (shallower attentional slopes) were faster readers (shorter reading times). Reading scores, on the other hand, did not correlate with attentional efficiency (Pearson's R = 0.1, 95% CI = −0.4 to 0.5, $p = 0.67$). For completeness, we also calculated search efficiencies in the target-absent trials (difference between conjunction search slope and feature search slope). As in previous studies (Wolfe, 1998) there was a strong positive correlation between target-present and target-absent search efficiencies (Pearson's R = 0.55, 95% CI = 0.1 to 0.8, $p = 0.0094$). This measure of search efficiency also correlated with reading speed (R = 0.52, 95% CI = 0.1 to 0.8 $p = 0.02$) but again not with reading score (R = −0.21, 95% CI = −0.6 to 0.2 $p = 0.35$).
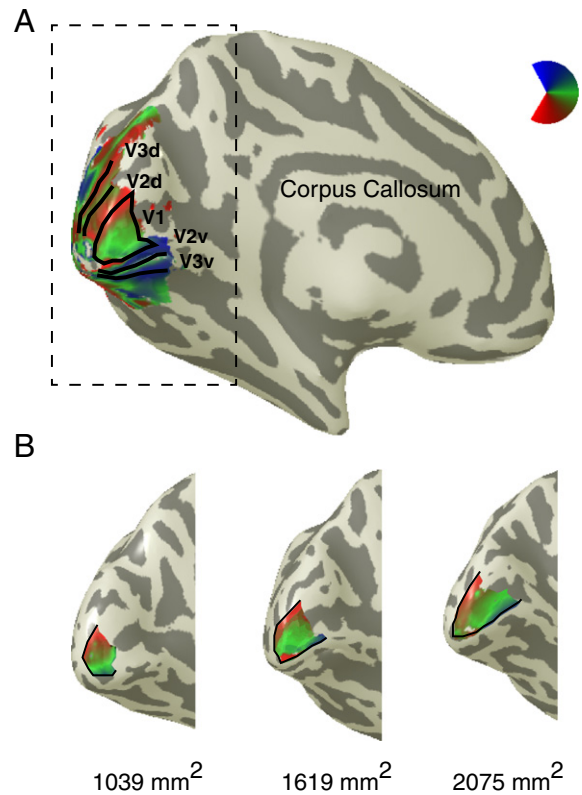

Fig. 2. Visual field map of V1 and individual variations in the size of V1. Panel A shows the polar angle reversals and visual area outlines (V1, V2 and V3) of a single participant's left hemisphere on an inflated representation of their cortical surface. Light and dark shading indicate gyri and sulci, and the corpus callosum is labelled to clarify the orientation of the inflated surface. The colour on the inflated brain indicates the angle (with respect to central fixation, as shown in the visual field inset) that most effectively stimulated each location. It can be seen that the left V1 forms a distinct representation of the right visual field along the horizontal meridian (green). Its dorsal boundary is formed by the reversal into lower vertical meridian (red), while its ventral boundary is at the upper vertical meridian (blue) transition. Panel B shows an expanded view of the surface around the occipital pole (dotted lines) overlaid with the region of V1 that was active in response to a 12° (diameter) stimulus, in the left hemispheres of three different participants. (From left to right — examples of participants with small, average and large functional V1s with their respective surface areas denoted below).

We then examined the relationship between the functional surface area of V1 and these behavioural measures. A significant negative correlation was found (Fig. 3B) between attentional slope in target-present trials and V1 size confirming our hypothesis that a larger functional V1 does indeed relate to increased attentional efficiency (Pearson's R = −0.57, CI: −0.80 to −0.18, $p = 0.0075$, Bonferroni correction for multiple comparisons: α = 0.017). Interestingly, the target-absent search slopes did not correlate with V1 size (R = −0.33, CI: -0.7 to 0.1, $p = 0.14$). The measures of reading fluency, both reading scores (R = 0.04, CI: -0.4 to 0.5, $p = 0.9$) and reading speed (R = −0.09, CI: -0.5 to 0.4, $p = 0.7$) (Fig. 3C) showed no correlation with V1 size. Furthermore, we found that the correlation between attentional efficiency and the surface area of the retinotopic cortex was specific to V1 and did not extend to V2 (Fig. 4A; R = −0.11, CI: -0.3 to 0.5, $p = 0.6$) or V3 (Fig. 4B; R = −0.4, CI: −0.7 to 0.03, $p = 0.07$). Since the confidence intervals for these correlations overlapped, we also performed an analysis to directly test for significant differences between the correlation values. V2 had significantly lower correlations than V1 but this was not the case for V3 (V1 versus V2; Williams' test for comparing two correlations with a common variable t(18) = −2.7, $p = 0.01$, V1 versus V3; t(18) = −7.8, $p = 0.4$). A multiple regression analysis was run to predict attentional efficiency using V1 size, V3 size and reading as predictors. Overall the model was a good predictor of attention F(3,16) = 11.5, $p < 0.0005$, $R^2 = 0.683$, adjusted $R^2 = 0.623$. However, only V1 size (not V3) and
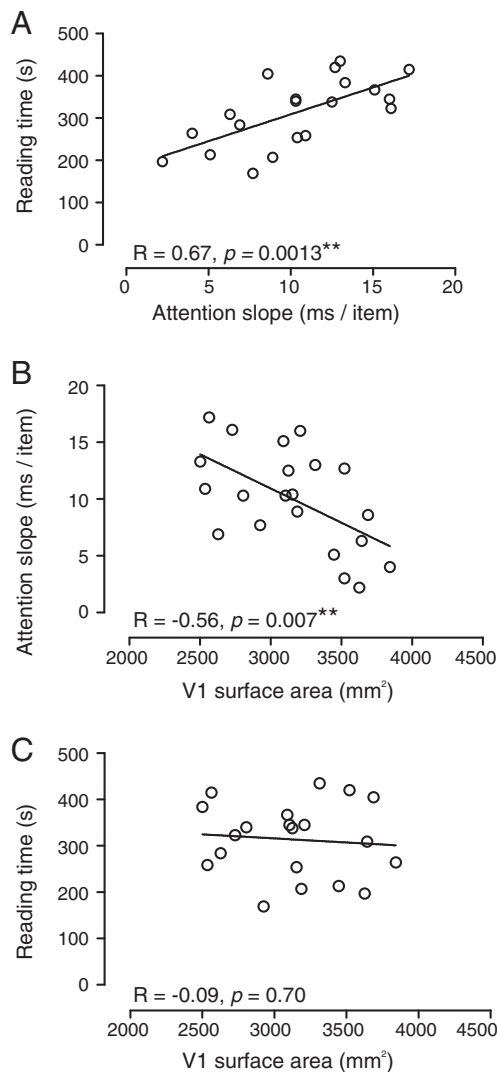
Fig. 3. Relationships between reading speed, attention and functional size of V1. Correlations between (A) attention slope and reading time (N = 20); (B) size of V1 and attention slope (N = 21); and (C) size of V1 and reading time (N = 20). Shorter reading times indicate faster reading speeds and shallower attentional slopes indicate better attentional efficiency.

reading speed added significantly to the prediction of attention (V1 size: $\beta = -0.5$, $p = 0.003$, V3 size: $\beta = 0.085$, $p = 0.56$, reading speed: $\beta = 0.61$, $p = 0.001$).

With regards to attention and V1, not only did participants with better attentional search abilities (shallower attentional slopes) have

an overall larger functional area of V1 (Fig. 3B), but a significant hemispheric asymmetry was also noted (Fig. 5). The surface area of only the left V1 showed a significant correlation with attention (left: Pearson's R = − 0. 60, CI: − 0.8 to − 0.2, $p = 0.004$ and right: R = − 0.14, CI: − 0.5 to 0.3, $p = 0.54$). However the correlations themselves were not significantly different (left V1 versus right V1: Williams' test $t(18) = -1.7$, $p = 0.11$). A similar hemispheric bias was not seen for reading speed (left: Pearson's R = − 0.09, CI: − 0.5 to − 0.36, $p = 0.70$ and right: R = − 0.12 CI: − 0.5 to 0.3, $p = 0.61$).

We further tested whether the correlations between V1 and attention also existed within separate eccentricity bands of 1° width. We used the number of voxels as an indicator of the volume of V1 at each eccentricity and only considered voxels whose pRF centres were within 6 degree eccentricity (the region actually encoding the stimulus) to control for cortical magnification factor. We found that while the overall correlation of activity within 1° to 6° eccentricity bands was significant (Pearson's R = − 0.4, 95% CI = − 0.7 to − 0.01, p = 0.04), when individual eccentricity bands were considered, only the outer bands showed significant correlation (see Table 1).

Discussion

We report a significant relationship between the functional size of V1 and the efficiency of top–down attention, indicating that V1 could indeed play a crucial role in attentional modulation. This is consistent with integrative models of visual processing that propose that feedback from dorsal areas to the primary visual cortex gate signals that enter the ventral stream destined for inferotemporal cortical areas that are involved in object recognition (Bullier, 2001; Bullier et al., 2001; Vidyasagar, 1999). This feedback is conceived (Vidyasagar, 1999; Vidyasagar and Pammer, 2010) as a spotlight of attention that, during visual search tasks, uses the location information from a parietal cortical priority map (Bisley and Goldberg, 2010; Itti and Koch, 2001; Serences and Yantis, 2006; Verghese et al., 2013) to sequentially guide the sites of facilitation on the striate cortical representation. Such a gating process would be particularly important in highly cluttered scenes and would potentially benefit from a larger surface area of V1. Top–down feedback from the posterior parietal cortex to lower visual areas such as V5/MT has been electrophysiologically identified (Saalmann et al., 2007). Furthermore, many studies have shown attentional modulation of V1 neuronal responses with both facilitation of the locus of interest and suppression of the surrounding visual field (Gandhi et al., 1999; McAdams and Reid, 2005; Vidyasagar, 1998). When processing highly cluttered scenes, top–down feedback carrying a spatial attention signal must target the fine-grained representation of the visual field in V1 (Vidyasagar, 1999) rather than subsequent ventral stream areas where the receptive field sizes become progressively larger (Boussaoud et al., 1991; Kastner et al., 2001). A larger stimulus representation in V1 may then be associated with increased inter-areal connectivity between V1 and the higher processing areas. This may explain why those subjects
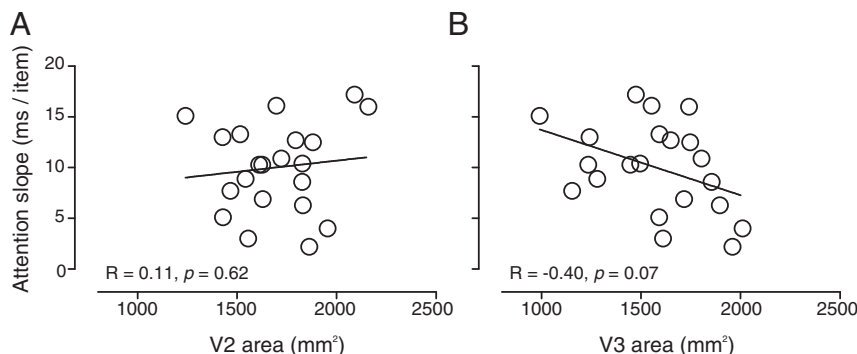

Fig. 4. Correlations of V2 and V3 with attention. (A) No significant correlations were found between V2 surface area and attention or (B) V3 and attention.
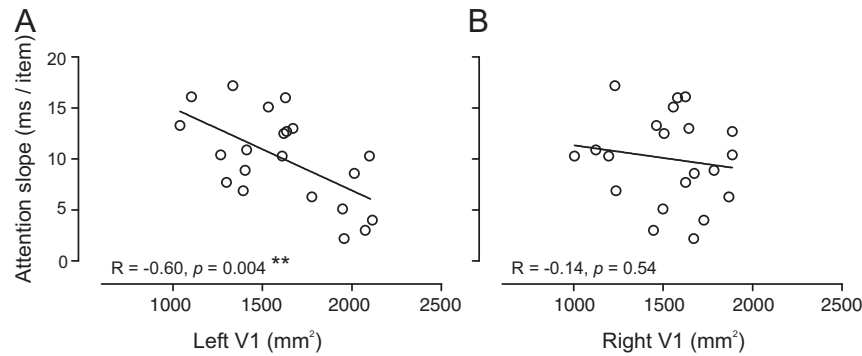
Fig. 5. Hemispheric asymmetry for V1 and efficiency of attention. (A) Significant negative correlation (indicated by **) was observed between functional size of left V1 and the attentional slope. (B) No correlation was found between size of right V1 and the attentional slope.

with larger V1 were faster with serial visual search, especially when searching for the target within larger sets. Interestingly, visual search efficiency in target-absent trials did not correlate with V1 size. This may have been because participants had been encouraged to perform as accurately as possible. Hence, target-absent trials would have been terminated with great reluctance after scanning each item. While a large V1 could potentially scale the spotlight or allow faster cycles of the attentional spotlight, the termination criteria would still vary depending on how conservative the participants were and their search strategy such as pattern of eye movements. We believe that target-present trials better represent the attentional effect.

It remains unclear whether differences in the size of functional V1 relate to cortical patterning during maturation or are a product of experience-dependent plasticity. Sigman et al. (2005) studied changes in BOLD activation in subjects who had been trained on a conjunction search task similar to ours. They noted a significant increase in V1 BOLD signal in the retinotopic areas V1 and V2 following training. However, given that we observed a nearly three-fold range in the functional size of V1, we consider it unlikely that such differences relate solely to experience. Regardless, these results are consistent with our hypothesis that functional enlargement of V1 underpins greater efficiency of top–down attentional signals that modulate activity in V1.

While V1 is certainly important in predicting attention, one cannot discount the role of the various fronto-parietal networks that underlie attention. For instance, a previous diffusion tensor imaging (DTI) study showed that the white matter integrity of superior and inferior longitudinal fasciculus, which corresponds with the dorsal and ventral fronto-parietal attention networks also predict performance in conjunction searches (Bennett et al., 2012).

Reading is one of the uniquely human functions that not only involves many areas and interconnecting pathways across the brain, but also crucially depends on sequential visuo-spatial attentional processing of letter strings in the text (Facoetti et al., 2006; Valdois et al., 2004; Vidyasagar, 1999; Vidyasagar and Pammer, 1999, 2010).

The present study confirmed that those with faster reaction times in the serial search task were also faster readers. On the other hand, reading scores as a measure of general reading ability did not relate to the efficiency of selective attention, possibly due to a ceiling effect for the cohort of adult university readers who participated in our study. Furthermore, there was no significant relationship between reading scores (including reading speeds) and the functional size of V1. This suggests that while visuo-spatial attention itself is an important determinant of reading speeds, there are factors other than V1 size, such as the strength of both feedforward and feedback connections between V1 and the extra-striate areas and beyond that may play a more decisive role in the relationship between selective attention and reading. A recent whole-brain analysis of connectivity has in fact identified a host of pathways between various cortical areas that show disruption in the reading impaired that are not apparent in activation-based analysis of individual brain regions (Finn et al., 2013).

We note that the relationship between the functional size of V1 for central vision and efficiency of attention was present only for the left hemisphere, albeit the correlation was not significantly different from that of the right hemisphere. It has however been shown that, conjunction searches that require processing on a fine spatial scale show a left hemisphere bias (Fecteau et al., 2000; Poynter and Roberts, 2012). These studies demonstrated that when the target in a visual search task was presented in the right visual field (hence projected to the left hemisphere), conjunction searches were faster than when the target was presented in the left visual field. The ability to perform local processing effectively in visual search tasks at a fine spatial scale, especially when they involve more complex objects as in conjunction search, may hence depend critically on left V1. The study by Schwarzkopf et al. (2011) also noted a similar hemispherical asymmetry with regard to a size contrast illusion but they were unable to replicate this in their later study (Schwarzkopf et al., 2013). The idea of specialisation within V1 is however rapidly gaining popularity, with other studies identifying different sub-populations of V1 neurons that show maximal activation depending on the type of attention-demanding task being performed (orientation or contrast discrimination) (Scolari et al., 2012; Verghese et al., 2012). In fact, a recent study by Schwarzkopf and colleagues (Song et al., 2013) reported an association between the size of V1 and an individual's sensitivity to fine discrimination versus contextual modulation of orientation features. The authors suggest that this shift from globally- to locally-oriented perception with increasing cortical surface area may be due to not just a scaling of stimulus size but also scaling of intra-cortical connections specific to the feature. This feature-specific model could also potentially account for our findings of faster detail oriented conjunction searches being associated with large V1s. While the hemispherical asymmetry we observed may be a genetic trait, it is also possible that it is a consequence of a lifetime of tasks that involve the use of the right side of the visual field for most near tasks in a world where most people are right-handed.

Table 1
Relationship between number of voxels in each eccentricity band in V1 and performance in conjunction search: For target-present trials better attentional efficiency (shallower slopes) was associated with increased number of voxels in the left V1 (as seen from the negative correlation indices). This reached significance only for the outer eccentricity band indicated by the * (Bonferroni's correction, $\alpha = 0.01$).

Eccentricity bands	Left		Right	
	Pearson's R	p value	Pearson's R	p value
1 to 2	−0.4204	0.0578	−0.1604	0.4874
2 to 3	−0.2435	0.2876	−0.1767	0.4436
3 to 4	−0.1769	0.443	−0.129	0.5774
4 to 5	−0.3362	0.1362	0.06477	0.7803
5 to 6	−0.5787	0.006*	−0.06346	0.7846

Conclusions

In summary, we find that the size of the central 12 degree visual field representation in V1, relates to the efficiency of top–down attentional processes in a simple visual search task. Furthermore, attentional efficiency itself correlates positively with reading speed. The lack of a direct correlation between the functional size of V1 and reading ability suggests that complex cognitive functions such as reading may involve other neural substrates, including changes in white matter connectivity (Yeatman et al., 2013). This sets the stage for future investigations into the neural correlates underlying the relationship between visuo-spatial attention and reading.

Acknowledgments

Conflict of interest

The authors declare no competing financial interests.

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