NeuroImage 93 (2014) 47–52

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

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

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ARTICLE INFO

Article history:
Accepted 19 February 2014
Available online 28 February 2014

Keywords:
Visual attention
Primary visual cortex
fMRI
Reading
Visual search

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.

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

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http://dx.doi.org/10.1016/j.neuroimage.2014.02.023
1053-8119/

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 × 1 × 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/m^2) 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/m^2). 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

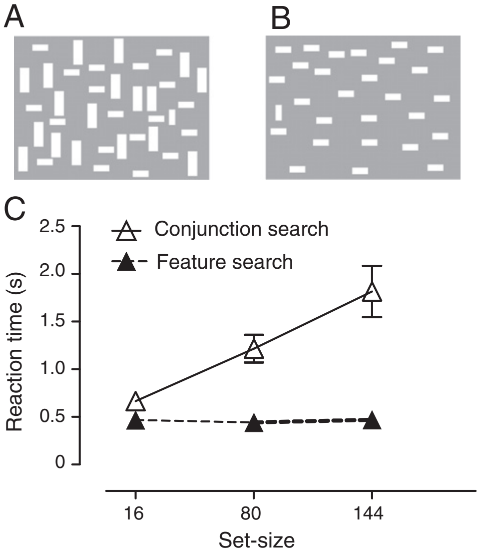

Fig. 1. Visual search task design. A) Conjunction search display. B) Feature search display. C) Search slopes in conjunction and feature search tasks for one of the participants. The target was a small vertical bar. The difference between these slopes is referred to as the *attentional slope*, and was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