NeuroImage 147 (2017) 339–345

Contents lists available at ScienceDirect

NeuroImage

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

Spatiotopic updating across saccades revealed by spatially-specific fMRI adaptation

Scott L. Fairhall[a,*], Jens Schwarzbach[b], Angelika Lingnau[c], Martijn Gerbrand Van Koningsbruggen[d], David Melcher[a]

[a] Center for Mind/Brain Sciences, University of Trento, Trento 38068, Italy
[b] Department of Psychiatry and Psychotherapy, University of Regensburg, Regensburg, Germany
[c] Royal Holloway University of London, Department of Psychology, Surrey, UK
[d] Center for Neuroscience and Cognitive Systems@UniTn, Italian Institute of Technology, Trento 38068, Italy

ABSTRACT

Brain representations of visual space are predominantly eye-centred (retinotopic) yet our experience of the world is largely world-centred (spatiotopic). A long-standing question is how the brain creates continuity between these reference frames across successive eye movements (saccades). Here we use functional magnetic resonance imaging (fMRI) to address whether spatially specific repetition suppression (RS) is evident during trans-saccadic perception. We presented two successive Gabor patches (S1 and S2) in either the upper or lower visual field, left or right of fixation. Spatial congruency was manipulated by having S1 and S2 occur in the same or different upper/lower visual field. On half the trials, a saccade was cued between S1 and S2, placing spatiotopic and retinotopic reference frames in opposition. Equivalent RS was observed in the posterior parietal cortex and frontal eye fields when S1-S2 were spatiotopically congruent, irrespective of whether retinotopic and spatiotopic coordinates were in accord or were placed in opposition by a saccade. Additionally the post-saccadic response to S2 demonstrated spatially-specific RS in retinotopic visual regions, with stronger RS in extrastriate than striate cortex. Collectively, these results are consistent with a robust trans-saccadic spatial updating mechanism for object position that directly influences even the earliest levels of visual processing.

1. Introduction

We perceive the visual world to be stable despite the fact we make frequent saccades that completely alter visual input. Compounding this issue, topographic visual representations in the brain are in eye-centered (retinotopic) rather than world-centered (allocentric/spatiotopic) coordinates. The issue of how the brain creates continuity between retinotopic and spatiotopic references frames over successive eye movements is a long-standing question (for review, see Melcher, 2011).

A critical aspect of visual stability is the spatial updating of salient objects across saccadic eye movements. This process would allow the brain to keep track of the most important items in the scene, either by continuously updating retinotopic maps based on a copy of the eye-movement command ("remapping": Duhamel et al., 1992; for review, see Wurtz et al., 2011) or by explicitly representing spatiotopic coordinates (for review, see Burr and Morrone, 2011). If this spatial updating process includes information about the object, then it could allow the visual system to integrate information about that object over time, rather than starting afresh with each new fixation (Melcher and Morrone, 2003; Melcher and Colby, 2008). A number of studies have reported behavioral correlates of such trans-saccadic updating processes (Prime et al., 2006; Van Eccelpoel et al., 2008; Wittenberg et al., 2008; Demeyer et al., 2009; Ong et al., 2009; Fracasso et al., 2010; Fabius et al., 2016), although the neural mechanisms that underlie these processes remain a matter of debate.

At present, there are two main lines of neuroimaging evidence for spatial updating in humans. The first set of studies have presented a single stimulus for a time period prior to a horizontal saccadic eye movement that would bring that stimulus into the opposite hemifield (Merriam et al., 2003; Medendorp et al., 2005). They compared trials in which a pre-saccadic stimulus was present to those in which a saccade was made with a blank screen. The logic behind these studies is that a greater response in the hemisphere where the stimulus would have been after the saccade reflects an active remapping of the stimulus representation. One limit to these studies is that they investigate only

* Correspondence to: Center for Mind/Brain Sciences, University of Trento, Trento, Corso Bettini 31, I-38068 Rovereto, Italy.
E-mail address: Scott.fairhall@unitn.it (S.L. Fairhall).

http://dx.doi.org/10.1016/j.neuroimage.2016.11.071
Received 17 July 2016; Accepted 28 November 2016
Available online 29 November 2016
1053-8119/

the pre-saccadic stimulus and not whether the updating of this stimulus influences processing of the stimulus after the saccade. A second set of studies has measured processing of a post-saccadic stimulus based on the presence of a pre-saccadic stimulus. In particular, these studies have focused on object processing in inferior temporal cortex (McKyton and Zohary, 2007), motion processing in MT/MST (d'Avossa et al., 2007) and, most recently, on memory for an oriented grating (Dunkley et al., 2016). However, given that there was only a single stimulus on the screen that was presented in the same spatial location before and after the saccade, it leaves open the possibility that the changes in fMRI signal reported in such studies reflect a more general and high-level effect of repetition rather than a spatially-specific adaptation.

The question of whether saccadic updating in the brain is spatially specific, or not, remains a key issue for theories of visual stability (Bays and Husain, 2007). We investigated this question using a variant of previous studies that have measured repetition suppression (RS, or 'fMRI-adaptation': Grill-Spector et al., 2006) across saccades (McKyton and Zohary, 2007; Golomb et al., 2011). In general, a repeated stimulus should evoke a weaker fMRI response than a novel stimulus (Grill-Spector et al., 1999). Here, we introduced a manipulation in which the post-saccadic stimulus was either in the same or different location (upper/lower hemifield) from the pre-saccadic stimulus. This allowed us to distinguish retinotopic from spatiotopic representations while discounting more general effects of simply repeating the same stimulus. This was accomplished by comparing RS for trials in which the two stimuli were shown in the same versus different locations. Based on previous neurophysiological evidence and the theory of object-based remapping (Melcher and Colby, 2008), we hypothesized that spatial congruency effects would be present in frontal and parietal areas implicated in spatial maps and saccades, as well as in early visual areas involved in processing the stimulus.

2. Methods

2.1. Participants

Nine individuals participated in this study (4 female, mean age: 31.6). All participants were highly trained in running eye movement studies. Participants gave informed consent and all procedures were approved by the University of Trento Human Research Ethics Committee.

2.2. Stimuli and procedure

Stimuli were presented via a coil-mounted mirror and a rear-projected screen using ASF (A Simple Framework; Schwarzbach, 2011) based on the Psychophysics Toolbox (Pelli, 1997). Two fixation crosses were presented in the left and right visual field, separated by 7° of visual angle. Probe stimuli, 2° flickering Gabor patches, were presented 2° above or below the horizontal meridian (see Fig. 1).

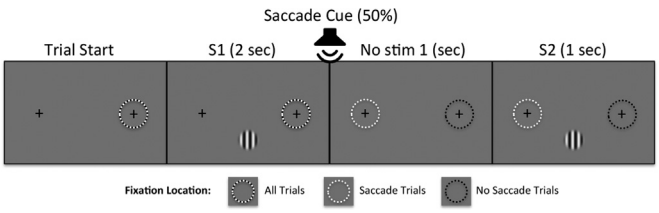

Fig. 1. Example of spatially congruent trial. The trial starts with fixation on one of two fixation crosses (here the right). The first Gabor (S1) is presented for 2 sec. A 100 msec auditory cue (50% of trials) instructs the participant to saccade to the other cross. Following a 1 sec interstimulus interval, S2 is presented for 1 sec. The location was either retinotopically and spatiotopically congruent (no saccade trials) or only spatiotopically congruent (saccade trials). For a complete breakdown of trial types, see Table 1.

Table 1
Condition permutations. Conditions were determined by the presence or absence of a saccade between S1 and S2, the presence or absence of S1, of S2, and whether S2 was at the same or different location as S1.

Condition Name	Saccade	S1	S2	Same Location	N-trials
	Feature				
Fixation only					96
$S1_{NoSacc}$		✔			192
$S2_{NoSacc}$-*same*		✔	✔	✔	96
$S2_{NoSacc}$-*different*		✔	✔		96
Saccade only	✔				96
$S1_{Sacc}$	✔	✔			192
$S2_{Sacc}$-*same*	✔	✔	✔	✔	96
$S2_{Sacc}$-*different*	✔	✔	✔		96

Over twelve ~15 min runs participants performed a total of 960 trials. There were 384 trials where only S1 was presented, 192 where S2 was presented in the same location as S1 and 192 trials where S2 was presented in the different upper/lower visual field. On half of these trials, a sound cued subjects to saccade to the alternate fixation cross in between S1 and S2 presentation. In addition, 96 trials were fixation only and 96 trials were saccade only (see Table 1). In alternating runs, participants began each trial fixating on the left or right fixation cross and each combination of upper/lower, left/right visual field was fully counterbalanced across the design.

Non-baseline trials initiated with the two-second presentation of S1. A one-second period was given for participants to make the change in fixation position in between S1 and S2 on saccade trials. To ensure vigilance, on 80% of trials the fixation cross at the correct fixation position turned green. This small change in the hue of the cue was only detectable when looking directly at the fixation point. The colour change cued participants to report the orientation of the most recently presented stimulus (horizontal or vertical). All participants performed correctly (mean 96.1%, sd 2.9%) in this task. On no-saccade trials, participants maintained fixation during the blank interval between S1 and S2. Fixation and saccade trials were run interleaved, so that participants did not know in advance whether a given stimulus would appear in the upper or lower half of the screen, whether they would be cued to make a saccade during the blank interval, or whether the fixation cross would turn green. Prior to the study, outside the scanner, participants were trained to criterion (no incorrect eye movements or missed probes).

2.3. Data acquisition

MRI data was collected on a 4 T head scanner (Bruker Biospin Medspec) at the Center for Mind/Brain Sciences, University of Trento, using a USA Instruments eight-channel phased-array head coil. Over the 12 runs, approximately ~12000 volumes of 17 anterior/posterior-commissure aligned slices were acquired over twelve runs (image matrix=70×64, repetition time=1000 ms, echo time=33 ms, flip angle=61°, slice thickness=5 mm, gap=0.75 mm, with 3×3 mm in plane resolution).

An additional high-resolution (1×1×1 mm^3) T1-weighted MPRAGE sequence was performed (sagittal slice orientation, centric phase encoding, image matrix=256×224 [read×phase], field of view=256×224 mm [read×phase], 176 slices with 1 mm thickness, GRAPPA acquisition with acceleration factor=2, duration=5.36 min, repetition time=2700, echo time=4.18, TI=1020 ms, 7° flip angle).

2.4. MRI analysis

Analysis was performed in SPM12b (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). The first four volumes of each run were discarded. All subsequent images were corrected for head movement. Runs were rejected if slice coverage was unsatisfactory or the presence of severe motion artifacts was detected. If one run was rejected the corresponding run in the opposite field was also removed. This resulted in the removal of a total of 14/108 runs (range: 0–4 removed runs per subject). For each fMRI run, images were separately coregistered with the high-resolution anatomical image then normalized to the standard SPM T1 template (MNI stereotactic space), resampled to a 3 mm isotropic voxel size, and spatially smoothed using an isotropic Gaussian kernel of 4 mm FWHM. The time series at each voxel for each participant were high-pass filtered at 128 s.

Subject-specific β weights were derived through a general linear model (GLM). For each subject, the data were best-fitted at every voxel using a combination of effects of interest. These were delta functions representing the onset of either S1 or S2 (see below), convolved with the SPM8 hemodynamic response function. There were 14 regressors in each run. S1 and S2 were modeled as separate events. S1 was modeled as occurring either in the upper or lower visual field. S2 events were modeled as a function of the upper-lower visual field and whether this occurred in the same or different visual field as S1 see Table 1). These six event-types (2 for S1, 4 for S2) were modeled separately depending on whether or not a saccade was cued, creating 12 regressors. In additions. the two control conditions (the fixation only trials and saccade only trials) were modeled explicitly to facilitate analysis. The six motion regressors were also included as regressors of no interest.

As each run alternated left or right initial-fixation (and therefore right-left visual field presentation of S1), a total of 28 experimental regressors were entered into a factorial design for the second-level random-effects analysis.

Unless otherwise stated, data were thresholded at an initial voxel-wise p-value of $p < .001$ and corrected for multiple comparisons at the cluster level using the family-wise error as implemented in SPM12b.

ROI definition was accomplished in Marsbar (http://marsbar.sourceforge.net). Voxels were extracted from the intersection of the appropriate 'localizer' contrast (threshold: $p < .001$) and a sphere centered at the local activation peak. The radius of this sphere was 4.5 mm in retinotopic brain regions and 12 mm in the *a priori* analysis of the FEF non-retinotopic analysis. In retinotopic analyses, functional images were co-registered with the surface rendering and automated anatomical labeling in Freesurfer (http://freesurfer.net) to permit peak-location within striate and extrastriate cortex for each visual quadrant and the generation of averaged group maps for the generation of the flattened cortex in Fig. 2 and supplementary figure 1 (Fischl et al., 2008).

3. Results

3.1. Spatially-specific repetition suppression in frontal-parietal regions

The main focus of our analysis was the presence of spatially-specific adaptation effects when S1 and S2 were shown in the same spatial location on the screen (both upper or both lower) compared to when they were shown in different spatial locations. First, we confirmed that the presence or absence of a saccade had little effect on the processing of S2 once the effect of the saccade itself had been linearly subtracted (contrast: [$S2_{noSacc}$ > fixation-only] and [$S2_{Sacc}$ > saccade-only], panels b & c, Fig. 2). In both conditions a comparable network was evident, which consisted of frontoparietal regions: the superior parietal lobe (SPL), intraparietal sulcus (IPS) and frontal eye fields (FEF) as well as ventral and dorsal visual regions (see Table 2 and Fig. 2a–c). There were no significant differences between saccade and no-saccade conditions in frontoparietal regions even at very lenient thresholds ($p < .05$; extent > 10 voxels). This apparent linearity of the effect of the saccade on the processing of S2 meant we were able to directly compare saccade and no-saccade trials in terms of the processing of S2 and any spatially-specific adaptation effects.

To investigate specifically whether adaptation effects resulting from the spatial consistency of S1 and S2 were similarly robust to saccades, we assessed spatially-specific adaptation effects (S2 different location to S1 > S2 same location as S1). This revealed adaptation in a subset of those frontoparietal regions responsive to S2: the SPL, FEF and the parietal-occipital junction (POJ; see Fig. 2). Again, there were no significant differences between saccade and no-saccade conditions, even at lenient thresholds (at a voxel $p < .01$, the largest cluster was 29 voxels and had an associated corrected p-value of .89). For completeness, we include the beta values at ROIs centered at peak adaptation location in Fig. 2g. In this illustrative analysis (it is highly circular and not fit for inference) there is no indication that adaptation effects are driven by a single condition.

The inferential whole brain analysis did revealed similar spatial congruency effects for saccade and no-saccade trials in the SPL and POJ (see Fig. 2:e, f and Table 2). However, the adaptation effect in the FEF evident across all trials (Fig. 2d) did not survive corrections for whole brain inferential analysis motivating an ROI analysis. To fully explore whether there were FEF differences in spatially-specific adaptation in saccade and no-saccade conditions, the FEF was localized using the statistically independent response to all S2 stimuli (Fig. 2a; see also methods). Within ROIs in both hemispheres, adaptation was evident for both saccade and no-saccade conditions (adaptation P-values < .025, one-tailed) which did not differ from one another ($t < 1$).

3.2. Spatial adaptation in early visual cortex

The high tolerance of frontoparietal systems to change in retinotopic coordinates raises the question of whether spatiotopic adaptation occurs early in the visual processing hierarchy. We found that, contingent on spatiotopic consistency, a stimulus in the opposite visual field and represented in the opposite hemisphere prior to a saccade has a strong influence on the neural response to a second stimulus in the opposite visual field and cortical hemisphere in early visual cortex. We demonstrated this by performing an ROI analysis in early visual cortex (Fig. 3). Visual regions responsive to the Gabor patch were identified in each visual quadrant using the response from the independent no-saccade trials ($S1_{noSacc}$ and $S2_{noSacc}$, contrast: upper versus lower visual field). Clear distinctions between striate and extrastriate responses were confirmed by anatomical, surface-based, labeling (Fischl et al., 2008). Although stereotaxic atlases located the group average coordinates for the extrastriate region well within BA18 (V2) rather than BA19 (V3), responses have been designated 'extrastriate' in deference to the uncertainty of V2/V3 distinctions in individual participants (Table 3).

Responses to S2 following a saccade were strong in both striate (mean beta, 24.0; SEM, 1.83) and extrastriate cortex (mean 21.3; SEM, 2.3) and positive in all subjects. Due to this high signal strength, we could express adaptation effects in terms of the percent difference between the response to spatiotopically inconsistent trials (e.g. upper left VF → lower right VF) and spatiotopically consistent trials (e.g. upper left VF → upper right VF). Striate cortex showed modest adaptation (~5%; $p < .05$, one-tailed) compared to extrastriate cortex

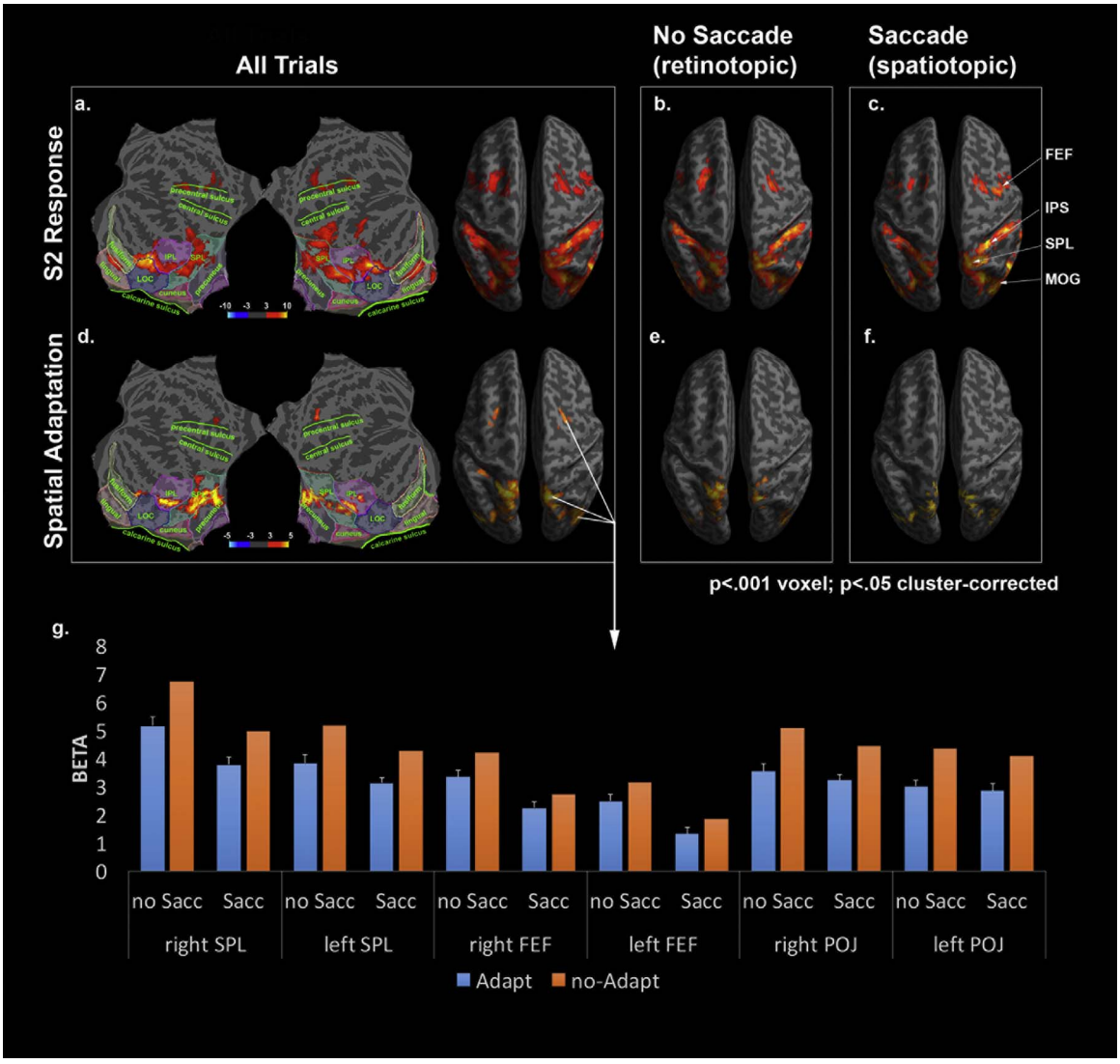

Fig. 2. Whole brain analysis (t-values) of response to S2 (upper row) and spatially-specific adaptation (bottom row) for all trials, no saccade trials (retinotopic and spatiotopic adaptation) and saccade trials (spatiotopic adaptation only). For transparency, descriptive beta plots in g. show the relatively consistent pattern of adaption effects across conditions (inference on these ROIs is not appropriate due to analytic circularity; error bar: 1 SE of the difference between adapt and no-adapt trials). Abbreviations. LOC: lateral occipital cortex; IPL: inferior parietal lobe; SPL: superior parietal lobe; FEF: frontal eye field; IPS: intraparietal sulcus; MOG: middle occipital gyrus.

(~12%; $p < .0001$, one-tailed), The difference between striate and extrastriate cortex adaptation was significant ($P < .01$, two-tailed).

4. Discussion

In this study, we found spatially-specific repetition suppression for trials in which a stimulus was presented in the same world-centered location but different retinotopic locations before and after a saccade. We can divide the regions involved into two functional clusters. The first set of areas, the frontal eye fields (FEF) and posterior parietal cortex (PPC), have previously been implicated in the representation of spatial saliency maps that keep track of important items and update these representations across saccades (Duhamel et al., 1992; Gottlieb, 2007; Crapse and Sommer, 2008; Melcher and Colby, 2008). Specifically, it has been shown that these areas are involved in attention to salient items and that neurons in these regions change their receptive fields around the time of saccades. There is evidence that this relationship is causal: TMS to FEF and IPS can interfere with spatial updating tasks (van Koningsbruggen et al., 2010; for review, see Prime et al., 2006). Our study provides new insight into the role of frontal and parietal regions. We show that updating in these regions is robust and spatially specific to the point that RS in the trans-saccadic (spatiotopic) condition was comparable to the no-saccade condition. As described in the Introduction, spatial selectivity in non-retinotopic coordinates across a saccade is consistent with either remapping of retinotopic coordinates or non-retinotopic coordinate systems (for review, see Melcher and Morrone, 2015). Non-retinotopic coordinates might be based on allocentric information (such as the screen position), multisensory representations or head/body-centered coordinates. There may in fact be more than one mechanism underlying spatial (and feature) updating. It is currently a matter of debate, for example, whether changes in receptive fields around the time of saccades reflect true remapping such as would be required for spatial updating or, instead, shifts in attention towards the saccadic target (Zirnsak et al., 2014). The current results provide evidence for the former account, a complete spatial updating of the stimulus representation, even for items that are not the saccade target.

We also found spatially-specific RS effects in retinotopic visual areas. Although these effects were stronger for extra-striate than striate cortex, even striate cortex showed significant RS when S2 was shown in the same spatial location as S1. This suggests that trans-saccadic updating influences even the first stages of cortical processing and

Table 2
Location, extent and significance of the response to S2 and spatially specific adaptation for all trials (Fig. 2a and d).

	Hemi	Region	Cluster Extent (voxels)	P-value (corrected)	Peak t-value	*x*	*y*	*z*
Response to S2 (all trials)	left	MOG	1715	< .001	10.68	−45	−67	5
	left	pIPS			7.20	−27	−70	29
	left	SPL			6.87	−21	−-61	53
	right	MOG	2269	< .001	10.21	42	−67	-1
	right	IPS			8.28	27	−70	32
	right	SPL			7.56	15	−61	62
	left	FEF	168	< .001	4.81	−27	11	50
	right	FEF	126	< .001	4.78	24	5	53
	right	IFG	103	< .001	4.73	42	8	32
	left	IFG	91	< .001	4.67	−42	5	29
Spatially Specific Adaptation	right	SPL	1444	< .001	6.89	15	−58	59
	left	SPL			6.35	−12	−52	50
	left	POJ			6.10	−39	−76	20
	right	POJ			5.35	36	−82	26
	right	FEF	35	.002	4.43	21	−4	50
	left	FEF	31	.004	4.03	−27	8	47

Table 3
Group average stereotaxic (MNI) coordinates for striate and extrastriate ROIs.

	Hemifield	Left			Right		
		x	***y***	***z***	***x***	***y***	***z***
Striate	**Upper**	−12	−92	3	12	−90	9
	Lower	−4	−88	−2	6	−88	−5
Extrastriate	**Upper**	−16	−95	14	17	−92	23
	Lower	−15	−83	−9	16	−81	−8

provides important evidence for the ongoing debates on whether object representations are updated across saccades ('object pointer theory'; Melcher and Colby, 2008) or, instead, that more abstract "attention pointers" are updated but visual representations remain unaffected (Cavanagh et al., 2010). While both theories would predict effects in frontal-parietal saliency maps (although attentional pointers should result in enhanced rather, than suppressed, activity), only the object pointer theory (Melcher and Colby, 2008) would predict spatial updating in visual areas. Indeed, spatial updating in visual areas would seem to be important to explain spatiotopic visual effects, such as feature integration ((Hayhoe et al., 1991; Melcher and Morrone, 2003; Prime et al., 2006; Gordon et al., 2008; Van Eccelpoel et al., 2008; Wittenberg et al., 2008; Demeyer et al., 2009; 2010; Fracasso et al., 2010; Demeyer et al., 2011; Melcher and Fracasso, 2012; Fabius et al., 2016) or feature adaptation (Melcher, 2005; Ong et al., 2009; Biber and Ilg, 2011; Seidel Malkinson et al., 2012; Zimmermann et al., 2013; Cha and Chong, 2014; Wolfe and Whitney, 2015). One of the criticisms of previous behavioral studies showing spatiotopic effects is that visual areas are obviously retinotopic, calling into question whether these effects are neurally plausible. Some remapping-related activity in retinotopic visual areas for single flashes has been previously reported in neurophysiological studies of non-human primates and in human fMRI (Nakamura and Colby, 2002; for review, see Hall and Colby, 2011). The current findings go further, in showing spatiotopic adaptation effects, not just changes in receptive fields at the time of saccades.

In a recent study, Dunkley et al. (2016) reported RS in inferior parietal cortex and the supramarginal gyrus, as well as repetition summation in an area of extrastriate cortex (possibly V4) for a similar task in which a grating was presented before and after a saccade. Unlike the current study, the location of the stimulus was not varied spatially across trials, so they compared performance for trials in which

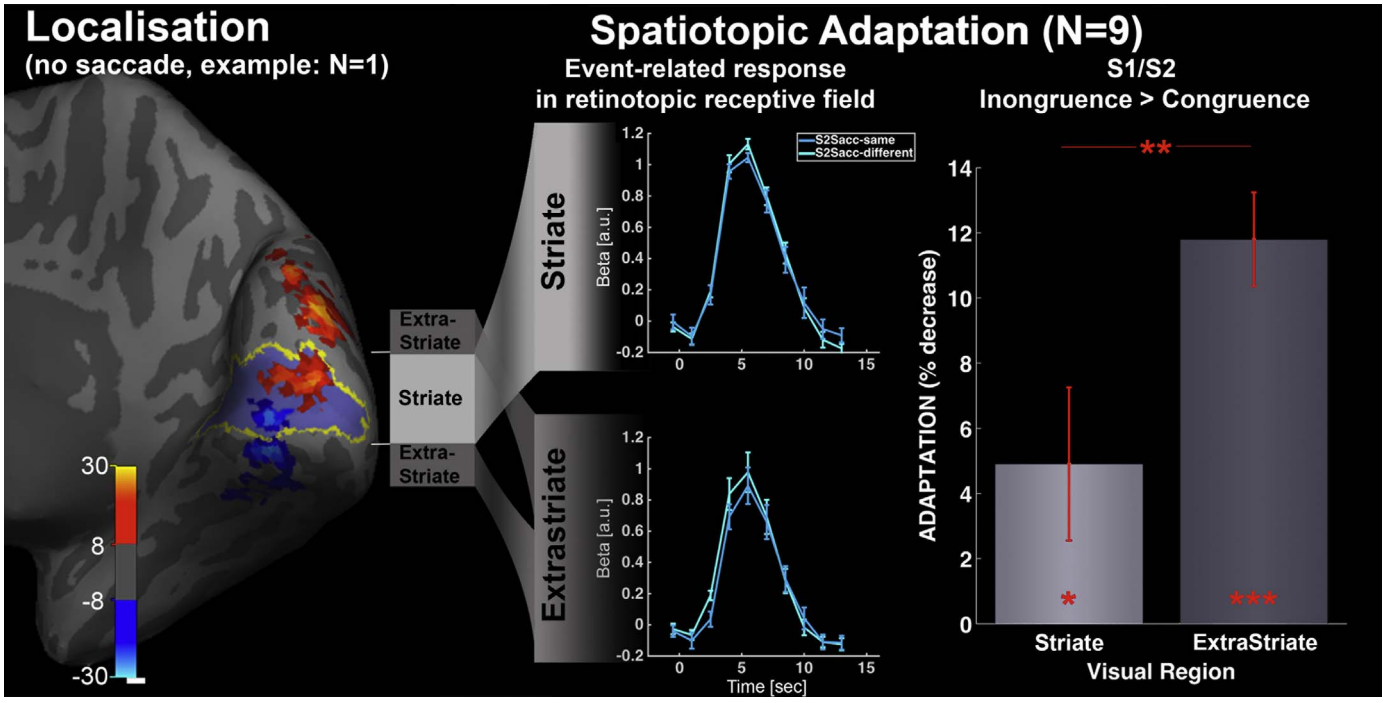

Fig. 3. Spatially specific adaption in early visual cortex. Localisation: Example of localization in the right hemisphere of one subject (this procedure was carried out for each subject). Retinotopic regions responding to the Gabor were identified from the independent 'no-saccade' trials. Eight ROIs were created per participant (four visual quadrants by 2 visual regions). The delineation between striate and extrastriate was confirmed with automatic anatomical labelling (Fischl et al., 2008; see purple/yellow underlay). V2/V3 distinctions were not attempted, as the separation between these regions was uncertain in individual participants. For striate/extrastriate locations for individual participants, see supplementary figure S1. Group-Level Event-Related Response: The response of S2 following a saccade was extracted from each ROI when S2 fell within its receptive field. Values were averaged across quadrants. S1/S2 adaptation: The %-reduction from spatiotopically inconsistent and spatiotopically consistent trials calculated. This revealed modest adaptation effects in striate cortex (~5%; $p < .05$) compared to robust (~12%; $p < .0001$) and significantly stronger ($P < .01$) effects in extrastriate cortex. (Error bars=SEM, *$p < .05$, **$p < .01$, ***$p < .001$).

the grating orientation was the same to when it differed across saccades. Those RS results were interpreted as evidence for potential neural correlates for trans-saccadic memory for orientation, but did not allow for a clear understanding of the spatial reference frame of the effects. In contrast, they did show feature-specificity of the adaptation effect, consistent with updating of visual features (orientation) of an object across saccades. It is also useful to compare the current results to a previous study showing both retinotopic and spatiotopic RS for repeated visual scenes in parahippocampal cortex (Golomb et al., 2011). Although that study focused only on scene-defined ROIs in higher-level visual cortex, the authors did find that RS occurred in a way that was consistent with an active updating of visual representations across saccades. We found strong RS already in extrastriate cortex, suggesting that the spatiotopic RS found in that study might arise already in early visual areas.

Previous studies suggest that fMRI repetition suppression reflects a number of factors, including neuronal adaptation, attention and perceptual expectations (Summerfield et al., 2008; Larsson and Smith, 2012; Kovacs et al., 2013). In our study, participants could not predict the location of S2 based on S1, or even that there would be an S2 at all. Thus, it seems unlikely that our effects reflect expectations. Similarly, there was no reason to shift attention to a particular S2 location, given the inability to predict the location (or presence) of S2 and the fact that stimuli were shown long enough to allow attention to be shifted as needed. Moreover, an attention shift would tend to increase the response to S2, rather than reduce it, showing the opposite pattern of results to those found here. In the current study, the dual task required saccades between target locations (for detecting the probe) and maintaining in memory the orientation of the most recently viewed stimulus (for the orientation memory task). One simple explanation for the current pattern of results is that participants were paying attention to S1 and updating its object representation across the saccade. Such an updating process would result in the brain treating S2 as the same stimulus when it was spatially-matched, resulting in robust repetition suppression. It is interesting that, within PPC, RS was maximal in the SPL. Both the IPS and SPL are implicated in retinotopic object-representation (Sereno et al., 2001). However recently the SPL has been additionally implicated in spatiotopic object representations via a structural/functional connection to the supplementary eye-fields (SEFs; Szczepanski et al., 2013). RS in the SPL may indicate that our stimuli were being tracked in object-centered terms in both saccade and no-saccade conditions.

Overall, the current results provide evidence for theories of visual stability that posit the spatial updating of salient objects across saccadic eye movements in frontal-parietal saliency maps and in visual processing areas (Melcher and Colby, 2008; Melcher, 2011). These results imply that, although the visual system is retinotopic, visual perception does not begin completely anew with each fixation. Instead, the brain actively predicts the outcome of saccades for the spatial location of salient objects. On the one hand, spatial updating would serve visual stability by reducing confusion about matching objects across glances. On the other hand, most theories of repetition suppression see it as a form of efficiency, in which the brain is able to more effectively process an expected or repeated stimulus (Grill-Spector et al., 2006). The present findings imply that spatial updating may serve not only to reduce the negative outcome of saccades, but also to take advantage of the predictability in visual input across saccades to increase the efficiency of the visual system.

Acknowledgements

The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP/2007–2013: ERC Grant Agreement n. 313658). This research was supported by the Provincia Autonoma di Trento and the Fondazione Cassa di Risparmio di Trento e Rovereto.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuroimage.2016.11.071.

References

Bays, P.M., Husain, M., 2007. Spatial remapping of the visual world across saccades. Neuroreport 18, 1207–1213.
Biber, U., Ilg, U.J., 2011. Visual stability and the motion aftereffect: a psychophysical study revealing spatial updating. PloS One 6, e16265.
Burr, D.C., Morrone, M.C., 2011. Spatiotopic coding and remapping in humans. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 366, 504–515.
Cavanagh, P., Hunt, A.R., Afraz, A., Rolfs, M., 2010. Visual stability based on remapping of attention pointers. Trends Cogn. Sci. 14, 147–153.
Cha, O., Chong, S.C., 2014. The background is remapped across saccades. Exp. Brain Res. 232, 609–618.
Crapse, T.B., Sommer, M.A., 2008. The frontal eye field as a prediction map. Progress. Brain Res. 171, 383–390.
d'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D.C., Morrone, M.C., 2007. Spatiotopic selectivity of BOLD responses to visual motion in human area MT. Nat. Neurosci. 10, 249–255.
Demeyer, M., De Graef, P., Verfaillie, K., Wagemans, J., 2011. Perceptual grouping of object contours survives saccades. PloS One 6, e21257.
Demeyer, M., De Graef, P., Wagemans, J., Verfaillie, K., 2009. Transsaccadic identification of highly similar artificial shapes. J. Vision. 9 (28), (21-14).
Demeyer, M., De Graef, P., Wagemans, J., Verfaillie, K., 2010. Parametric integration of visual form across saccades. Vision. Res. 50, 1225–1234.
Duhamel, J.R., Colby, C.L., Goldberg, M.E., 1992. The updating of the representation of visual space in parietal cortex by intended eye movements. Science 255, 90–92.
Dunkley, B.T., Baltaretu, B., Crawford, J.D., 2016. Trans-saccadic interactions in human parietal and occipital cortex during the retention and comparison of object orientation. Cortex 82, 263–276.
Fabius, J.H., Fracasso, A., Van der Stigchel, S., 2016. Spatiotopic updating facilitates perception immediately after saccades. Sci. Rep. 6, 34488.
Fischl, B., Rajendran, N., Busa, E., Augustinack, J., Hinds, O., Yeo, B.T., Mohlberg, H., Amunts, K., Zilles, K., 2008. Cortical folding patterns and predicting cytoarchitecture. Cereb. Cortex 18, 1973–1980.
Fracasso, A., Caramazza, A., Melcher, D., 2010. Continuous perception of motion and shape across saccadic eye movements. J. Vision. 10, 14.
Golomb, J.D., Albrecht, A.R., Park, S., Chun, M.M., 2011. Eye movements help link different views in scene-selective cortex. Cereb. Cortex 21, 2094–2102.
Gordon, R.D., Vollmer, S.D., Frankl, M.L., 2008. Object continuity and the transsaccadic representation of form. Percept. Psychophys. 70, 667–679.
Gottlieb, J., 2007. From thought to action: the parietal cortex as a bridge between perception, action, and cognition. Neuron 53, 9–16.
Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn. Sci. 10, 14–23.
Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., Malach, R., 1999. Differential processing of objects under various viewing conditions in the human lateral occipital complex. Neuron 24, 187–203.
Hall, N.J., Colby, C.L., 2011. Remapping for visual stability. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 366, 528–539.
Hayhoe, M., Lachter, J., Feldman, J., 1991. Integration of form across saccadic eye movements. Perception 20, 393–402.
Kovacs, G., Kaiser, D., Kaliukhovich, D.A., Vidnyanszky, Z., Vogels, R., 2013. Repetition probability does not affect fMRI repetition suppression for objects. J. Neurosci.: Off. J. Soc. Neurosci. 33, 9805–9812.
Larsson, J., Smith, A.T., 2012. fMRI repetition suppression: neuronal adaptation or stimulus expectation? Cereb. Cortex 22, 567–576.
McKyton, A., Zohary, E., 2007. Beyond retinotopic mapping: the spatial representation of objects in the human lateral occipital complex. Cereb. Cortex 17, 1164–1172.
Medendorp, W.P., Goltz, H.C., Vilis, T., 2005. Remapping the remembered target location for anti-saccades in human posterior parietal cortex. J. Neurophysiol. 94, 734–740.
Melcher, D., 2005. Spatiotopic transfer of visual-form adaptation across saccadic eye movements. Curr. Biol.: CB 15, 1745–1748.
Melcher, D., 2011. Visual stability. Philos. Trans. R. Soc. Lond. Ser. B, Biol. Sci. 366, 468–475.
Melcher, D., Colby, C.L., 2008. Trans-saccadic perception. Trends Cogn. Sci. 12, 466–473.
Melcher, D., Fracasso, A., 2012. Remapping of the line motion illusion across eye movements. Exp. Brain Res. 218, 503–514.
Melcher, D., Morrone, M.C., 2003. Spatiotopic temporal integration of visual motion across saccadic eye movements. Nat. Neurosci. 6, 877–881.
Melcher, D., Morrone, M.C., 2015. Non-retinotopic visual processing in the brain. Vis. Neurosci. 32, E017.
Merriam, E.P., Genovese, C.R., Colby, C.L., 2003. Spatial updating in human parietal cortex. Neuron 39, 361–373.
Nakamura, K., Colby, C.L., 2002. Updating of the visual representation in monkey striate and extrastriate cortex during saccades. Proc. Natl. Acad. Sci. 99, 4026–4031.
Ong, W.S., Hooshvar, N., Zhang, M., Bisley, J.W., 2009. Psychophysical evidence for

spatiotopic processing in area MT in a short-term memory for motion task. J. Neurophysiol. 102, 2435–2440.
Pelli, D.G., 1997. The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat. Vision. 10, 437–442.
Prime, S.L., Niemeier, M., Crawford, J.D., 2006. Trans-saccadic integration of visual features in a line intersection task. Exp. Brain Res. 169, 532–548.
Schwarzbach, J., 2011. A simple framework (ASF) for behavioral and neuroimaging experiments based on the psychophysics toolbox for MATLAB. Behav. Res. Methods 43, 1194–1201.
Seidel Malkinson, T., McKyton, A., Zohary, E., 2012. Motion adaptation reveals that the motion vector is represented in multiple coordinate frames. J. Vision., 12.
Sereno, M.I., Pitzalis, S., Martinez, A., 2001. Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. Science 294, 1350–1354.
Summerfield, C., Trittschuh, E.H., Monti, J.M., Mesulam, M.M., Egner, T., 2008. Neural repetition suppression reflects fulfilled perceptual expectations. Nat. Neurosci. 11, 1004–1006.
Van Eccelpoel, C., Germeys, F., De Graef, P., Verfaillie, K., 2008. Coding of identity-diagnostic information in trans-saccadic object perception. J. Vision. 8 (29), (21-16).
van Koningsbruggen, M.G., Gabay, S., Sapir, A., Henik, A., Rafal, R.D., 2010. Hemispheric asymmetry in the remapping and maintenance of visual saliency maps: a TMS study. J. Cogn. Neurosci. 22, 1730–1738.
Wittenberg, M., Bremmer, F., Wachtler, T., 2008. Perceptual evidence for saccadic updating of color stimuli. J. Vision. 8 (9), 1–9.
Wolfe, B.A., Whitney, D., 2015. Saccadic remapping of object-selective information. Atten. Percept. Psychophys. 77, 2260–2269.
Wurtz, R.H., Joiner, W.M., Berman, R.A., 2011. Neuronal mechanisms for visual stability: progress and problems. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 366, 492–503.
Zimmermann, E., Morrone, M.C., Fink, G.R., Burr, D., 2013. Spatiotopic neural representations develop slowly across saccades. Curr. Biol.: CB 23, R193–R194.
Zirnsak, M., Steinmetz, N.A., Noudoost, B., Xu, K.Z., Moore, T., 2014. Visual space is compressed in prefrontal cortex before eye movements. Nature 507, 504–507.