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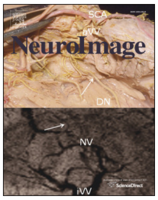

Spatial attention enhances object coding in local and distributed representations of the lateral occipital complex

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ABSTRACT

The modulation of neural activity in visual cortex is thought to be a key mechanism of visual attention. The investigation of attentional modulation in high-level visual areas, however, is hampered by the lack of clear tuning or contrast response functions. In the present functional magnetic resonance imaging study we therefore systematically assessed how small voxel-wise biases in object preference across hundreds of voxels in the lateral occipital complex were affected when attention was directed to objects. We found that the strength of attentional modulation depended on a voxel's object preference in the absence of attention, a pattern indicative of an amplificatory mechanism. Our results show that such attentional modulation effectively increased the mutual information between voxel responses and object identity. Further, these local modulatory effects led to improved information-based object readout at the level of multi-voxel activation patterns and to an increased reproducibility of these patterns across repeated presentations. We conclude that attentional modulation enhances object coding in local and distributed object representations of the lateral occipital complex.

1. Introduction

Attention is a cognitive process that enables us to focus on certain aspects of the environment for the benefit of improved performance (Bashinski and Bacharach, 1980; Cameron et al., 2002; Carrasco et al., 2000; Hawkins et al., 1990). One way in which attention has been found to impact neural processing is through an amplification of neural responses to attended spatial locations, objects, or features (for review, see Treue, 2003). In the visual domain, attentional amplification has been found throughout the visual processing hierarchy, from the earliest stage of visual neural processing in the lateral geniculate nucleus (O'Connor et al., 2002), primary visual cortex (Gandhi et al., 1999; Martínez et al., 1999; Somers et al., 1999), up to high-level visual cortices (Murray and Wojciulik, 2004; O'Craven et al., 1999; Serences et al., 2004) and the frontal lobes (Gitelman et al., 1999). However, the nature of attentional modulation remains a topic of debate. A number of studies have reported that attention leads to a multiplicative scaling of neuronal responses (Di Russo et al., 2001; McAdams and Maunsell, 1999; Treue and Martínez Trujillo, 1999; Treue and Maunsell, 1999), which results in an increase of a neuron's signal to noise ratio. In contrast, other studies reported results that violated the predictions of the multiplication hypothesis, by showing that spatial attention leads to increased neural responses in visual areas in the absence of any visual stimulation (Kastner et al., 1999; Luck et al., 1997; Ress et al., 2000; Silver et al., 2007). According to these studies, attentional modulation involves an unspecific baseline shift of activity.

A common approach to investigate the effects of visual attention is the recording of neural responses across a range of a stimulus parameter (e.g., orientation of motion direction) both in the presence and absence of attention. In this way, previous studies have examined the attentional modulation of single-neuron (McAdams and Maunsell, 1999; Motter, 1993; Treue and Martínez Trujillo, 1999) or voxel (Saproo and Serences, 2010, 2014) tuning profiles. However, a complicating factor for the investigation of attentional modulation in high-level object-coding areas like the human lateral occipital complex (LOC) is the lack of analogous neuronal tuning functions. Similarly, the analysis of contrast response functions – a technique that has been used to study the nature of attentional modulation for low-level visual stimuli (Reynolds et al., 2000; Williford and Maunsell, 2006) – is problematic, because object-related neuronal responses become increasingly invariant to contrast along the visual hierarchy (Avidan et al., 2002; Rolls and

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Baylis, 1986) and this invariance may itself depend on attention (Murray and He, 2006). In the present work we therefore used a different approach by exploiting the fact that the LOC represents objects in a distributed fashion across ensembles of neural populations (Haxby et al., 2001; Rice et al., 2014). At the spatial resolution of fMRI this distributed code is expressed in a differential preference of voxels for a given stimulus, likely representing the cumulative stimulus preference of neurons within these voxels. Thus, if attention causes an amplification of neural activity as opposed to a mere baseline shift, these preferences should be augmented with attention, and as a consequence single- and multi-voxel responses should become more informative about the stimuli encoded in these voxels.

In the present study we presented human participants with objects under conditions of spatial attention and inattention in a functional magnetic resonance imaging (fMRI) experiment. We had two aims. First, we sought to probe the nature of attentional modulation of visual object responses in the LOC as described above, by examining whether attentional modulation increased with a voxel's preference for a given object in the absence of attention, or whether the modulation was independent of object preference. In a second step we investigated whether these local modulatory effects of attention resulted in a more informative and reliable object code. To this end we used a mutual information metric (Saproo and Serences, 2010; Serences et al., 2009) to assess whether single-voxel responses became more informative about object identity with attention. At the multi-voxel pattern level we examined how these local changes affected the quality of object representations through pattern similarity and classification-based analyses.

2. Materials and methods

2.1. Disclosure

A previous article (Guggenmos et al., 2015) was based on the same fMRI dataset, but pursued a different research question and orthogonal analyses.

2.2. Participants

Eighteen healthy participants (11 female, mean age ± SEM, 23.4 ± 0.8 years) took part in the experiment for payment after giving written informed consent. The study was conducted according to the declaration of Helsinki, and approved by the local ethics committee.

2.3. Experimental design

Our key experimental manipulation was to direct participants' spatial attention to either an object (attended condition) or a noise stimulus (unattended condition). Overall the experimental design comprised the factors attention (attended, unattended) as a factor of interest, as well as object (camera, watering can, chair), configuration (intact, split) and side of presentation (left, right) as factors of no interest. Configuration was manipulated by minimally scrambling (half-splitting) the objects, but note that the analyses in this article were based on intact objects only. Within each of 8 experimental runs, an object appeared in 4 trials in each attention condition (in 2 trials per side of presentation). The order of presentation was randomized across the 48 trials of each run.

2.4. Experimental procedures

In each trial (Fig. 1A), participants viewed a stimulus display that contained an object and a noise stimulus on either side of a central fixation cross. Spatial attention was manipulated by means of a brightness discrimination task that was performed either on the object (attended condition) or the contralateral noise stimulus (unattended condition). A trial (Fig. 1A) started with a blank fixation screen for 3300 ms ± 2000 ms, after which one half of a central black fixation diamond turned red, indicating the side to which attention should be directed. Following this cue and a short fixed interval (250 ms), four repetitions of the stimulus–response phase appeared. Each stimulus–response phase lasted 1500 ms and comprised the presentation of the stimulus screen (500 ms), a pattern mask (133 ms) and a response screen (867 ms). The object appeared on one side of the fixation cross (offset 3.84° of visual angle) and a noise stimulus at the same offset on the other side of the stimulus screen. All visual stimuli subtended 3.81 by 3.81° of visual angle. A brightness change occurred 283 ms after stimulus onset simultaneously on both the object and the noise stimulus, such that they became independently and randomly either darker or lighter. Participants were instructed to press a button on the response box when the stimulus on the cued side became darker. Responses were counted as valid within a time window of 1000 ms after stimulus offset. In each repetition of the stimulus–response phase, the same object was shown at the same position. The noise stimulus, while also presented at the same position, was randomly generated for each repetition.

To independently identify object-responsive regions of the lateral occipital complex (LOC) in each participant (Malach et al., 1995), we Q4

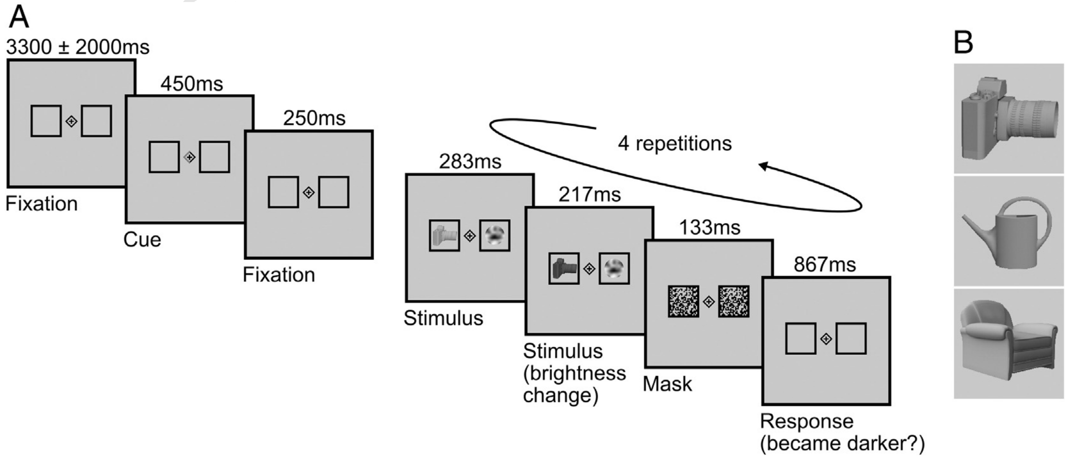

Fig. 1. Experimental procedures and stimuli. A. In each trial a cue indicated the side to which attention should be directed. Subsequently, four repetitions of the stimulus–response phase appeared, during each of which participants had to detect a decrease in brightness of either the object (attended condition) or the noise stimulus (unattended condition). B. The stimulus set consisted of three objects in an intact and half-split configuration.

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conducted a localizer run with 5 blocks of intact objects, 5 blocks of split objects and 10 blocks of grid-scrambled versions of the objects in randomized order. Blocks lasted for 15.8 s during which 20 images were presented for 600 ms each, followed by 200 ms blank screen. Pairs of identical objects were shown left and right of fixation, equaling the configuration of the main experiment in eccentricity and size. Participants performed a one-back task on the object pairs, in which they had to indicate via button press whenever the same stimulus display appeared twice in a row.

2.5. Stimuli

Stimuli were generated with Psychophysics Toolbox 3 (http://psychtoolbox.org) and projected with a Sanyo LCD projector at 60 Hz. The stimulus set consisted of three grayscale objects (camera, watering can, chair) based on realistic three-dimensional models presented either intact or half-split (Fig. 1B). The objects were selected for representing non-overlapping man-made categories to increase the discriminability of evoked neuronal activation patterns. The noise stimuli matched the objects in terms of spatial extent and complexity to ensure that there would be no performance difference. They were randomly generated for each trial by sampling a 9 × 9 random binary matrix, scaling the matrix to 216 × 216 pixels, applying a low-pass filter with a cut-off frequency of 0.02/pixel and cropping pixels outside a circle of 216 pixels diameter. This procedure resulted in circular grayscale stimuli with randomly distributed smooth patches that approximately matched the objects in terms of spatial extent. Both the objects and the noise stimuli were scaled to grayscale RGB values between 50 and 205. To generate these brightness changes, the underlying RGB histograms were shifted up or down by 50 (the image background remained constant with an RGB value of 200). The pattern masks were generated for each trial by sampling an 18 × 18 random binary matrix and scaling the matrix to 216 × 216 pixels.

2.6. Eyetracking

Eyetracking data were successfully collected in 16 of 18 subjects using an infrared video eyetracking system (iView XTM MRI 50Hz, SensoMotoric Instruments, Teltow, Germany). For each run, the horizontal eye movement data were low-pass filtered and drift corrections were performed. As a measure of fixation reliability, we computed the percentage of recorded eye gaze positions during stimulus presentation within a 1.93° visual angle circle around the center of the fixation cross. This radius corresponded to the eccentricity of the inner edges of the two stimulus-containing boxes (see Fig. 1A). In addition, we computed the number of saccades to the intact objects and the noise stimuli, separately for the attended and the unattended condition. Saccades were defined as events of at least three consecutive data points in velocity space exceeding a velocity criterion of 30°/s. Saccades were counted as object-directed or noise-directed saccades, when their endpoint was located within the object-containing box, or the noise-containing box, respectively.

2.7. FMRI data acquisition and preprocessing

FMRI data were acquired on a 3-Tesla Siemens Trio (Erlangen, Germany) scanner using a gradient echo planar imaging (EPI) sequence and a 12-channel head-coil. We recorded 8 experimental runs of 214 whole-brain volumes each, and one LOC localizer run of 242 volumes (TR = 2 s, echo time (TE) 25 ms, flip angle 78°, 33 slices, 3 mm isotropic resolution, interslice gap 0.75 mm). In addition, a high-resolution T1-weighted image was acquired (TR = 1.9 s, echo time (TE) 2.51 ms, flip angle 9°, 192 slices, resolution 1 mm isotropic). The data of the experimental runs were realigned using SPM8 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London). Data analyses for the main experiment were generally performed in native subject space. An exception was an illustrative display of the whole-brain group-level T-maps for the main effect of attention, for which we generated spatially normalized (MNI) and smoothed (8 mm Gaussian kernel) volumes. Preprocessing of the localizer data included realignment, spatial normalization to an MNI template and smoothing (8 mm Gaussian kernel).

2.8. FMRI data analysis

2.8.1. First-level general linear models (GLMs)

For each participant we estimated a GLM including the stimulus-onset regressors, accounting for the factors attention (attended, unattended), object (camera, can, chair) and configuration (intact, split). The onsets of each experimental regressor were set to the beginning of the stimulus–response phase. In addition, six motion parameters were included as regressors-of-no-interest. All experimental regressors were modeled as stick functions and convolved with a canonical hemodynamic response function.

The GLM for the functional localizer comprised regressors for objects and scrambled objects and six motion parameters. The experimental regressors were modeled as boxcar functions with durations equal to the block lengths (15.8 s) and convolved with a canonical hemodynamic response function as implemented in SPM8.

2.8.2. Region of interest procedures

Our region of interest (ROI) was the LOC, a functionally defined region that responds more to images of objects than their counterparts and stretches from the lateral occipital cortex to posterior fusiform gyrus (Grill-Spector et al., 1999). We anatomically constrained Q5 the LOC by a bilateral composite mask of the inferior occipital cortex, middle occipital cortex and the posterior half of the fusiform gyrus (derived from the AAL Atlas, Tzourio-Mazoyer et al., 2002). Then Q6 the LOC ROI was defined as the intersection of the anatomical mask and the functional localizer based on the t-contrast *intact objects* > *scrambled objects* of the functional localizer at a significance level of $p < 0.05$ (family-wise error (FWE) corrected at the whole-brain level). Note that this t-contrast was a group-level t-contrast, because the statistical power in the first-level localizer contrasts was not sufficient to define individual ROIs in all participants at the $p_{FWE} < 0.05$ level. To ensure a homogenous generation of the LOC ROI for all participants we thus first defined the LOC ROI in group-level (MNI) space and subsequently reverse-normalized the generated ROI to each participant's native space.

2.8.3. Quantifying changes in mean BOLD activity

To estimate neural activity in the LOC ROI and its dependence on attention, we extracted the voxel-wise beta values for attended and unattended objects separately and averaged across objects and voxels. This procedure resulted in single values representing the average BOLD response to attended and unattended objects.

To visualize the spatial extent of the attentional modulation at a whole-brain level, we performed a group-level repeated-measures ANOVA with factors attention and object and computed the post-hoc contrast *attended* > *unattended*. This analysis was based on normalized and smoothed data. Voxels were considered statistically significant at a level of $p < 0.05$, FWE-corrected at the whole-brain level.

2.8.4. Analyzing attentional modulation as a function of object preference

We next analyzed whether the attentional modulation depended on the preference of a voxel for a given object. We reasoned that if attention leads to an amplification of neural responses, the difference between a voxel's attentional modulation for the preferred object and the modulation for the non-preferred objects should increase as a function of object preference. By contrast, if attention led to an unspecific baseline shift irrespective of a voxel's preference for the presented object, the attentional modulation should not differ between the

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presentations of the voxel's preferred and non-preferred object. We therefore defined a preference index PI(i) for each object i and each voxel based on the data of the unattended condition:

$$\mathrm{PI}(i) = \beta_{\mathrm{unatt}}(i) - \langle\beta_{\mathrm{unatt}}(\ i)\rangle \ ,$$

where $\beta_{\mathrm{unatt}}(i)$ and $\beta_{\mathrm{unatt}}(\backslash i)$ are the voxel-wise beta values in the unattended condition for object i and all objects except i (denoted as "not i": \i) respectively; the symbol <> denotes the average operation (here across objects). PI was based on the unattended condition to circumvent the potential issue that the object preference of a voxel in the attended condition might not be independent of the magnitude of the attention effect. To compute the strength of the attentional modulation for an object i relative to the other objects \i, we defined a relative attentional modulation index RAI(i) as follows:

$$\mathrm{RAI}(i) = \beta_{\mathrm{att}}(i) - \beta_{\mathrm{unatt}}(i) - \langle\beta_{\mathrm{att}}(\ i) - \beta_{\mathrm{unatt}}(\ i)\rangle \ ,$$

where $\beta_{\mathrm{att}}(i)$ and $\beta_{\mathrm{att}}(\backslash i)$ are the voxel-wise beta values in the attended condition for object i and all objects except i respectively.

Finally, we quantified the RAI as a function of PI. To preclude a selection bias we used a leave-one-run-out procedure, such that PI and RAI were computed on independent data. The leave-one-run-out procedure was performed for each object i separately as follows. In each fold, we sorted the pooled voxels from the LOC ROI according to PI(i) based on data from all but one experimental runs. We then divided the sorted voxels into 10 equinumerous bins (deciles) according to PI(i) and computed the average RAI(i) for the voxels in each bin based on the data of the held-out run. Subsequently, we computed an average RAI across objects for each bin, resulting in a single RAI for each bin.

2.8.5. Computing the mutual information between BOLD response and presented objects

To investigate whether attention increased object information encoded in the activity of individual voxels, we used a mutual information (MI) metric. MI estimates the extent to which the uncertainty about one variable Y (here: BOLD response to the object being presented) is reduced by measuring another variable X (here: the object being presented) (cf. Saproo and Serences, 2010; Serences et al., 2009). The mutual information (MI) measure is defined as the difference of the total entropy $H(X)$ and the noise entropy $H(X|Y)$:

$$\begin{aligned}\mathrm{MI}(X;Y) &= H(X) - H(X|Y)\\ &= -\sum_{x\in X} p(x)\log_2 p(x) - \left(-\sum_{y\in Y} p(y)\sum_{x\in X} p(x|y)\log_2 p(x|y)\right).\end{aligned}$$

Thus we subtract from the total entropy $H(X)$, which corresponds to the overall dynamic range of responses, the noise entropy, which is a measure for the noise in the data conditional on each presented object. The remainder quantifies to what degree the variation in the BOLD signal is informative about the presented object. To compute the total and noise entropies, estimated BOLD responses were transformed into a discrete variable (X) by dividing the entire range of responses into a set of 10 equinumerous bins (deciles). This discretization was based on the pooled range of responses from all voxels in either the attended or the unattended condition after subtracting out the respective mean activation levels of the attended and the unattended condition. This subtraction was done to avoid errors in the binning process due to additive shifts attributed to attention (Saproo and Serences, 2010). In the above formulation, $p(x)$ corresponds to the frequency with which a response in a given voxel falls into bin x. The noise entropy term $H(X|Y)$ additionally required the computation of the probability $p(y)$ of each object y – 1/3 in our case, given that the experiment consisted of three equally often appearing objects – and $p(x|y)$, which corresponds to the frequency with which a response in a given voxel falls into bin x, given object y was presented. We normalized the mutual information for each participant to a range between 0 and 1 by dividing MI(X;Y) by the total entropy $H(X)$ (Kojadinovic, 2005). A normalized MI value of 0 indicates that BOLD response X and object label Y are completely independent, whereas a normalized MI value of 1 indicates that response X gives complete information about the object label Y. The MI metric was applied to the responses of attended and unattended objects separately.

2.8.6. Analyzing the effects of attention at the multi-voxel pattern level

To assess the effect of attention at the multi-voxel pattern level, we examined object-related activation patterns with and without attention by means of a pattern similarity measure and support vector machine (SVM) classification. The two methods are complementary in the sense that the similarity measure provided a transparent quantification of the reproducibility (*within-object pattern similarity*) across runs, whereas the SVM classification assessed the amount of information that can be read out from these activation patterns.

2.8.7. Support vector machine classification

Support vector machine classification (SVM) was performed using *The Decoding Toolbox* (Hebart et al., 2014) with a linear C-SVM and a fixed cost parameter ($c = 1$). We quantified object information in the LOC for attended and unattended objects. We trained the classifier to discriminate between objects based on multi-voxel activation patterns in the LOC ROI in native subject space (Haynes and Rees, 2005; Kamitani and Tong, 2005). A leave-one-run-out cross-validation procedure was used, such that in each of 8 folds the classifier was trained on the beta maps of seven runs and tested on the left out eighth run. We performed pair-wise decoding between the three pairs of objects (camera–can, camera–chair, can–chair) separately for the attended and the unattended condition. Subsequently the decoding accuracies were averaged across folds and object pairs.

2.8.8. Pattern similarity analysis

The pattern similarity analysis was based on z-transformed correlations between activation patterns in the LOC ROI. The *within-object pattern similarity* (WPS) measured the correlation between the patterns evoked by the same object across the 8 runs (separately for attended and unattended objects). For each object this led to $8 \cdot (8 - 1) / 2 = 28$ correlation coefficients for the pairwise combinations of runs, which were z-transformed and averaged across permutations and objects. This procedure yielded a single within-object pattern similarity value for both the attended and the unattended condition. As a control analysis, we also computed the *between-object pattern similarity* (BPS). BPS was assessed analogously to WPS, except that the correlation coefficients were computed between patterns evoked by different objects, resulting in three between-object comparisons (camera–can, camera–chair, can–chair). To avoid an overestimation of pattern similarity due to within-run autocorrelations, we excluded all within-run comparisons (Mumford et al., 2014).

3. Results

3.1. Behavioral results and fixation control

Participants detected and reported brightness changes of the objects and the noise stimuli highly accurately (performance > 98%), indicating focused attention on the correct stimulus. On average, 98.3 ± 0.8% (mean ± SEM) of recorded eye gaze positions during stimulus presentation were within the fixation area, demonstrating that the participants maintained fixation throughout the experiment. There was no difference in the overall number of saccades between the attended and the unattended condition (attended: 3.1 ± 1.6 saccades in the experiment; unattended: 3.6 ± 2.2; $p = 0.43$, $t(15) = -0.80$, two-tailed t-test), and neither was there a difference with respect to the number of object-directed (attended: 2.9 ± 1.6; unattended: 0.9 ± 0.6; $p = 0.19$,

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$t(15) = 1.36$) or noise-directed saccades (attended: 0.2 ± 0.2; unattended: 2.8 ± 2.0; $p = 0.22$, $t(15) = -1.26$). The interaction of saccade direction (object-directed, noise-directed) and attention (attended, unattended) was not significant ($p = 0.21$, $F(1,15) = 1.71$, repeated-measures ANOVA). These results, as well as the low absolute number of object- or noise-directed saccades, indicate that differences between the neural correlates of the attended and the unattended condition are unlikely to ensue from effects of eye movements.

3.2. Attention amplifies responses to objects in the lateral occipital complex

To examine the influence of covert attention on neural activity, we compared the overall average BOLD response for attended and unattended objects within the LOC averaged over objects and sides of presentation. Attended objects led to a significant increase of neural activation ($p < 0.001$, $t(17) = 5.00$, Cohen's $d = 1.17$; Fig. 2A).

In order to test whether the effect of the attention manipulation was confined to object-selective cortex, we quantified the overlap between the thresholded ($p_{FWE} < 0.05$) whole-brain T-maps of the contrasts *attended* > *unattended* (main experiment) and *intact* > *scrambled* (functional localizer). We found that 94.8% of the voxels showing an effect in the attention contrast overlapped with voxels classified as object-selective (Fig. 2B). Thus our focus on the LOC was justified by the spatial extent of the attentional modulation. It should be noted, however, that the attended and the unattended conditions differed only with respect to the attended stimulus type (object vs. noise pattern), but neither systematically with respect to low-level features (likely canceling out effects of attention in earlier visual areas in the contrast attended > unattended) nor with respect to task (likely canceling out effects of attention in executive cortices). The spatial restriction of attentional modulation to LOC therefore reflects a deliberate property of our design, rather than the absence of attentional modulation in other brain areas.

3.3. Attention modulates neural activity as a function of object preference

We reasoned that if attention led to an amplification of neural activity (as opposed to a mere baseline shift), the attentional modulation should be greater for a voxel's preferred object relative to its non-preferred objects. An analysis of a voxel's attentional modulation for a given object in dependence of its preference for the object should thus be informative about the specificity of the attentional modulation. To quantify the difference between the attentional modulation for preferred and non-preferred objects, we computed a relative attentional modulation index (RAI). Further, we determined a preference index (PI) for each voxel based on the mean response to a given object relative to the response of the other objects in the unattended condition. We hypothesized that RAI should increase as a function of PI.

To this end, we used a leave-one-run-out procedure, in which we sorted the voxels according to their PI, divided the voxels into 10 equinumerous bins (deciles) and computed the average RAI for each bin. We found that the RAI increased as a function of PI (linear slope [mean ± SEM]: 0.066 ± 0.022, $p = 0.009$, $t(17) = 3.00$, two-tailed t-test against the null hypothesis of a slope of zero; Fig. 3). In direct comparison, the average RAI for preferred objects ($PI > 0$ [mean ± SEM]: 0.18 ± 0.06) was greater than the average RAI for non-preferred objects ($PI < 0$: −0.17 ± 0.06) ($p = 0.011$, $t(17) = 2.86$, Cohen's $d = 0.67$). These results show that the modulation of neural activity through spatial attention comprises an amplificatory component and is not due to a baseline shift only.

3.4. Attention increases the mutual information between BOLD responses and object identity

To test whether the increase of neural activity increased a voxel's information about the presented objects, we computed the mutual information for attended and unattended objects. We found that attention increased the mutual information of a voxel's responses about the objects presented ($p < 0.001$, $t(17) = 5.72$, Cohen's $d = 1.35$). The percentage of voxels showing higher mutual information in the attended relative to the unattended condition was 55.1% ± 0.9% (mean ± SEM across participants), which was significantly different from the chance level of 50% ($p < 0.001$, $t(17) = 5.81$). Thus, attention reduced the uncertainty of BOLD responses about object identity, implying enhanced object coding at the level of single voxels.

3.5. Attention enhances object representations at the pattern level

A growing body of evidence suggests that the LOC codes object not by means of individual neurons or neuronal populations, but across multiple distributed neuronal populations (Haxby et al., 2001; Rice et al., 2014). Thus, if attention has an enhancing effect on sensory representations, the above finding of object-specific local modulation by attention should improve the quality of multi-voxel activation patterns.

In a first step we assessed the effect of attention on the reproducibility of activation patterns by computing the within-object pattern similarity (WPS) of activation patterns across repeated presentations of the same object, separately for attended and unattended object presentations. We found that attention significantly increased WPS ($p < 0.001$, $t(17) = 10.51$, two-tailed t-test; Fig. 4A), indicating that attention improved the reproducibility of responses at the pattern level. However, in a control analysis we found that attention also led to a considerable increase of the between-object pattern similarity (BPS; $p < 0.001$, $t(17) = 9.73$, two-tailed t-test). If the increase in reproducibility for the same object (WPS) was outweighed by a simultaneous increase of the ambiguity between different objects (BPS), nothing is gained. We therefore directly compared WPS and BPS and found that the increase in WPS was greater than the increase in BPS ($p < 0.001$, $t(17) = 4.22$), indicating that attention led to a functionally relevant improvement of the reproducibility of multi-voxel activation patterns.

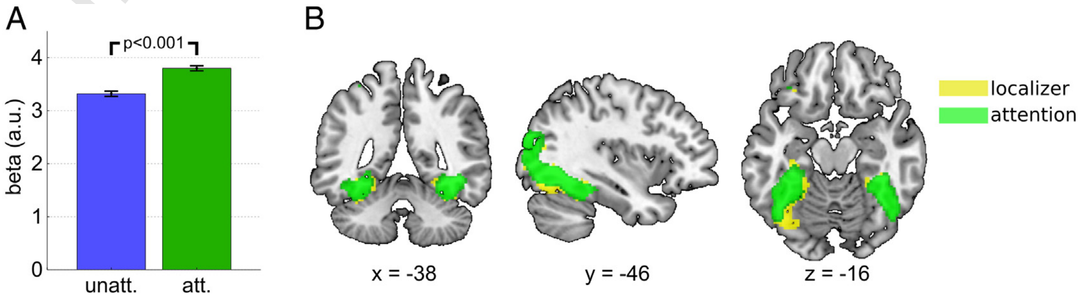

Fig. 2. Modulatory effect of attention. A. LOC ROI. The bars represent average beta values of the LOC ROI for the attended and unattended condition, averaged across objects and sides of presentation. Error bars denote SEM corrected for between-subject variance (Cousineau, 2005). Statistical comparison was based on a two-tailed t-test. B. Whole-brain analysis. Overlay of object-selective voxels (based on the independent functional localizer, intact > scrambled, thresholded at $p_{FWE} < 0.05$, colored in yellow) and voxels showing a significant effect of attention (attended > unattended, thresholded at $p_{FWE} < 0.05$, colored in green).

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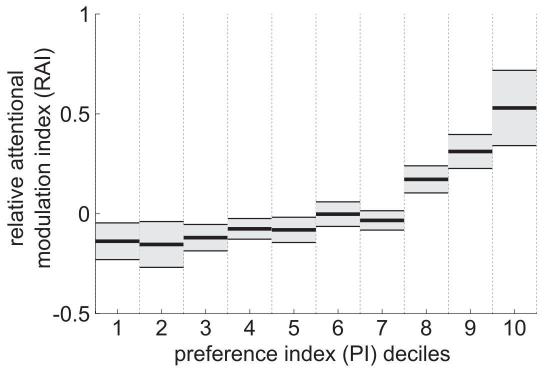

Fig. 3. Relative attentional modulation as a function of object preference. The relative attentional modulation index (RAI) quantifies the attentional modulation for a given object relative to the average modulation of the other objects. For each participant voxels were binned into deciles according to their object preference index (PI). The plot shows the averaged RAI for each preference bin. Error bars denote SEM corrected for between-subject variance (Cousineau, 2005).

In a second step we directly assessed how attention affected the readout of object information from the LOC by performing support vector machine classification between objects. Decoding accuracies were significantly above chance in both the attended (66.6% ± 2.0%; $p < 0.001$, $t(17) = 8.36$, two-tailed t-test against the chance decoding accuracy of 50%) and the unattended condition (54.8% ± 1.8%; $p = 0.017$, $t(17) = 2.66$; Fig. 4B). Importantly, classification performance was significantly and markedly greater in the attended compared to the unattended condition ($t(17) = 4.74$, $p < 0.001$, Cohen's $d = 1.12$). Thus, the attentional modulation of neuronal responses increased object information in the LOC at the multi-voxel pattern level.

3.6. Enhanced readout at the pattern level is linked to the local increase in mutual information, but not mean activation

Finally, we assessed whether the attentional modulation at the single-voxel level was related to the enhancement of object representations at the pattern level. In the single-voxel-level analyses we found that attention led to an increase of (1) BOLD signal, and (2) the mutual information. We therefore correlated – across participants – both effects with the increase in decoding accuracy. We found that the increase in decoding accuracy correlated with the increase in mutual information (Pearson's $r = 0.59$, $p = 0.009$), but not with the increase in BOLD activation ($r = 0.01$, $p = 0.96$). A direct comparison confirmed that the increase in mutual information explained significantly more variance than the BOLD increase ($p = 0.034$, z-score $= 2.11$, Steiger's z-test; Steiger, 1980). Although the absence of a significant contribution of the BOLD increase is surprising (possibly caused by ceiling effects of the BOLD increase), the relationship between mutual information and decoding accuracy suggests that the local attentional modulation of neuronal responses increases the information content of object representations at the pattern level.

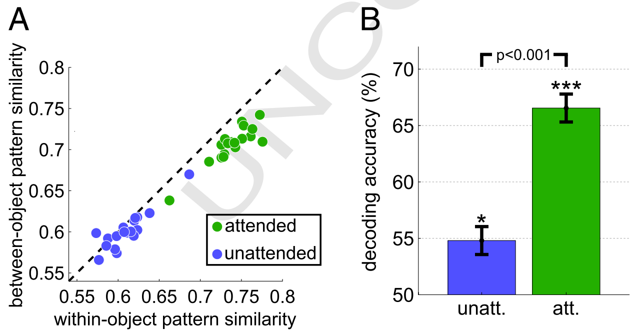

Fig. 4. Pattern level. A, between-object and within-object pattern similarity within the LOC ROI. Each dot represents one participant. The dashed diagonal line indicates identical within- and between-object similarity of activation patterns. Attention leads to a shift of data points below the diagonal line, indicating higher pattern similarity for repeated presentations of the same object compared to the pattern similarity of different objects. Between-subject variance was removed for illustration. B, SVM decoding results based on percent correct classification (decoding accuracy). Error bars denote SEM corrected for between-subject variance (Cousineau, 2005). Statistical comparison was based on a two-tailed t-test.

4. Discussion

We examined tuning-dependent attentional modulation of object representations in the LOC and the resulting enhancement of object representations at the single-voxel level and the multi-voxel pattern level. At the single-voxel level we found that (1) responses in the LOC were considerably stronger when an object was attended relative to when a noise stimulus was attended; (2) the relative attentional modulation (the attentional modulation for a given object relative to the average modulation of other objects) increased as a function of a voxel's preference for the given object; and (3) mutual information between a voxel's responses and object identity increased, demonstrating that responses became more informative about a presented object when the object was attended compared to when it was unattended. All three results provide evidence against a mere baseline-shift effect of attention. Further analyses showed that these local changes resulted in increased object information at the level of multi-voxel patterns and increased similarity of these patterns across multiple presentations, indicating increased reproducibility of distributed neuronal responses.

4.1. Effects of attention at the level of individual voxels

A key goal of this study was to investigate whether the observed increase in activity involved amplificatory attentional modulation, or merely an unspecific baseline shift. Previous neuroimaging studies reported that neural activity increased with attention in high-level visual cortex (Baldauf and Desimone, 2014; Connor et al., 1997; Murray and Wojciulik, 2004; O'Craven et al., 1999; Serences et al., 2004), and showed that the effects of attention were specific to coarse functional modules, such as parahippocampal place area (PPA) or fusiform face area (FFA). However, given that objects are known to be coded across distributed neuronal ensembles in visual cortex (Haxby et al., 2001; Rice et al., 2014), it is desirable to analyze attentional modulation at a more fine-grained level, thereby accounting for the differential tuning of neuronal populations within these areas. Here we provide evidence for voxel-wise object-specific attentional modulation of responses in the LOC by identifying a relationship between attentional modulation and object preference. The consistent increase of the relative attentional modulation across preference levels suggests that subtle difference in preference measured in the absence of attention became amplified as attention was directed to the objects. Our additional information-theoretic analyses indicated that such attentional modulation effectively increased the information of voxel-wise responses about object identity, in line with previous work on orientation coding in V1, which likewise found an increase in mutual information with attention (Saproo and Serences, 2010).

How do these results relate to the multiplicative gain hypothesis of attention derived from neurophysiological recordings in monkeys (McAdams and Maunsell, 1999; Treue and Martínez Trujillo, 1999)? It should be noted that a direct comparison between the BOLD responses in our study and spiking activity in these previous studies is difficult for two reasons: first, BOLD responses are more closely related to the local field potentials and hence synaptic activity than to spiking neuronal activity (Ekstrom, 2010; Logothetis, 2003; Logothetis et al., 2001); and second, efficient event-related fMRI designs such as ours do not permit inferences about the absolute level of stimulus-related BOLD activity, which would be necessary to quantify the ratio between attended and

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unattended responses analogous to the ratio of firing rates in these previous neurophysiological studies. Nevertheless, our results do provide indirect evidence for the multiplicative gain as opposed to a mere baseline shift hypothesis. Consider the result of increased attentional modulation with object preference. A voxel's preference for a given object may indicate that, for a fixed number of neurons tuned to different objects, the tuning curves of neurons are biased more towards the given object than to the other objects. Alternatively, it may indicate that for a fixed bias towards the given object an overall greater number of neurons prefer the given object. Importantly, in both cases an unspecific baseline shift would lead to an equal increase of neural activity for preferred and non-preferred objects, which is at odds with our results. To illustrate why the increase in MI provides evidence for a multiplicative gain mechanism as opposed to a pure baseline shift explanation, it is helpful to consider two objects A and B and a hypothetical voxel consisting of neurons with a preference for, e.g., object A. In case of a pure baseline shift the voxel would show increased responses to both objects and neural responses would therefore not become more informative about whether object A or B was presented. In contrast, in case of multiplicative scaling, attention will lead to greater response amplification for object A compared to object B, increasing the dynamic range of responses and resulting in increased mutual information between neural responses and presented objects. Thus, the increase in mutual information by attention provides a second line of evidence in favor of a multiplicative gain mechanism and against a pure baseline shift explanation.

4.2. Effects of attention at the multi-voxel pattern level

At the level of multi-voxel activation patterns we found improved decodability of attended relative to unattended objects, which is in accordance with similar reports for early (Jehee et al., 2011; Kamitani and Tong, 2005) and high-level visual areas (Pratte et al., 2013; Reddy and Kanwisher, 2007). This result demonstrates that the attentional modulation increased the information content of distributed object representations in the LOC, potentially benefitting information readout from the LOC by high-level executive cortices. An analysis of pattern similarity showed that attention increased the reproducibility of activation patterns of the same object. Such an increase in reproducibility would be expected on the assumption of a multiplicative attentional scaling mechanism, where neuronal responses become amplified without an equivalent increase of the noise (which increases as the square-root of the signal). Another possibility is that the increase in reproducibility is the result of more discrete neural processing with attention, as proposed for conscious relative to non-conscious percepts (Sackur and Dehaene, 2009; Schurger et al., 2010). When discrete decisions are reached at each (object) processing stage, before they are dispatched to the next stage, the resulting activation patterns might become more stereotypical and reproducible.

A number of previous fMRI studies have used MVPA to study the effects of attention on neural responses (Esterman et al., 2009; Jiang et al., 2013; Pratte et al., 2013; Reddy and Kanwisher, 2007; Reddy et al., 2009; Tamber-Rosenau et al., 2011). In particular, Reddy and Kanwisher (2007) and Reddy et al. (2009) investigated the decodability of complex stimuli in high-level visual cortex when they were presented alongside a second object and were either attended or unattended. Reddy and Kanwisher (2007) found that information about object categories encoded in multi-voxel activation patterns was strongly reduced to the point of being abolished when attention was diverted. In the present study we showed that multi-voxel responses were reduced, but still informative about object categories even when attention was diverted. This difference may be explained by the fact that participants in the study by Reddy and Kanwisher (2007) directed their attention to complex distractor stimuli (which, in addition, were the relevant stimuli in other trials), whereas participants in our study viewed noise stimuli in the unattended condition. It is conceivable that the absence of high-level visual cortex information for unattended objects in Reddy and Kanwisher (2007) was caused by distractor-related neural responses interfering with the activation pattern of the unattended target object. Along similar lines, Reddy et al. (2009) interpreted the informational gain for attended objects (or loss for unattended objects) in the biased competition framework. According to this view, attention serves to disambiguate the overlapping multi-voxel patterns of different objects through a shift towards the pattern of the currently attended object. Aside from investigating the effect of attention in sensory cortices, other studies have successfully used MVPA to study the initiation and control of attentional shifts. For instance, Esterman et al. (2009) and Tamber-Rosenau et al. (2011) showed that spatial patterns of brain activity within the medial superior parietal lobule reliably differentiated between several domains of cognitive attentional control at a given moment. Thus, in our and previous studies, MVPA presented a powerful technique to probe distributed neural underpinnings of different attentional phenomena, from the initiation of attentional shifts to the modulation of sensory representations.

4.3. Linking the single-voxel and the multi-voxel pattern level

Finally, we linked the effects of attention at the single-voxel level with the effects at the pattern levels by correlating the increase in decoding accuracy of multi-voxel activation patterns to the increase in either BOLD signal or mutual information. Unexpectedly, we found that the increase in mean activation was not related to the increase in decoding accuracy. This negative finding could indicate that the attentional manipulation in our paradigm operated in a range, in which effects at the pattern level were insensitive to the overall magnitude (e.g., because the BOLD increase was at maximum). Alternatively, as the overall effect of attention likely involves both a multiplicative component and a baseline shift, the unspecific baseline shift component might have masked the effect of the relevant multiplicative component. In contrast, we found that the increase in mutual information explained a considerable amount of variance of improvements in pattern-based decoding. This result demonstrates that the increase of object information at the single-voxel level substantially translated to an enhanced object code at the pattern level. This link is informative, as the information content encoded in the linear combination of voxels can show strong gains, while information encoded in the individual voxel may show only small changes (for examples of such scenarios see Haynes and Rees, 2006). It is currently not clear whether the distributed object code in LOC represents the immediate neural correlate of perception, or whether it reflects object processing prior to perception. In either case our data indicate that the enhancement of sensory representations through attention – which may directly or indirectly underlie perceptual improvements – is not a phenomenon that solely emerges at the level of distributed object fingerprints. Instead, the improvement in pattern decoding likely represents the cumulative result of informational gains in multiple local units of LOC.

4.4. Implications for mechanisms of visual attention

The results of the present study corroborate the notion that behavioral benefits of attention are based on an enhanced stimulus processing in sensory brain areas (Bisley, 2011). Our finding that the magnitude of attentional modulation increased with object preference suggests a response gain mechanism that magnifies stimulus-driven responses as a function of response strength without attention. Importantly, our information-theoretic analyses demonstrate that the attentional modulation effectively increases object information encoded in high-level visual cortex, which may facilitate the readout in executive cortices and thus benefit perceptual decision making. A unifying theoretical framework for such attentional modulation of neural activity is provided by the normalization model of attention (Reynolds and Heeger, 2009). The model describes the modulation of attention by two processes: a

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multiplication of neuronal responses by an attention field and a division (normalization) by a suppressive drive. Thus, our observed differences between neural responses to attended and unattended objects may not only be caused by a boost of neural processes tuned to the attended object, but also by a suppression of activity related to the unattended object. Another key aspect of the model is that it makes specific predictions regarding the effect of different attentional strategies on neural activity. According to the model, a purely spatial attention strategy causes a scaling of the entire tuning curves (because the attention field is then assumed to be constant across feature dimensions), whereas a purely feature-based attention strategy causes a sharpening of tuning curves. The fact that our brightness discrimination task emphasized spatial attention strategies over feature-based strategies may thus explain the strong amplitude modulation of the BOLD response in our study. Future neuroimaging studies could test whether our findings of tuning-dependent attentional modulation and information-theoretic gains through endogenous visual spatial attention generalize to other forms of attention, e.g. to involuntary (exogenous) shifts of attention or to other sensory modalities.

In conclusion, our results show that visual spatial attention modulates neural activity as a function of voxel-based object preferences. Through these modulatory processes, attention enhances object coding both at the single-voxel and pattern level, which may give rise to improved perception and perceptual decisions.

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