RAPID REPORT | Sensory Processing

Typical visual-field locations enhance processing in object-selective channels of human occipital cortex

Daniel Kaiser¹ and Radoslaw M. Cichy^{1,2,3}

¹Department of Education and Psychology, Freie Universität Berlin, Berlin, Germany; ²Berlin School of Mind and Brain, Humboldt-Universität Berlin, Berlin, Germany; and ³Bernstein Center for Computational Neuroscience Berlin, Berlin, Germany

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Kaiser D, Cichy RM. Typical visual-field locations enhance processing in object-selective channels of human occipital cortex. J Neurophysiol 120: 848-853, 2018. First published May 16, 2018; doi:10.1152/jn.00229.2018.-Natural environments consist of multiple objects, many of which repeatedly occupy similar locations within a scene. For example, hats are seen on people's heads, while shoes are most often seen close to the ground. Such positional regularities bias the distribution of objects across the visual field: hats are more often encountered in the upper visual field, while shoes are more often encountered in the lower visual field. Here we tested the hypothesis that typical visual field locations of objects facilitate cortical processing. We recorded functional MRI while participants viewed images of objects that were associated with upper or lower visual field locations. Using multivariate classification, we show that object information can be more successfully decoded from response patterns in objectselective lateral occipital cortex (LO) when the objects are presented in their typical location (e.g., shoe in the lower visual field) than when they are presented in an atypical location (e.g., shoe in the upper visual field). In a functional connectivity analysis, we relate this benefit to increased coupling between LO and early visual cortex, suggesting that typical object positioning facilitates information propagation across the visual hierarchy. Together these results suggest that object representations in occipital visual cortex are tuned to the structure of natural environments. This tuning may support object perception in spatially structured environments.

NEW & NOTEWORTHY In the real world, objects appear in predictable spatial locations. Hats, commonly appearing on people's heads, often fall into the upper visual field. Shoes, mostly appearing on people's feet, often fall into the lower visual field. Here we used functional MRI to demonstrate that such regularities facilitate cortical processing: Objects encountered in their typical locations are coded more efficiently, which may allow us to effortlessly recognize objects in natural environments.

functional connectivity; multivariate pattern analysis; object representations; real-world regularities; scene statistics

INTRODUCTION

To optimally perform in everyday situations, the human visual system has adapted to the structure of its environment. A key aspect of this adaptation is the sensitivity to regular

patterns in the input. For example, it has been proposed that the characteristic distribution of specific visual features across the environment determines the perceptual organization of these features (Purves et al. 2011). Our everyday environments are structured not only in their basic visual properties but also in their high-level content, such as their spatial object structure (Bar 2004; Biederman 1972; Chun 2000; Kaiser et al. 2014; Oliva and Torralba 2007; Wolfe et al. 2011). Within a scene, objects do not appear in an unorganized manner but frequently occupy similar locations. For example, hats are commonly seen on people's heads, while shoes are most often seen on the ground. When objects frequently occupy similar locations in the world, they-unless directly fixated-also frequently occupy similar retinotopic locations. As we wander around the world, hats will most often fall in the upper visual field and shoes in the lower visual field.

Here we propose that the brain exploits such regularities in typical visual field locations to facilitate object processing. Specifically, we hypothesize that object representations in ventral visual areas are tuned to typical object locations. Object-selective regions of the ventral and lateral visual cortex are sensitive to the retinotopic location of objects (Cichy et al. 2011; Golomb and Kanwisher 2012; Hong et al. 2016; Kravitz et al. 2010; Schwarzlose et al. 2008), which suggests that object and location information could be integrated there (Kravitz et al. 2008). Such an integration may arise from experience with typical object locations: When an object is preferentially activating retinotopically constrained neural populations, these populations become tuned to an objectlocation conjunction. This tuning would facilitate the processing of the object when it appears in its typical location.

Furthermore, object-selective regions have characteristic functional connections with retinotopic early visual regions (Uyar et al. 2016). We hypothesize that typical visual field locations may thus not only shape object representations in higher-level regions but also influence how these representations are connected to retinotopically organized lower-level regions. Such an experience-based strengthening of interregion connectivity may facilitate information flow in object-process-ing channels (Kaiser and Haselhuhn 2017). This facilitation may streamline the progression from retinotopically organized feature information in early visual cortex toward object representations on higher levels.

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Address for reprint requests and other correspondence: D. Kaiser, Dept. of Education and Psychology, Freie Universität Berlin, Habelschwerdter Allee 45, 14195 Berlin, Germany (e-mail: danielkaiser.net@gmail.com).



Fig. 1. Stimuli and paradigm. *A*: we used 6 objects (10 exemplars each) that were associated with either upper or lower visual field locations. These associations were validated in 2 ways. First, we automatically extracted within-scene object positions from a large database of labeled scene photographs (Russell et al. 2008). Additionally, we asked a set of participants to freely place the objects on the screen to best match their real-world locations. Both measures confirmed the spatial associations of the objects. Scatterplots show the relative horizontal and vertical positions within a scene/on the screen, respectively. Crosses indicate the mean object position and its standard deviation in both directions. *B*: in the functional MRI experiment, single objects were shown in their typical or atypical positions for 150 ms, followed by a variable intertrial interval. Participants were asked to detect occasional 1-back repetitions on an object level (e.g., 2 shoes in a row). Colors are shown for illustration purposes only. Note that because of copyright restrictions we cannot show the original object images here; for stimulus examples, see Kaiser et al. (2018).

To test these hypotheses, we ran a functional MRI (fMRI) experiment. We selected everyday objects that were reliably associated with upper or lower visual field locations (Fig. 1*A*) and presented them in their typical location vs. the atypical location in the visual field (Fig. 1*B*). Using multivariate decoding and functional connectivity analyses, we obtained two key results: First, in object-selective lateral occipital cortex (LO), object information could be more successfully retrieved from multivoxel response patterns for typically positioned, compared with atypically positioned, objects (Fig. 2). Second, the regularity benefit in object decoding was accompanied by an increase in connectivity along the object-processing hierarchy, most prominently between retinotopic early visual cortex and LO (Fig. 3). Together our results provide evidence for object-processing channels along the visual hierarchy that are

tuned to the typical visual field location of an object. These processing channels may be an optimal adaptation to complex but regular environments.

MATERIALS AND METHODS

Participants. Seventeen healthy adults (mean age 24.5 yr, SD = 3.9 yr; 11 women, 6 men) with normal or corrected-to-normal vision completed the experiment. All participants provided written informed consent and received monetary reimbursement or course credits for participation. All procedures were approved by the local ethical committee and were in accordance with the Declaration of Helsinki.

Stimuli. The stimulus set consisted of grayscale images of six

objects (Fig. 1A). For each object, 10 exemplars were collected. We

chose these six objects because we believed they were strongly V1 LO FG **PPA** typical atypical 55.5 51.5 eqularity effect egularity effect egularity effect egularity effect % decoding % decoding 55.5 decoding % decoding 51 52.5 55 55 50.5 52 54.5 54.5 0 51.5 -2

Fig. 2. Multivariate decoding results. Decoding accuracy was computed by first performing pairwise decoding analyses between all conditions in each region of interest (ROI); subsequently, accuracies were averaged for all decoding analyses within typically and atypically positioned objects, respectively (see MATERIALS AND METHODS). In lateral occipital cortex (LO), decoding performance was significantly higher when the objects were positioned typically rather than atypically. Error bars reflect the standard error of the difference. Scatterplots show the regularity effect (i.e., the decoding difference) for each participant. $*P_{corr} < 0.05$. ROI masks shown for illustrative purposes are taken from a representative participant. V1, early visual cortex; FG, fusiform gyrus; PPA, parahippocampal place area.

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Downloaded from www.physiology.org/journal/jn by \${individualUser.givenNames} \${individualUser.surname} (087.077.023.230) on August 21, 2018. Copyright © 2018 American Physiological Society. All rights reserved. V1 - LO

V1 - FG





0.05

0.88

0.84



0.15

0.1

0.05

regularity effect

connectivity (r)

0.66

0.62







Fig. 3. Functional connectivity results. Functional connectivity was computed by correlating the activation time courses for each pairing of region of interests (ROIs) and for the typical and atypical conditions separately (see MATERIALS AND METHODS). Crucially, functional coupling between visual cortex (V1) and lateral occipital cortex (LO) was significantly enhanced when the objects were positioned typically, rather than atypically. Error bars reflect the standard error of the difference. Scatterplots show the regularity effect (i.e., the connectivity difference) for each participant. Asterisk ($P_{corr} < 0.05$) and star ($P_{corr} = 0.057$) indicate significant and trending differences. ROI masks shown for illustrative purposes are taken from a representative participant. FG, fusiform gyrus; PPA, parahippocampal place area.

associated with particular visual field locations: three of them should appear mostly in the upper visual field (lamp, airplane, and hat) and three mostly in the lower visual field (carpet, boat, and shoe). To validate these putative associations with upper/lower parts of the visual field, we used two different measures (Fig. 1A).

First, the typical within-scene location of each object was assessed by automatically extracting object positions from a large number of labeled images (>10,000) contained in the LabelMe toolbox (Russell et al. 2008). For each object, we extracted its typical within-scene location by computing the mean pixel coordinate of the area labeled as belonging to the object and then averaged these coordinates across all available scenes (2,251 for lamp, 1,054 for plane, 327 for hat, 292 for carpet, 871 for boat, and 325 for shoe). Confirming the validity of our object selection, typical within-scene locations were significantly higher on the vertical axis for objects associated with upper visual

field locations than for objects associated with lower visual field locations, for all pairwise comparisons of objects (all t > 11.4, P <0.001).

Second, we used a complementary approach in which we asked an independent group of participants (n = 70 for lamp/carpet, n = 60 for airplane/boat, and n = 65 for hat/shoe) to explicitly judge the objects' typical location in the environment. Participants were asked to freely place the object on a computer screen in the location where they expected it to appear with the highest probability under natural circumstances. As expected, the vertical locations chosen by the participants differed significantly between objects associated with the upper and lower visual fields, for all pairwise comparisons (all t >6.04, P < 0.001). Together, both tests strongly corroborate the associations between the objects and their typical locations, thus validating our stimulus selection.

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To avoid low-level, image-based confounds, the images were matched for overall luminance (Willenbockel et al. 2010). Additionally, to explicitly assess the stimuli's low-level visual similarity, we computed pixelwise similarity between all 60 images (i.e., 6 objects, 10 exemplars each), in a pairwise fashion. First, pixel intensity values were correlated between all object exemplars. We then tested whether pixel-based similarity was higher for objects associated with the same visual field location (e.g., an airplane and a hat) than for objects associated with different visual field locations (e.g., an airplane and a shoe), separately for all exemplars. Comparing all possible within-location and between-location comparisons revealed no difference (t[1,498] = 0.50, P = 0.62), indicating that objects associated with upper vs. lower locations did not differ in simple visual properties.

Paradigm. On every trial, one object exemplar (~3° visual angle) was presented in an upper or lower location (3.25° vertical eccentricity) for 150 ms, followed by a variable intertrial interval (jittered between 2 s and 3 s, in steps of 250 ms) (Fig. 1B). Stimulus presentation was controlled with the Psychtoolbox (Brainard 1997). Participants were asked to detect one-back repetitions on an object level (e.g., 2 different airplanes). Repetitions occurred on 13% of the trials and equally often for typically and atypically positioned repetition targets. Participants performed accurately on this task (mean accuracy 94%, SD = 3%), with no difference in accuracy between typically and atypically positioned targets (t[16] = 1.59, P = 0.13). Each run consisted of 138 trials: 120 trials covered each object exemplar in each location once (i.e., 2 locations, 6 objects, and 10 exemplars), and 18 trials contained one-back repetitions. The repetition trials were excluded from all fMRI analyses. Trial order was randomized, with the constraint that there were exactly 18 one-back object repetitions in each run. Fourteen participants completed the whole experiment consisting of eight runs, one participant completed only seven, and two participants completed only six runs. Runs started and ended with brief fixation periods; each run lasted 6 min 16 s.

Each participant additionally completed a functional localizer designed to identify object-selective voxels. This run consisted of 25 blocks. In 10 blocks, different everyday objects were shown, and in 10 blocks phase-scrambled versions of the objects were shown, alternating between object and scrambled blocks. Within each block (16-s duration), 32 stimuli were shown (200-ms stimulus, 300-ms interstimulus blank). Additionally, five baseline blocks (where only a fixation cross was shown throughout the block) were interleaved at random positions. Participants were instructed to maintain fixation on a central red fixation dot while passively viewing the stimuli. The run started and ended with brief fixation periods, amounting to a total duration of 6 min 50 s.

MRI acquisition and preprocessing. MRI data were acquired with a 3T Siemens Tim Trio Scanner equipped with a 12-channel head coil. T2*-weighted gradient-echo echo-planar images were collected as functional volumes (TR = 2 s, TE = 30 ms, 70° flip angle, 3-mm³ voxel size, 37 slices, 20% gap, 192-mm field of view, 64×64 matrix size, interleaved acquisition). Additionally, a T1-weighted image (MPRAGE; 1-mm³ voxel size) was obtained as a high-resolution anatomical reference. Preprocessing was done in MATLAB with SPM12 (https://www.fil.ion.ucl.ac.uk/spm/). The functional volumes were realigned and coregistered to the T1 image. Volumes collected during the localizer run were additionally smoothed with an 8-mm full-width half-maximum Gaussian kernel.

Region of interest definition. We restricted our analyses to four regions of interest (ROIs) (see Fig. 2). Two regions were defined functionally with data from the functional localizer run, and two regions were defined based on template masks.

For the definition of functional ROIs, we first modeled the functional localizer data in a general linear model (GLM) with six predictors (1: object condition, 2: scrambled condition, 3–6: movement regressors). To assess object selectivity, we computed a *t*-contrast between the GLM weights for objects and scrambled objects. We defined two object-selective ROIs in LO and fusiform gyrus (FG) by intersecting the *t*-contrast maps from the functional localizer with anatomical masks (lateral/inferior occipital cortex and fusiform cortex, respectively, taken from WFUpickatlas for SPM), which were inverse normalized into individual subject space. Then, within the two anatomical masks and separately for each hemisphere, we selected the 250 most object-selective voxels from these *t*-contrasts (this selection offered comparable voxel counts with the early visual cortex ROI, see below).

As a retinotopically organized low-level region, we anatomically identified an early visual cortex (V1) ROI for each hemisphere by inverse-normalizing a probabilistic V1 mask (Wang et al. 2015) into individual- subject space (average ROI size: left 251 voxels, right 271 voxels). To assess whether typically positioned objects are more strongly linked to activations in scene-selective cortex, we also targeted the parahippocampal place area (PPA). To identify PPA, a probabilistic group mask for this region (Julian et al. 2012) was inverse-normalized into individual subject space (average ROI size: left 99 voxels, right 80 voxels).¹

All analyses were done for each hemisphere separately. The resulting data were averaged across hemispheres before statistical testing.

Multivariate analysis. Multivariate analyses were carried out with the CoSMoMVPA toolbox (Oosterhof et al. 2016) and were done for each participant separately. For each ROI, we extracted the responses for every trial from the realigned functional volumes after shifting the time course of volumes by 6 s to account for the hemodynamic delay. For every run separately, voxelwise responses were normalized by subtracting the mean response of the voxel across all trials.

Decoding analysis was performed with linear discriminant analysis classifiers in a leave-one-run-out scheme: classifiers were trained on data from all but one run and tested on the remaining run. This procedure was repeated until each run was left out once, and decoding accuracy was averaged across these repetitions. The analysis was done pairwise for all possible classifications between the six objects in the two locations. Subsequently, within each ROI, decoding accuracies for all classifications between typically positioned objects (e.g., hat in upper visual field vs. shoe in lower visual field) and atypically positioned objects (e.g., shoe in upper visual field vs. hat in lower visual field), respectively, were averaged. This yielded two average decoding accuracies for each ROI: one for decoding between typically positioned objects and one for decoding between atypically positioned objects.

To test for a more generic signature of regularity in object locations, we directly decoded typical vs. atypical positioning, independently of the object that was shown. Notably, in this analysis classifiers could not utilize object information but could only rely on regularity information that generalized across objects. For this analysis, all trials where the objects were positioned typically or atypically, respectively, were treated equally. As above, classifiers were trained and tested in a leave-one-run-out scheme.

Connectivity analysis. To investigate how positional regularity influences information propagation in visual cortex, we performed an interregion connectivity analysis. First, as for the multivariate analysis, we extracted voxelwise responses for each ROI. We extracted trialwise responses from the realigned functional volumes after shifting the time course of volumes by 6 s. For every run separately, voxelwise responses were normalized by subtracting the mean response of the voxel across all trials. Second, responses were averaged across all voxels belonging to each ROI, so that for each ROI one activation value was available for each trial. Third, we sorted these activation values by object positioning: one subset contained all trials with typically positioned objects. This procedure yielded two vectors of activations values, forming two "time series" of activation:

¹ As no functional data were available for localizing PPA in individual participants, analyses in PPA might have been less sensitive than analyses in the functionally localized object-selective ROIs.

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one time series for typically positioned objects and another for atypically positioned objects.

Finally, functional connectivity was computed separately for typically and atypically positioned objects. For this we correlated the time series of all ROIs in a pairwise fashion. The rationale is that when two regions are more strongly connected their activation time series should correlate more than when the regions are weakly connected. In this analysis, 12 connectivity values were obtained for every participant (i.e., 6 ROI combinations, separately for typically and atypically positioned objects). All individual participant correlations were Fisher transformed before statistical analysis.

Statistical testing. Differences between typically and atypically positioned objects were assessed with paired, one-sided *t*-tests, with a significance threshold of $\alpha = 0.05$. For each analysis, *t*-tests were Bonferroni corrected for the number of tests performed (either across ROIs or ROI-to-ROI connections). We report both uncorrected and corrected *P* values.

RESULTS

Positional regularities boost object decoding in LO. For each ROI, we carried out multivariate analysis by performing pairwise linear discriminant analysis decoding for all combinations of the 12 conditions (i.e., 6 objects in 2 locations) and subsequently averaging the results of different subsets of these pairwise analyses.

When all available pairwise decoding results were averaged, above-chance decoding was found in all ROIs (all t[16] > 3.48, P < 0.0015, $P_{corr} < 0.006$), suggesting that response patterns in all ROIs contained reliable information about the different experimental conditions.

To test the key prediction that typically positioned objects are processed more efficiently than atypically positioned objects, we compared decoding performance for all classifications within typically and within atypically positioned objects, respectively. Crucially, we observed enhanced decoding for typically positioned objects in LO (t[16] = 2.62, P = 0.009, $P_{corr} = 0.037$), whereas no differences were found in the other ROIs (all t[16] < 0.71, P > 0.24, $P_{corr} > 0.98$) (Fig. 2). These results show that in LO object information can be more successfully retrieved for typically positioned objects, suggesting that LO representations are tuned to typical visual field locations.

In a two-way regularity classification analysis, we additionally decoded between typical and atypical positioning irrespective of the object shown. This direct decoding of regularity yielded close-to-chance accuracies in all ROIs (V1: 49.7%, LO: 50.3%, FG: 49.6%, PPA: 49.2%), none of which exceeded chance level (all *t*[16] < 0.70, P > 0.12, $P_{corr} > 0.49$). These results suggest that the effect of typical positioning in LO reflects enhanced object processing rather than a more unspecific difference between typically and atypically positioned objects (e.g., a generic signature of stimulus familiarity).

Positional regularities increase connectivity in object-processing channels. To test whether the processing of typically positioned objects is related to a facilitation of interregion functional connectivity, we correlated the response fluctuations for each pairwise combination of ROIs separately for typically and atypically positioned objects. When objects were positioned in their typical locations, connectivity was qualitatively higher in all regions. Notably, statistical testing revealed a significant increase in connectivity between V1 and LO when objects were positioned typically rather than atypically (t[16] = 3.12, P = 0.003, $P_{corr} = 0.020$) (Fig. 3). A similar, trending effect was observed for connectivity between LO and PPA (t[16] = 2.61, P = 0.010, $P_{corr} = 0.057$). No connectivity modulations were found for the other comparisons (all t[16] < 1.73, P > 0.05, $P_{corr} > 0.31$). This finding suggests that the facilitated processing of typically positioned objects can be linked to an increase in functional coupling along the visual hierarchy, most prominently between V1 and object-selective LO.

DISCUSSION

Here we show that typical visual field locations enhance representations in object-selective processing channels of the occipital cortex. Using multivariate decoding, we demonstrate that object information can be more accurately retrieved from LO when the object is positioned in its typical retinotopic location. This facilitated readout of object information may reflect a more efficient representational format for typically positioned objects. Results from a functional connectivity analysis indicate that typical positioning also enhances coupling between visual areas. Most prominently, V1 and LO were more strongly connected when the object was positioned typically. This coupling may streamline information flow between these regions, where retinotopic feature information from V1 is efficiently routed to object representations in LO.² Together, these findings provide evidence for a location-specific tuning in visual object processing that is shaped by the spatial statistics of our everyday environments.

Our results highlight location-specific coding as an organizational principle for object information. This principle may shape the representation of various types of visual input (Kaiser and Haselhuhn 2017). For example, previous fMRI studies on face part coding have demonstrated that cortical representations for face parts are strongest when the parts appear in their typical visual field locations (Chan et al. 2010; de Haas et al. 2016). Using approaches similar to our study, these investigations demonstrated that typical retinotopic locations facilitate multivariate decoding of face parts (e.g., eyes are best represented in the upper visual field), predominantly from response patterns in lateral/inferior occipital regions. This convergence of results suggests that experience with typical retinotopic locations can shape visual representations in different domains.

Our effects emerged in lateral occipital regions rather than in more anterior areas of the fusiform or parahippocampal cortex. This might be because processing in lateral occipital regions is both object specific and still bound to retinotopic locations. In contrast to regions further up the processing hierarchy that are more location tolerant, this makes LO particularly sensitive to be shaped by extensive experience with typical object visual field locations. This notion is consistent with previous electrophysiological results, where benefits of typical positioning emerged within the first 150 ms of processing (Issa and DiCarlo 2012; Kaiser et al. 2018), compatible with a modulation of feedforward processing in LO.

 $^{^2}$ Whether the increased interregion connectivity indeed reflects an increased information transfer between regions must be explicitly shown in future studies. On the basis of the present data, alternative explanations based on shared variations in signal-to-noise characteristics across regions cannot be conclusively refuted.

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The enhanced cortical processing of typically positioned objects may be a valuable mechanism for boosting object perception. Recently, we have shown that typical positioning in the visual field facilitates an object's access to visual awareness (Kaiser and Cichy 2018), suggesting that their enhanced cortical representation allows typically positioned objects to compete more efficiently in interocular suppression (Cohen et al. 2015). This advantage in competing for cortical representation may be particularly beneficial in natural environments, where large numbers of objects challenge the brain's limited ability to process multiple stimuli concurrently. As a strategy to reduce resource overlap in multiple-object coding, the brain may exploit regularity structures in natural scenes (Torralba et al. 2006; Wolfe et al. 2011). Our results highlight one facet of incorporating such regularity structures: the brain may partly separate the processing of different objects into retinotopically tuned channels. Such channels can streamline the processing across retinotopic populations in early visual and object-selective populations (as evidenced by the increase in V1-LO connectivity) and may potentially support the construction of coherent scene representations (as evidenced by the increase in LO-PPA connectivity). Our findings could thus highlight a beneficial mechanism for efficient scene parsing, where object information is preferentially routed along retinotopically tuned processing channels.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

D.K. and R.M.C. conceived and designed research; D.K. performed experiments; D.K. analyzed data; D.K. and R.M.C. interpreted results of experiments; D.K. prepared figures; D.K. drafted manuscript; D.K. and R.M.C. edited and revised manuscript; D.K. and R.M.C. approved final version of manuscript.

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