Statistical learning of frequent distractor locations in visual search involves regional signal suppression in early visual cortex

Bei Zhang[1*], Ralph Weidner[2], Fredrik Allenmark[1], Sabine Bertleff[3], Gereon R. Fink[2,4], Zhuanghua Shi[1], Hermann J. Müller[1]

[1] General and Experimental Psychology, Ludwig-Maximilians-Universität München, 80802, München, Germany

[2] Cognitive Neuroscience, Institute of Neuroscience and Medicine (INM-3), Research Centre Jülich, 52428, Jülich, Germany

[3] Traffic Psychology and Acceptance, Institute for Automotive Engineering (ika), RWTH Aachen University, 52074, Aachen, Germany.

[4] Department of Neurology, University Hospital Cologne, Cologne University, 50937, Cologne, Germany

* Corresponding author

Correspondence concerning this article should be addressed to **Bei Zhang**, General and Experimental Psychology, Ludwig-Maximilians-Universität München, 80802, Munich, Germany. Email: beizhangbrain@gmail.com. Phone: +49 89 2180 16587. Fax: +49 89 2180 5211.

Running Title: Spatial Distractor Signal Suppression in Early Visual Cortex

Abstract

Observers can learn the locations where salient distractors appear frequently to reduce potential interference – an effect attributed to better suppression of distractors at frequent locations. But how distractor suppression is implemented in the visual cortex and within the frontoparietal attention networks remains unclear. We used fMRI and a regional distractor-location learning paradigm (Sauter et al. 2018, 2020) with two types of distractors defined in either the same (orientation) or a different (colour) dimension to the target to investigate this issue. fMRI results showed that BOLD signals in early visual cortex were significantly reduced for distractors (as well as targets) occurring at the frequent versus rare locations, mirroring behavioural patterns. This reduction was more robust with same-dimension distractors. Crucially, behavioural interference was correlated with distractor-evoked visual activity only for same- (but not different-) dimension distractors. Moreover, with different- (but not same-) dimension distractors, a colour-processing area within the fusiform gyrus was activated more when a distractor was present in the rare region versus being absent in the display and more with a distractor in the rare versus the frequent location. These results support statistical learning of frequent distractor locations involving regional suppression in the early visual cortex and point to differential neural mechanisms of distractor handling with different- versus same-dimension distractors.

Keywords: distractor suppression, early visual cortex, functional magnetic resonance imaging (fMRI), statistical learning

Introduction

In everyday life and experimental scenarios, such as, the additional-singleton paradigm (Theeuwes 1992), attention is often distracted or ‘captured’ by salient but goal-irrelevant stimuli (Folk and Remington 1998; Hickey et al. 2006; Forster and Lavie 2008). However, with repeated exposure and practice (Kelley and Yantis 2009; Zehetleitner et al. 2012), distractor interference can be reduced via attentional control (Bacon and Egeth 1994; Leber and Egeth 2006; Müller et al. 2009; Gaspelin et al. 2017).

Moreover, observers can learn not only to prioritize locations for attentional selection where task-relevant targets are regularly encountered (Shaw and Shaw 1977; Geng and Behrmann 2005), but also to deprioritize locations where salient but irrelevant distractors frequently appear (Goschy et al. 2014; Leber et al. 2016; Ferrante et al. 2018; Sauter et al. 2018; Wang and Theeuwes 2018). Typically, in the latter studies, a salient distractor occurs with a higher likelihood at one, ‘frequent’ display location/subregion relative to the remaining, ‘rare’ locations/subregions. The consistent finding is that, over time, search becomes less impacted by distractors that appear at frequent than at rare locations. This effect is attributable primarily to a proactive suppression of frequent distractor locations: oculomotor capture is less likely when distractors occur at frequent (vs. rare) locations (Di Caro et al. 2019; Wang et al. 2019a; Sauter et al. 2020); and for frequent locations, an anticipatory suppression-related event-related component (P_D) is observed (Wang et al. 2019b). However, behavioural evidence indicates that the way suppression of likely distractor locations is implemented is influenced by how distractors are defined relative to the target (Sauter et al. 2018; Allenmark et al. 2019; Failing et al. 2019; Zhang et al. 2019; Liesefeld and Müller 2021): if target and distractor are defined in the same dimension (e.g., target and distractor are both orientation-defined), suppression appears to work at a supra-dimensional level of ‘attentional-priority’ computation, impacting both distractor and target signals – as compared to a level of dimension-specific ‘feature-contrast’ computation when they are defined in a different dimension (orientation-defined target, colour-defined distractor), in which case suppression typically impacts only distractor signals.

While a consensus is emerging as to the loci of learnt distractor-location suppression within the architecture of search guidance, how suppression is neurally implemented remains largely unclear. It is well-established that the frontoparietal network, including the inferior/superior parietal lobe (IPL/SPL), is involved in attentional control of distractor interference (de Fockert et al. 2004; Krueger et al. 2007), and top-down control can instigate preparatory activity to minimize capture by expected distractors (Serences et al. 2004; Ruff and Driver 2006; Munneke et al. 2011). For instance, presenting trial-by-trial precues indicating the likely target side as well as, on critical trials, the appearance of a distractor in the opposite hemifield, Ruff and Driver (2006) observed enhanced occipital-cortex activation in the hemisphere contralateral to the upcoming distractor during the cue period, and this was associated with reduced search costs later on. Yet, concerning top-down effects on distractor coding in early visual cortex, the evidence is mixed. For instance, Bertleff et al. (2016) found precuing of the target region to diminish distractor interference through increased activity in medial parietal regions involved in controlling spatial attention, rather than by down-modulating distractor signals in early visual cortex. In contrast, manipulating the overall likelihood with which a distractor could occur anywhere in the display, Won et al. (2020) reported distractor signalling in visual cortex to be diminished when distractors occurred more frequently, along with reduced distractor interference.

Thus, using functional magnetic-resonance imaging (fMRI) in Sauter et al.'s (2018, 2020) regional distractor-location learning paradigm, the current study aimed to examine whether visual-cortex signals at learnt distractor locations would be down-modulated to reduce distractor interference and what specific role the frontoparietal attention networks play in distractor handling. In particular, given the dissociative (behavioural) learning effects between distractors defined in the same versus a different dimension to the target (see above), we examined for differences in the neural mechanisms mediating distractor-location learning between the two types of distractor.

Materials and Methods

Participants

Thirty-two volunteers (mean age: 27.47 years; age range: 20-45 years; 18 female) were recruited, twenty-four at the Forschungszentrum Jülich and eight at the LMU Munich. Functional MRI data from six participants were excluded from the MRI analysis due to data quality (e.g., distortion) issues and/or head movements. Based on the effect size of significant preparatory visual activation of distractor suppression in Serences et al. (2004), for a power of 0.80 and an alpha of 0.05 (G*Power analysis) (Erdfelder et al. 1996), the required sample size would have been 24. However, to attain enough power and take into account potential drop-outs, 32 subjects were recruited. All participants were right-handed and reported normal or corrected-to-normal vision, including normal colour vision, and none had been diagnosed with a neurological or psychiatric disorder. Participants received 15 Euro per hour for their service. The study protocol was approved by the ethics committees of the German Society of Psychology (DGPs) and, respectively, the Psychology Department of the LMU Munich. Written informed consent was obtained from all participants before the experiment.

Apparatus

In preparation for the fMRI experiment, participants received behavioural training outside the scanner to become familiarized with the task. The training was conducted in a sound-reduced and moderately lit test chamber. Stimuli were presented on a 24-inch Samsung SyncMaster 2233 (Samsung Electronics Co., Ltd., Seoul, South Korea) screen at a 1280×1024 pixels screen resolution and a 120-Hz refresh rate. Stimuli were generated by Psychophysics Toolbox Version 3 (PTB-3) (Brainard 1997) based on MATLAB R2019 (The MathWorks® Inc). Participants viewed the monitor from a distance of 60 cm (eye to screen), and distance and fixation position were controlled by a forehead-and-chin rest and an EyeLink 1000 eye-tracker device. In the experiment proper (in the scanner), stimuli were presented on a 30-inch LCD screen mounted behind the scanner 245 cm away from the head coil. The stimulus settings and the parameters for MRI data acquisition were the same at the Forschungszentrum Jülich and the LMU Munich.

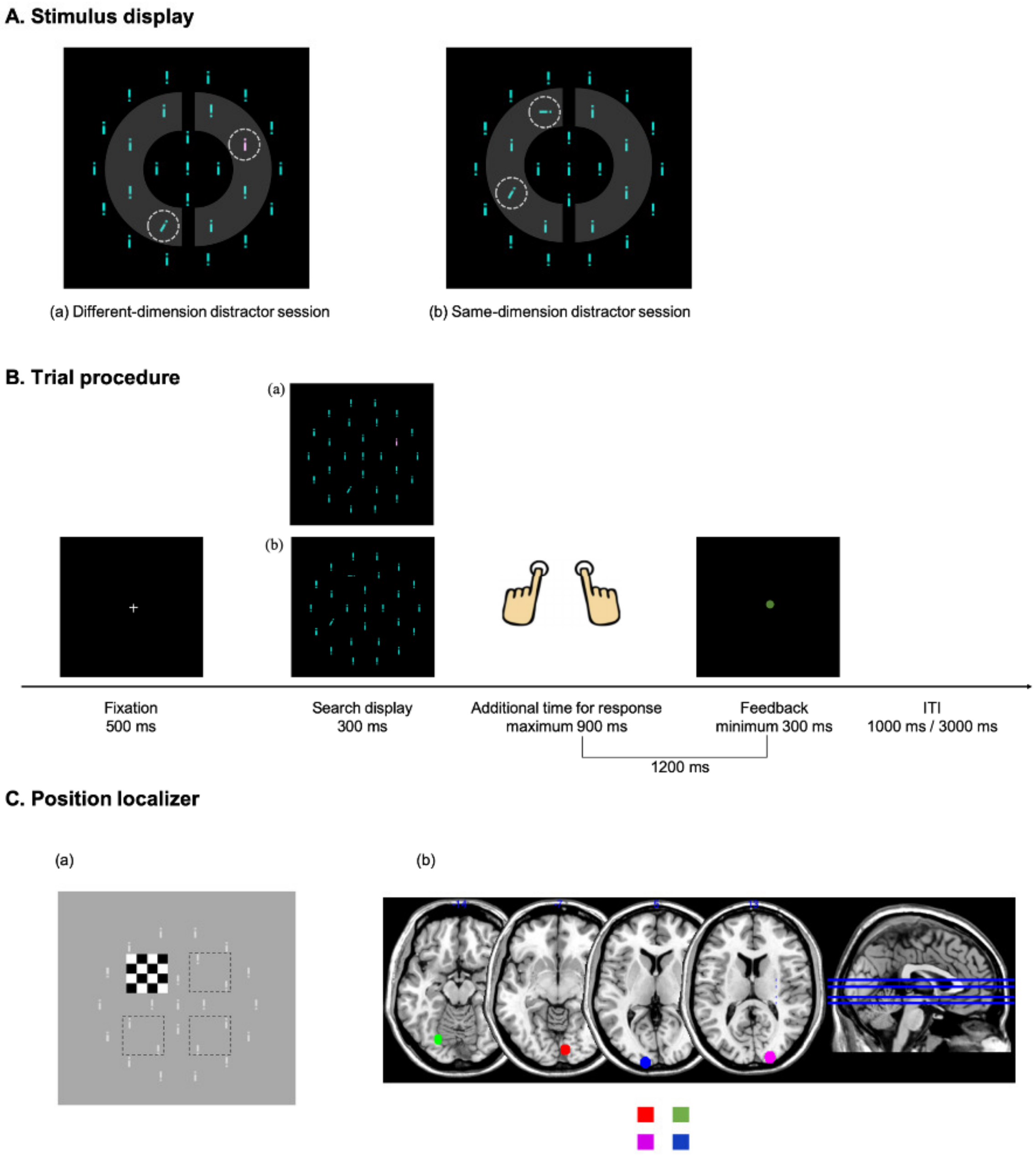
Visual Search Task

Stimuli

The stimuli used were essentially the same as in Sauter et al. (2018, 2020). The visual search displays consisted of twenty-seven turquoise (CIE [Yxy]: 29.6, 0.23, 0.37, measured on an equivalent display outside the scanner) upright or inverted ‘i’ shaped bars (0.10° of visual angle wide, 0.50° high; see search display in Figure 1A). One bar was positioned in the centre of the screen; the other bars were arranged on three imaginary concentric circles (around the centre) with radii of 1.25°, 2.50°, and 3.75° of visual angle containing 4, 8, and 14 items, respectively. The target was an item defined by a unique orientation difference compared to the vertically oriented nontarget items: it was tilted 30° to either the left or the right, with tilt direction randomized across trials. On a fraction of trials, one of the nontarget items, the singleton distractor (referred to as ‘distractor’ hereafter) was defined by either a different colour (red; CIE [Yxy]: 29.7, 0.30, 0.27; the *different-dimension distractor*) or a different orientation (a 90°-tilted, i.e., horizontally oriented ‘i’, the *same-dimension distractor*) compared to all the other items. The target and the singleton distractor only appeared at one of the eight positions on the middle circle, and they never appeared at the same location or adjacent to each other. The nontarget items on the outer and inner rings served to equate local feature contrast amongst the various singleton positions. All search items were presented on a black screen background (3.58 cd/m^2).

Note that the physical bottom-up saliency of the two types of distractors was determined in a pilot study (with different participants) in which the colour and, respectively, the orientation distractor were presented as response-relevant targets; that is, in separate blocks, they were the only singleton item in the display, to which participants had to make an eye movement as fast as possible. Following Zehetleitner et al. (2013), we took the (saccadic) reaction time to indicate the physical saliency of a given distractor stimulus. The results revealed that, while a similar proportion of first saccades was directed to the red and the horizontal target, 92% and 90%, respectively, the latencies of the first saccade were somewhat shorter for the red compared to the horizontal target, 166 ms vs. 184 ms, t(8.06) = -

2.93, p = .019, dz = 1.69. Thus, taking the two measures together: if anything, the physical saliency of the red singleton was somewhat higher than that of the horizontal singleton.


A. Stimulus display

(a) Different-dimension distractor session

(b) Same-dimension distractor session

B. Trial procedure

C. Position localizer

Figure 1. ***A.*** *Example of a search display in (a) the different-dimension distractor session: the search target is the 30-°tilted item (here, outlined by a white dashed circle, bottom-left of the middle ring), and the distractor is a red colour singleton (outlined by a white dashed circle, top-right of the middle ring); (b) the same-dimension distractor session: the search target is again the 30°-tilted item (outlined by a white dashed circle, bottom-left of the middle ring), and the distractor is a horizontal orientation*

singleton (outlined by a white dashed circle, top-left of the middle ring). Grey-shaded areas indicate the four potential target and distractor locations, and the left and right grey semicircles indicate the frequent and, respectively, rare distractor regions. Note that the dashed lines and grey areas are for illustration purposes only; they were not shown in the experiment. ***B.*** *Example of the trial procedure, described in more detail in the text.* ***C.*** *(a) Example of a checkerboard stimulus (here, top-left) serving as positional localizer for possible target and distractor locations; note that the black dashed-line squares and the grey 'i' stimuli are depicted here only for illustration purposes, i.e., they were not presented in the experiment. (b) The four VOIs induced by the position localizers are colour-coded, with a different colour for each of the respective localizer positions.*

Design

The two types of singleton distractor were introduced as a session factor in a within-group design: participants encountered only one type of distractor, either a different-dimension (i.e., colour) or a same-dimension (i.e., orientation) distractor, in either the first or the second experimental session (with order counterbalanced across participants); the two distractor sessions were conducted on consecutive days. In each session, the singleton distractor was presented in 60% of trials, the remaining 40% being distractor-absent trials. If a distractor was present, it appeared with 80% probability in one half of the search display (i.e., at one of the four positions on the middle semicircle on either the left or the right side – henceforth referred to as the 'frequent' distractor region) and with 20% probability in the other half (the 'rare' distractor region) (see Figure 1A). Within a given region, the distractor appeared equally often at each of the four possible locations, that is, with 20% frequency per location in the frequent region and 5% in the rare region. In contrast to the distractor, the target appeared with equal probability at each of the eight possible locations, that is, the frequency per location was the same for both regions.

Note that for each participant, the region in which the distractor appeared frequently was reversed between two experimental sessions (e.g., if the left half was frequent in session 1, the right half was frequent in session 2), to rule out carry-over of learning effects between the two types of distractors (in addition, the sessions were conducted on consecutive days, and the second session was preceded by 160 ‘unlearning’ trials with a spatially unbiased distribution of the distractor from the first session). The assignments of the frequent distractor region (left vs. right semicircle) and the type of distractor (same-dimension vs. different-dimension first) to the two sessions were counterbalanced across participants, thus avoiding possible confounds.

Further of note, the distractor type was manipulated as a within-subject factor in the present study: our participants had to learn the spatial distribution of one type of distractor first and then, after an unlearning phase, the opposite distribution with the other type of distractor. In previous studies (Sauter et al. 2018, 2019, 2020), we had used a between-subject design to avoid carry-over of acquired suppression strategies from one distractor type to the other. Based on finding dissociative target-location effects between same- and different-dimension distractors, we had proposed that statistical learning of distractor locations typically involves different levels of priority computation: the supra-dimensional priority map with same-dimension distractors (producing both a distractor- and a target-location effect) versus a level specific to the distractor-defining dimension with different-dimension distractors (producing only a distractor-location effect). Despite possible carry-over effects potentially weakening dissociative effects between the two distractor types, for the present fMRI study, we opted for a within-participant design to examine statistical distractor-learning effects within the same brain. Also, note that with different-dimension distractors, both dimension- and priority-map-based suppression are in principle feasible. Thus, even if observers start with a priority-map-based strategy (as indicated by them displaying a target-location effect), most will eventually revert to a dimension-based strategy (as indicated by observers losing the target-location, but not the distractor-location, effect) over extended task practice (Zhang et al. 2019).

Procedure

Each trial began with the presentation of a fixation cross in the middle of the screen for 500 ms, followed by the search display for a fixed duration of 300 ms (see Figure 1B). Participants were instructed to respond to the top vs. bottom position of the dot in the target ‘i’ by pressing the corresponding (left-/right-hand) response button (with stimulus-response assignment counterbalanced across participants) with two hands. Responses were to be made within 1200 ms of search display onset; otherwise, the trial was ‘timed out’. Following the response or time-out, feedback was provided in the shape of a coloured dot (0.4° of visual angle in diameter) presented in the screen centre: a green dot (RGB: 0, 255, 0) following a correct response and a red dot (RGB: 255, 0, 0) following an incorrect response or a time-out (i.e., too slow a response). A total time of 1200 ms was fixed for response and feedback: an additional maximum of 900 ms for response and a minimum of 300 ms for feedback (i.e., the feedback duration depended on the response time on a given trial). The intertrial interval (ITI) was 1000 ms or 3000 ms, randomly determined on each trial. Each experimental session consisted of 440 trials in total, subdivided into eight blocks of 55 trials. Five trials within each block presented a ‘search’ display of nontargets only (without a target or distractor item). On such trials, participants were to refrain from making a response (and they received ‘correct’ feedback for not responding); technically, these trials were treated as time-out trials. Breaks of 6 s duration separated the blocks. Before the MRI scanning, participants performed three training blocks outside the scanner (with the same type of distractor as in the first experimental session) to practice the task (i.e., finding the target ‘i’ and responding to the dot position within it) and start learning the biased (80%/20%) spatial distractor distribution (to increase the power for determining the brain regions involved in statistical distractor location learning in the scanner). Besides, before practicing the second session (also outside the scanner), participants completed four blocks (40 trials in each block) in which the singleton distractor was the same as in the first session but appeared equally often at two distractor regions (50%/50% distribution), to unlearn the spatial bias acquired for the first type of distractor. The number of unlearning trials was based on Ferrante et al. (2018), who found the distractor-location learning effect to be near-abolished within 144 ‘extinction’ trials.

In all experimental phases, participants were instructed to maintain fixation on the centre of the screen from the fixation cross’s appearance to the trial’s end. During practice (outside the scanner), compliance with this instruction was checked by monitoring participants’ eye movements using an eye-tracker device. In the scanner, eye movements could not be recorded, but participants reported that they had successfully maintained fixation on most of the trials. Note also that making eye movements would actually have been counterproductive given the brief (300-ms) display duration.

Position Localizer Task

To functionally identify the visual cortical representations corresponding to the various target and singleton distractor locations, a separate position localizer run was performed either before or after experimental session 1 (counterbalanced across participants). Participants were instructed to fixate the cross in the screen centre. They were then exposed to a contrast-reversing flickering checkerboard pattern that consisted of black and white mini-tiles (RGB: 0, 0, 0 and RGB: 255, 255, 255, respectively) flickering counter-phase at 8 Hz, with a height and width of 2°, which was presented successively in each quadrant of the visual field (see Figure 1C, left). Note that the localizer size covered two adjacent (target/distractor) locations in the search display. The localizer stimuli cycled through the four quadrants in clockwise direction, appearing at each location for 16 s with a 16 s break in-between for complete rounds, so that the localizer run took 4.27 min to complete.

MRI Measurement and Analysis

Data acquisition

MRI data were acquired on a 3.0 T TRIO Prisma MRI (Siemens, Erlangen, Germany) whole-body MRI system equipped with a 64-channel head matrix coil. Each participant was fitted with cushions in the head coil to help stabilize the head position. Participants viewed the monitor via an adjustable mirror positioned on top of the head coil. Functional images were obtained using a blood oxygenation level-dependent (BOLD) contrast sensitive gradient-echo echo-planar sequence. A total of 1355 images were acquired in each experimental session and, respectively, 244 images in each positional localizer run; scanning parameters: TR = 1200 ms, TE = 30 ms, flip angle = 70 degree, FOV = 192×192 mm, voxels size = 2 × 2 × 3 mm, slices number = 36, slice thickness = 3 mm. Structural MRI images (T1-weighted) were acquired from the sagittal plane using a three-dimensional magnetization-prepared rapid gradient-echo (MP-RAGE) pulse sequence; scanning parameters: TR =

1780 ms, TE = 2.51 ms, flip angle = 8 degree, FOV = 256 × 256 mm, voxel size = 0.9 × 0.9 × 0.9 mm, slice thickness = 0.9 mm.

Preprocessing

Functional-imaging data were processed with SPM12 (r7771) (Wellcome Centre for Human Neuroimaging, London, United Kingdom; https://www.fil.ion.ucl.ac.uk/spm/software/spm12) based on MATLAB R2019a. Functional images acquired in each experimental session were corrected for interslice time differences for every participant first. Next, the functional images from the main experiment and those from the position localizer functional images were corrected for head movement by affine registration in a two-pass procedure realigning individual functional images to their mean image. Participants who exhibited translation head motion of more than 3 mm or rotations of more than 3 degrees were excluded from further analysis. Each participant's mean image was then spatially normalized to a standard Montreal Neurological Institute (MNI) template using the 'unified segmentation' approach, and the resulting deformation field was applied to the individual functional images. The resulting images were smoothed with a 6-mm full width at half maximum (FWHM) Gaussian kernel to improve the signal-to-noise ratio and compensate for residual anatomical variations.

fMRI Analysis

Due to data quality issues (e.g., distortion) or large head movements during the visual search task, six out of the thirty-two participants were excluded from the functional MRI data analysis. To maximally use the available data, however, we included their good-quality behavioural and positional localizer data in the analysis.

Whole-brain analysis The first-level (individual-participant) analysis involved applying a general linear model (GLM), with the following regressors for each distractor-type session (i.e., the different- and the same-dimension distractor condition). There were three primary regressors: one coding (singleton) distractor-absent trials, one coding trials with a distractor appearing in the frequent region, and one coding trials with a distractor in the rare region. Also, the two manual-response conditions (left button press, right button press) were included as regressors to avoid a high implicit baseline (Monti 2011), along with an extra regressor for unused trials (trials with incorrect/missing responses). The hemodynamic response related to neural activity in each of the above conditions was modelled by the canonical hemodynamic response function and its first derivative, which can capture the late negative dip of empirical BOLD responses (Henson et al. 2002). Finally, six head-movement parameters were considered as covariates in the model to reduce potential confounding effects (Lund et al. 2005).

Based on the GLM, combining the two distractor-type conditions, we first calculated contrast images at the first level to examine the main effects of distractor interference in the frequent region (distractor frequent > distractor absent, and vice versa), of distractor interference in the rare region (distractor rare > distractor absent, and vice versa), and of distractor-location learning (distractor in the rare region > distractor in the frequent region, and vice versa). In addition, the interaction contrasts between each of the above effects and the two distractor types were also defined and calculated (e.g., the distractor-location learning × distractor-type interaction was calculated by comparing distractors in the frequent region vs. rare region for the different- vs. same-dimension distractor sessions). To test all the above effects for the two distractor types, differential contrast images were also calculated separately for each distractor-type condition (i.e., different-dimension distractor session: distractor in rare > frequent region, distractor in frequent > rare region; same-dimension distractor session: distractor in rare > frequent region, distractor in frequent > rare region). All individual contrast images were then taken to the group level and subjected to a one-sample t-test, with family-wise error (FWE) corrected at a cluster-defining voxel-level cut-off of $p < 0.05$ and a minimum cluster size of 5 contiguous voxels.

Volume-of-Interest (VOI) analysis Functional MRI data of the localizer stimuli (checkerboards) at the four positions corresponding to potential target/distractor positions were used to examine localized activation in early visual cortex (see Figure 1C). The first-level GLM model was estimated with four experimental regressors defined by the onset of visual stimulation at each of the four localizer positions, with a duration of 16 s. The hemodynamic response was again modelled by the canonical hemodynamic response function and its first derivative. Six head-movement parameters were included as covariates. Four individual contrast images were calculated by comparing each positional regressor with the other three regressors and then taken to the group level for one-sample t-tests at an extent threshold of $p < 0.05$ (FWE corrected) with a minimum cluster size of 5 contiguous voxels (Bertleff et al. 2016). The significantly activated clusters thus obtained turned out somewhat different in volume size for the four position localizers. To ensure identical volume sizes for the subsequent VOI analysis, the four localizer VOIs were defined as spheres, with the centre point of each sphere placed on the peak coordinate defined by the group maximum t value within the respective cluster and with a radius of 7 mm (see Figure 1C, right). The spheres' radius was determined based on the minimum volume size – consisting of 116 voxels – identified in a group-level analysis of the four localizer positions. In the next step, another set of first-level GLM models were estimated with four experimental regressors representing a *distractor* occurring at one of the localizer positions, separately for two distractor-type sessions. The hemodynamic response related to neural activity in the four distractor regressors was modelled by the canonical hemodynamic response function and its first derivative, with six head-movement parameters considered covariates in the model. Analogous GLM models were developed with four regressors representing a *target* appearing at one of the four positions, separately for two distractor-type sessions. Percent signal change (beta values) of each experimental regressor was extracted within the corresponding localizer VOIs for further examination (e.g., percent signal change for distractors appearing in the top-left positions was extracted within the VOI identified by the checkerboard localizer presented in the top-left quadrant).

Note that to examine for (and rule out) potential positional 'repetition-suppression' effects (Kristjánsson et al. 2007; Larson and Smith 2012) – that is, reduced neural activity generated by the second of two successive (in our case: distractor) stimuli appearing at the same location (in either the frequent or the rare distractor region) – we performed additional VOI (along with behavioural) analyses on the sub-sample of trials that *excluded* those trials on which the singleton distractor appeared at the same location as on the preceding trial (Supplementary-Materials Section S1). Furthermore, to more closely examine the visual activation patterns evoked by distractors (in the frequent vs. rare regions) in specific early retinotopic-cortex areas, we re-defined the four VOIs separately for each of the areas V1 to V4 – based on the early visual-cortex atlases from Wang et al.'s (2015) probabilistic visual-topography maps, adopting a 25% probability threshold combined across the left and right hemispheres and the dorsal and ventral areas. We then extracted the percent signal-change scores for each distractor regressor/location within the corresponding VOIs for each area V1–V4 (for details, see Supplementary-Materials Section S2).

Results

Behavioural Results

The error rate was overall higher in the same-dimension than in the different-dimension session (15.72% vs. 13.53%); and, compared to the distractor-absent baseline (12.68%), more errors were made on trials in which a distractor was present (in the rare region: 16.47%; in the frequent region, 15.78%). Further, the increased error rates caused by distractor presence were more marked with same- than with different-dimension distractors (see Figure 2a). This effect pattern was confirmed by a repeated-measures ANOVA with the factors Distractor (absent, present in the frequent region, present in the rare region) and Distractor Type (different-dimension distractor, same-dimension distractor), which revealed all effects to be significant: Distractor, $F(2, 62) = 15.01$, $p < .001$, $\eta_p^2 = .047$; Distractor Type, $F(1, 31) = 5.74$, $p = .023$, $\eta_p^2 = .031$; interaction, $F(2, 62) = 9.68$, $p < .001$, $\eta_p^2 = .027$.

This (interactive) effect pattern was mirrored in the RT results (Figure 2a), effectively ruling out differential speed-accuracy trade-offs. An analogous ANOVA of the mean RTs again revealed all effects to be significant: Distractor, $F(2, 62) = 115.97$, $p < .001$, $\eta_p^2 = .082$; Distractor Type, $F(1, 31) = 62.17$, $p < .001$, $\eta_p^2 = .132$; interaction, $F(2, 62) = 58.47$, $p < .001$, $\eta_p^2 = .055$. Response speed was overall slower with same- than with different-dimension distractors, and the presence of a distractor slowed RTs to the target (relative to the distractor-absent baseline). This slowing was more marked in the same- than in the different-dimension distractor condition; as depicted in Figure 2b, the interference effect was only some 8 ms with different-dimension distractors, $t(31) = 2.88$, $p = .007$, but ten times as high (81 ms) with same-dimension distractors, $t(31) = 13.9$, $p < .001$. This differential interference effect was significant ($t(31) = -12.1$, $p < .001$). Thus, even though the two types of distractor were balanced in terms of bottom-up saliency (see Method), same-dimension distractors caused considerably more RT interference than different-dimension distractors – replicating previous findings (e.g., Sauter et al. 2018, 2019; Liesefeld and Müller 2021).

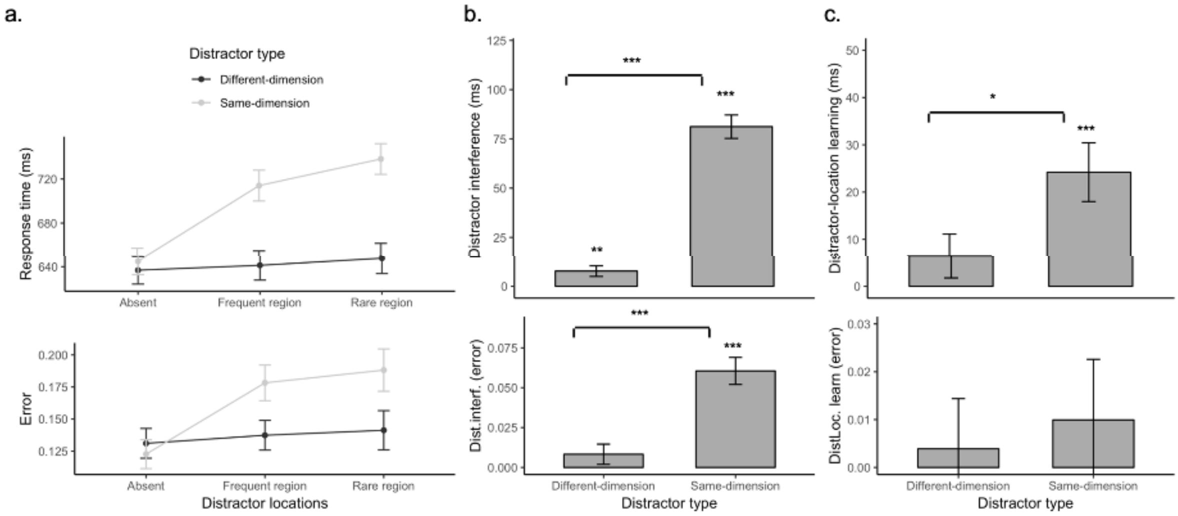


Figure 2. *Response times (RTs; upper panels) and error rates (lower panels) for the two distractor types. (a) Averaged RTs and error rates in the three distractor conditions, separately for the different- and same-dimension distractor sessions. (b) Distractor-interference effect, calculated as the difference between distractor-present and -absent trials, separately for the different- and same-dimension distractors. (c) Distractor-location learning effect, calculated as the difference between trials with a distractor presented in the rare vs. frequent region, separately for the different- and same-dimension distractors. Error bars depict 95% confidence intervals. * denotes $p < .05$, ** $p < .01$, *** $p < .001$.*

To quantify the effect of distractor-location learning, we calculated the RT difference between trials with a distractor presented in the rare region versus trials with a distractor presented in the frequent region. As depicted in Figure 2c, when a distractor appeared in the frequent region, RTs to the target were generally faster than with a distractor appearing in the rare region. Importantly, this difference was greater with same-dimension distractors, evidenced by a significant distractor-location effect in the same-dimension session (24-ms benefit, $t(31) = 3.96$, $p < .001$), but not in the different-dimension condition (6-ms benefit, $t(31) = 1.4$, $p = .17$). In any case, the larger (frequent- vs. rare-region) RT benefits obtained with same- than with different-dimension distractors (*t*(31) = -1.99, *p* = .05) closely replicate our previous findings (e.g., Sauter et al. 2018, 2019; Liesefeld and Müller 2021).

Of note, even though the target occurred with equal likelihood in both distractor regions, targets appearing at a location in the frequent region were responded to slower than targets in the rare region, the RT costs amounting to some 10 ms (combined across distractor-present and -absent trials) with different-dimension distractors (*t*(31) = 2.57, *p* = .015) and to 18 ms with same-dimension distractors (*t*(31) = 4.4, *p* < .001). Although the RT cost was about double the size in the same- versus the different-dimension condition, the difference was non-significant (*t*(31) = -1.21, *p* = .237). Thus, while statistical learning of distractor locations reduced the interference caused by distractors in the frequent region, this was associated with a cost: slowed processing of targets appearing in the frequent (distractor) region. Consistent with our previous behavioural studies, this cost effect was more marked, at least numerically, with same-dimension distractors. [In previous studies, there was either no cost with different-dimension distractors (e.g., Liesefeld and Müller 2021), or there was a cost initially, which, however, disappeared over extended task practice (i.e., 750 to 1,500 trials; Zhang et al. 2019) – indicative of a shift from priority-map- to dimension-based suppression.] Note that, even after excluding distractor-location repetition trials (on which the distractor occurred at the same location as on the preceding trial), the behavioural results essentially replicated the pattern of findings reported above (see Supplementary-Materials Section S1 and Figure S1).

VOI Results

Based on the human probabilistic cytoarchitectonic maps within the Anatomy Toolbox (Eickhoff et al. 2005), the group peak coordinates of the maximum *t*-values associated with each of the four flickering checkerboard localizers – that is, potential target/distractor positions – were localized to early visual cortex (V1 – V4; Figure 1C, right).

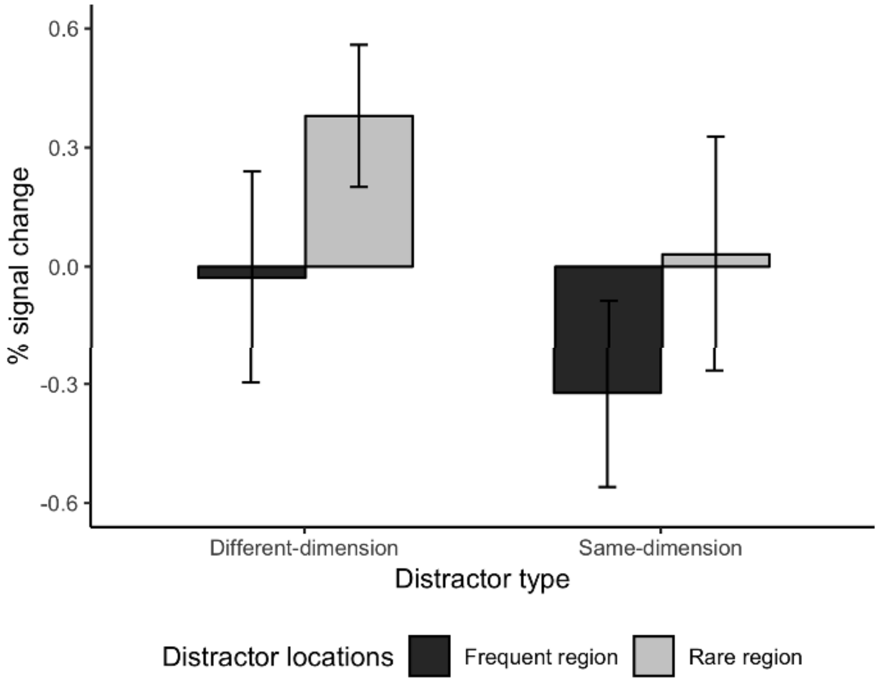


Figure 3. *Mean percent signal change (beta values) representing early visual-cortex activation by singleton distractors appearing in the frequent vs. the rare distractor region, separately for the different- and same-dimension distractor types. Error bars depict 95% confidence intervals.*

We first examined changes in the beta values representing activation at the specific localizer positions (VOIs) when the distractor appeared at a location in the frequent and, respectively, the rare region, for the two distractor types. To start with, we submitted the beta values to a three-way ANOVA with the within-subject factors Distractor Region (frequent region, rare region) and Distractor Type (different-, same-dimension distractor) and the between-subject factor Frequent Hemisphere (Group 1 with different-dimension distractors frequently appearing in the left region, i.e., the right VOIs, and same-dimension distractors frequently appearing in the right region, i.e., the left VOIs; Group 2 with the reversed frequent hemisphere relative to Group 1 for two distractor types). As the effect of the distractor-frequency manipulation did not differ between the two groups (non-significant main effect of Frequent Hemisphere, non-significant Frequent Hemisphere × Distractor Region or, respectively, Frequent Hemisphere × Distractor Type interactions, all $ps > .06$), we collapsed the beta values across the different assignments of the frequent distractor regions.

Figure 3 depicts the resulting beta values for distractor locations in the frequent and, respectively, rare distractor regions, separately for each distractor type. By visual inspection, and as confirmed by repeated-measures ANOVA of Distractor Type and Distractor Region, the beta values were overall lower for distractors appearing in the frequent versus the rare region (significant main effect of Distractor Region, $F(1, 25) = 5.19, p = .03, \eta_p^2 = .024$). This pattern is consistent with the idea that statistical learning of distractor locations is associated with stronger signal suppression in early visual areas coding frequent versus rare distractor locations. However, in contrast to the RT results, the beta values turned out little influenced by the factor Distractor Type (main effect, $F(1, 25) = 0.83, p = .37, \eta_p^2 = .017$); in particular, the effect of (frequent, rare) distractor region did not appear to be reduced in the different-, as compared to the same-, dimension distractor condition (non-significant Distractor Type × Distractor Region interaction, $F(1, 25) = 0.06, p = .81, \eta_p^2 = .0001$). However, as a weaker effect was expected from the RT pattern (see also Sauter et al. 2018, 2019; Liesefeld and Müller 2021), we conducted paired t-tests comparing the beta values between the frequent and rare distractor regions, separately for the two distractor types. These revealed the difference to be significant for the same-dimension condition (rare vs. frequent region: 0.031 vs. -0.322, $t(25) = 2.23, p = .04$), but not for the different-dimension condition (rare vs. frequent region: 0.38 vs. -0.028, $t(25) = 1.73, p = .10$). Thus, while early visual-cortex activation was generally reduced when a distractor occurred in the frequent (vs. the rare) region, this effect was statistically robust (i.e., consistent across participants) only with same-dimension distractors, but not with different-dimension distractors (in line with participants adopting more heterogeneous strategies of distractor handling with the latter distractor type; cf. Zhang et al. 2019).

Given this, we further examined whether early visual-cortex modulations play a role in generating the behavioural effects. To this end, we analysed the relationships between the beta values and the RT interference caused by distractors occurring in the frequent and, respectively, the rare region, for each of the two distractor-type conditions. The correlations are illustrated in Figure 4. As can be seen, the beta values were predictive of RT-interference magnitude only in the same-dimension condition (frequent region: $r = .51$ [95% confidence interval: .15 – .75], $p = .008$, $BF = 7.783$; rare region: $r = .40$ [CI: .01 – .68], $p = .04$, $BF = 2.254$), but not the different-dimension condition (frequent region: $r = -.19$ [CI: -.54 – .21], $p = .33$, $BF = 0.628$; rare region: $r = -.20$ [CI: -.55 – .20], $p = .31$, $BF = 0.647$). This pattern points to a critical role of the early visual signal modulations for behavioural distractor interference only with same-dimension distractors; in contrast, some other, or additional, distractor-handling mechanism must come into play with different-dimension distractors (see whole-brain results below).

Note that, even after excluding distractor-location repetition trials (with repetitions being more likely for the frequent vs. the rare region), the results of the VOI and correlation analyses remain consistent with the findings reported above: early visual-cortex activation was significantly reduced for distractors occurring at locations in the frequent versus the rare region $F(1, 25) = 4.98$, $p = .03$, and behavioural interference was correlated with distractor-evoked visual activity only for same- (but not different-) dimension distractors (frequent region: $r = .52$, $p = .006$, $BF = 9.61$; rare region: $r = .38$, $p = .05$, $BF = 2.00$) (see Supplementary-Materials Section S1, Figure S2 and S3). Moreover, this pattern was consistently observed in the various retinotopic visual-cortex areas V1–V3 (see Supplementary-Materials Section S2, Figures S4 and S5).

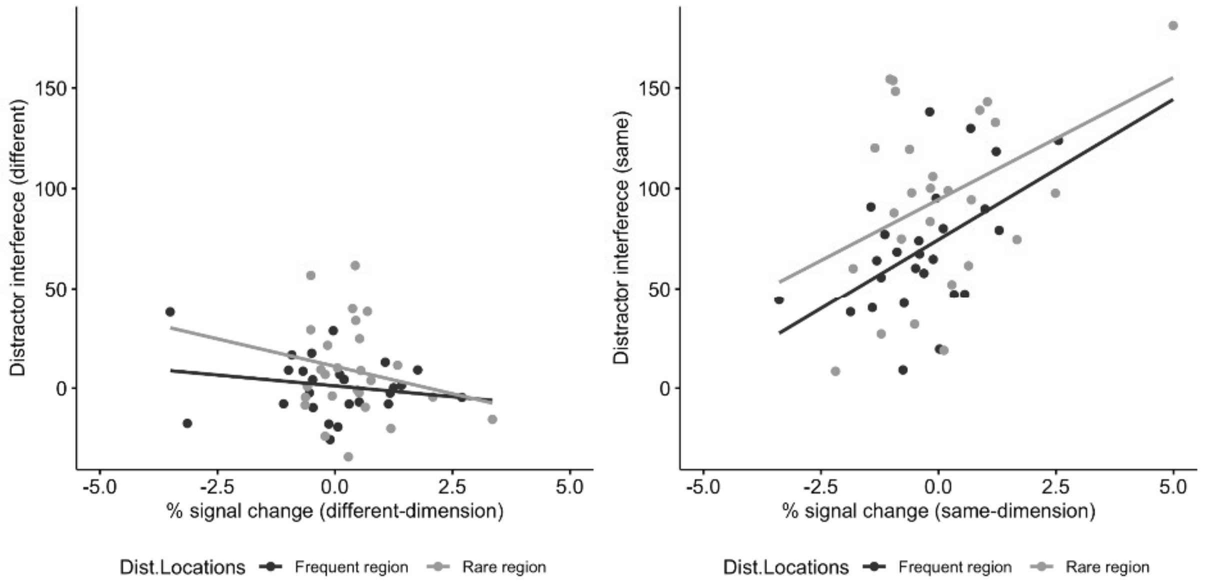


Figure 4. *Correlation between behavioural distractor interference effect (RTs) in the frequent region and the rare region with the respective percent signal changes for distractors in the frequent and rare region, separately for the different- (left panel) and the same-dimension distractor types (right panel).*

Of note, the beta values were not only reduced when a distractor occurred in the frequent (vs. the rare) region (see above), but also when a target appeared there (significant main effect of Target Location in frequent vs. rare region: $F(1, 25) = 5.56$, $p = .027$, $\eta_p^2 = .02$). Although the beta values were numerically more negative overall in the same-dimension condition, the main effect of Distractor Type was non-significant ($F(1, 25) = 0.74$, $p = .40$, $\eta_p^2 = .015$). Finally, the reduction was comparable between the two distractor-type conditions (Target-Location × Distractor-Type interaction: $F(1, 25) = 0.06$, $p = .81$, $\eta_p^2 = .00001$), even though it tended to be more robust in the same-dimension (rare vs. frequent region: 0.054 vs. -0.27, $t(25) = -2.25$, $p = .033$) than in the different-dimension distractor condition (0.382 vs. 0.004, $t(25) = -1.73$, $p = .10$). Even though the beta values for targets in the frequent region were somewhat higher than those for distractors, for both distractor types, this pattern is similar to the distractor-location effects (see above), and so likely reflecting the same mechanisms underlying statistical distractor-location learning.

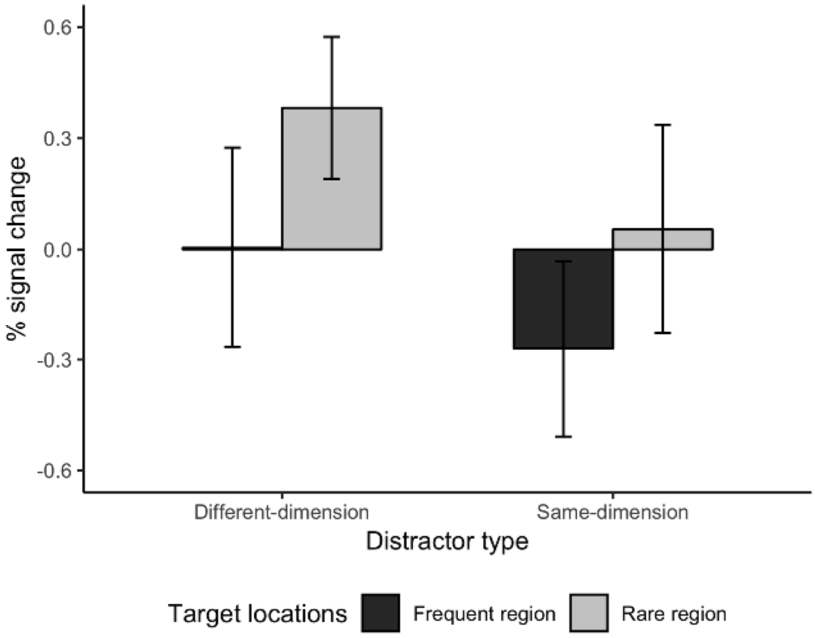


Figure 5. *Mean percent signal change (beta values) representing early visual-cortex activation by the target appearing in the frequent vs. the rare distractor region, separately for the different- and same-dimension distractor types. Error bars depict 95% confidence intervals.*

Whole-brain Results

Whole-brain results showed that the presence of a singleton distractor defined in a *different* dimension (namely, colour) relative to the (orientation-defined) target in the *rare* region invoked a BOLD response in left fusiform gyrus (FWE corrected, p < .05, see Figure 6 and Table 1), and the presence of a different-dimension singleton distractor in the *frequent* region invoked activation in precuneus (FWE corrected, p < .05, see Figure 6 and Table 1). Furthermore, compared to a (different-dimension) distractor appearing in the frequent region, a distractor in the rare region induced more robust activation in the left superior parietal lobule and the fusiform gyrus (FWE corrected, p < .05, see Table 1, Figure 6). In contrast to the different-dimension distractor, the presence of a distractor defined in the same dimension as the target in the frequent region was associated with more robust activation in the left superior parietal lobule, and distractor presence in the rare region appeared more associated with the right superior parietal lobule, typically in angular gyrus (FWE corrected, $p < .05$, see Table 1,

Figure 6). Critically, however, no significant clusters were found when comparing (same-dimension) distractors in the rare versus the frequent region.

Importantly, right middle frontal gyrus and bilateral superior parietal lobule were significantly activated when testing for the interaction between distractor interference in the frequent region (i.e., the factor 'distractor in the frequent region vs. distractor absent') and experimental session (i.e., the factor 'different- vs. the same-dimension distractor condition'), whereas there was no significant interaction between distractor interference in the rare region and experimental session. This pattern suggests that different neural mechanisms came into play to handle singleton distractors appearing in the frequent region with different-dimension (colour-defined) as compared to same-dimension (orientation-defined) distractors.

Table 1. Activations associated with contrasts defined by (A) Distractor in the rare region > Distractor absent; (B) Distractor in the frequent region > Distractor absent; (C) Distractor in the rare region > frequent region; and (D) Distractor in the frequent region > rare region, separately for the different- and same-dimension distractor types, as well as the interaction between two sessions.

Contrast	*Side*	*Region*	*Cluster size*	*Cluster peak coordinates*	*T value*
Different-dimension session					
(A) Distractor in the rare region > absent	L	Fusiform gyrus	41	-33, -57, -9	5.13
(B) Distractor in the frequent region > absent	L	Precuneus	47	-9, -54, 18	4.63
(C) Distractor in the rare region > frequent region	L	Fusiform gyrus	63	-33, -54, -6	5.13
	L	Superior parietal lobule	86	-21, -63, 33	4.82
(D) Distractor in the frequent region > rare region	No significant brain activation				
Same-dimension session					
(A) Distractor in the rare region > absent	R	Superior parietal lobule/Angular	38	27, -57, 51	4.78
(B) Distractor in the frequent region > absent	L	Superior parietal lobule	101	-18, -72, 45	5.36
(C) Distractor in the rare region > frequent region	No significant brain activation				
(D) Distractor in the frequent region > rare region	No significant brain activation				
Interaction between two sessions					
(A) Distractor in the rare region > absent	No significant brain activation				
(B) Distractor in the frequent region > absent	L	Superior parietal lobule	150	-15, -72, 45	5.51
	R	Middle frontal gyrus	66	36, 0, 51	5.02

	R	Superior parietal lobule	33	21, -57, 54	5.00

Coordinates (x, y, z) were defined in MNI space. Activations were all significant at $p < 0.05$ (FWE corrected), at the cluster level (based on $p < 0.001$, at the voxel level).

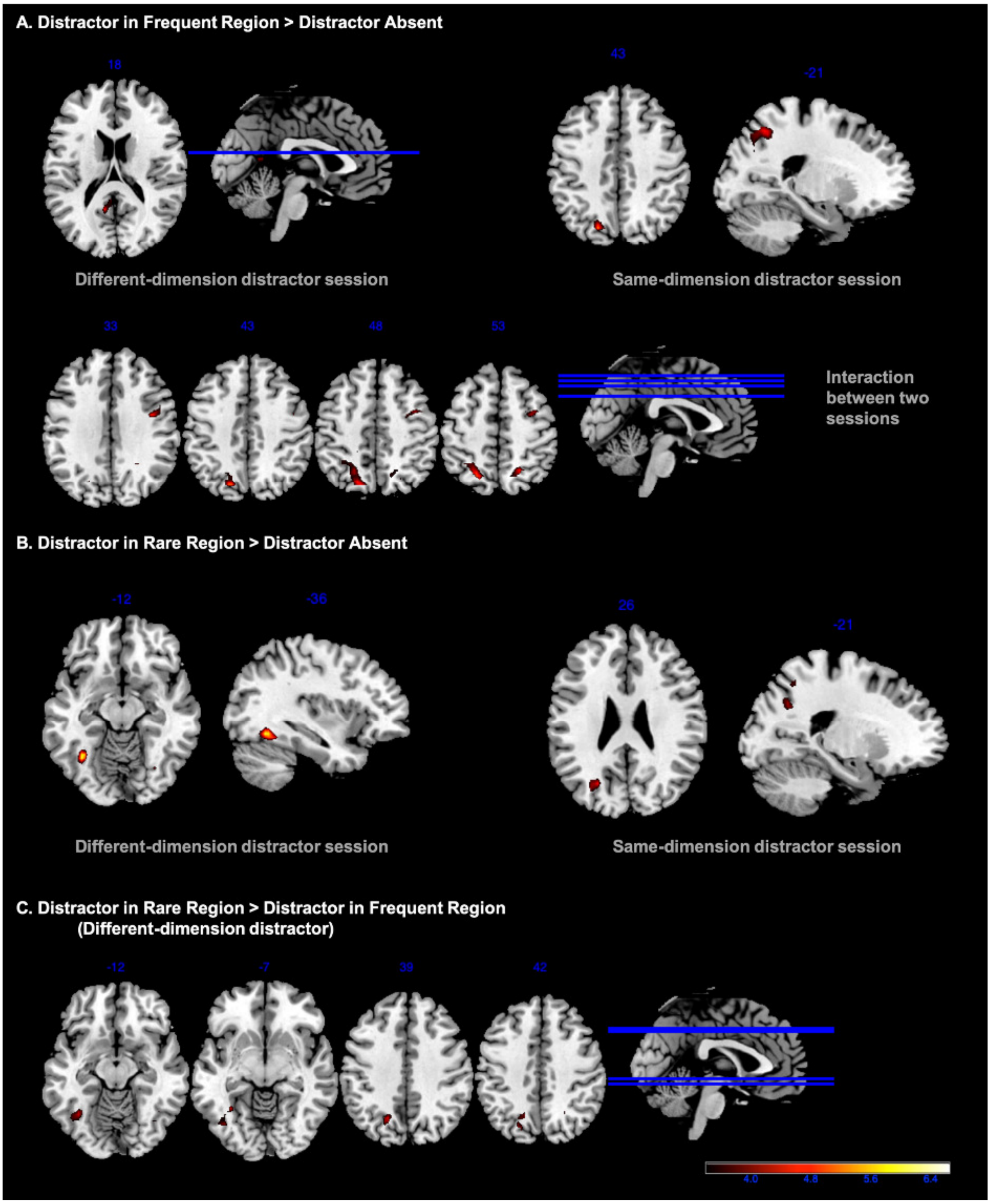


Figure 6. ***A.*** *Whole-brain activation patterns coloured in red-yellow reflect invoked BOLD signals driven mainly by the presence of salient distractors in the frequent region, for the distractor defined in a different dimension (i.e., colour) relative to the search-relevant target (top-left, different-dimension session), and for the distractor defined in the same dimension (i.e., orientation) as the target (top-right, same-dimension session), as well as the interaction difference between two distractor types (bottom), at* $p < .05$*, family-wise error- (FWE-) corrected at the cluster level.* ***B.*** *Whole-brain activation patterns coloured in red-yellow reflect invoked BOLD signals driven mainly by the presence of salient distractors in the rare region, for different-dimension distractors (left) and same-dimension distractors (right) at* $p < .05$*, FWE-corrected at the cluster level.* ***C.*** *Whole-brain activation patterns coloured in red-yellow depict increased BOLD signals when different-dimension (i.e., colour-defined) distractors appeared in the rare as compared to the frequent region, at* $p < .05$*, FWE-corrected at the cluster level.*

Order Factor

To check whether the counterbalanced session order influenced the observed pattern of results, we performed an additional analysis by separating the participants into two groups: participants who performed the different-dimension distractor session first and those performing the same-dimension distractor session first (hereafter referred to termed as ‘different-first’ and, respectively ‘same-first’ groups; we then examined the distractor-location learning effect separately for these two groups, for both the behavioural and the fMRI data.

Behaviourally, a mixed-design ANOVA of the distractor-interference effects (distractor-present minus distractor-absent conditions), with the within-subject factor Distractor type (different-dimension vs. same-dimension distractor) and the between-subject factor Session order (different-first group vs. same-first group), revealed significant main effects of both Distractor type, $F(1, 30) = 189.57$, $p < .001$, and Session order, $F(1, 30) = 9.50$, $p = .004$, the latter being due to participants who performed the different-dimension condition first showing overall larger distractor interference than participants who performed the same-dimension condition first. The Distractor-type × Session-order interaction was also significant, $F(1, 30) = 9.89$, $p = .004$: post-hoc analysis revealed that while the interference effect did not differ between the two groups for different-dimension distractors ($t(30) = 0.33$, $p = .75$), it was significantly larger for the different-first than for the same-first group for same-dimension distractors ($t(30) = 3.53$, $p = .001$) (see Figure S6a). That is, handling (the more difficult to handle) same-dimension distractors is made harder after having learnt to deal with different-dimension distractors (compared to learning to deal with same-dimension distractors 'from scratch'), perhaps because participants find it harder to discover, or switch to, the optimal control strategy for handling same-dimension distractors; by contrast, learning to handle (the easier to handle) different-dimension distractors is not similarly compromised by having first learnt to deal with same-dimension distractors. Despite this effect of Session order on the overall interference generated by same-dimension-distractors, the *distractor-location learning effect* itself was little affected by this factor (see Figure S6b): a mixed-design ANOVA of the distractor-location learning effect (RT distractor in rare region minus RT distractor in frequent region), with the factors Distractor type and Session order revealed neither the Session-order main effect nor the Session-order × Distractor-type interaction to be significant (*p*s > .46).

The latter tallies with a re-analysis of the VOI functional-imaging data (see Figure S7): an analogous, Distractor-type × Session-order ANOVA of the beta-value gradient (beta-value rare region minus beta-value frequent region) revealed no significant (main or interaction) effects involving the factor Session order (*p*s > .51). Accordingly, the (counterbalanced) order of the two distractor-type conditions did not alter the observed pattern of reduced early visual-cortex activation, along with the reduced behavioural interference, for distractors appearing in the frequent versus the rare region, for either distractor type.

Discussion

Combining fMRI with a statistical distractor-location learning paradigm, we manipulated whether the singleton distractor was defined within the same dimension (orientation) or a different dimension (colour) relative to the target. The behavioural results replicated previous findings: interference by a salient distractor was reduced when it appeared within the frequent, versus the rare, distractor region – evidencing adaptation of attentional guidance to the biased distractor distribution. Further, despite being equally (if not more) salient (see Methods), different-dimension distractors produced substantially less interference than same-dimension distractors, associated with a less marked frequent versus rare distractor-region effect. These behavioural effects were, to some extent, reflected in the fMRI results. BOLD signals in the early visual cortex were reduced for distractors occurring in the frequent versus rare region. [Importantly, this reduction was observed even when distractor-location repetition trials (which were more likely in the frequent region) were excluded from the analysis; this rules out a 'repetition-suppression' account of the gradient, according to which the gradient arises due to the a higher incidence of 'repetition-suppression' trials in the frequent region.] While the reduction was numerically similar in the two distractor conditions, it was more robust with same-dimension distractors, and crucially, behavioural interference correlated with distractor-evoked VOI activity exclusively for this type of distractor. A similar activity pattern was evident when (spatially unbiased) targets appeared in the frequent versus rare distractor region, mirroring a similar effect in the RTs. Whole-brain analysis revealed the involvement of parietal parts of the fronto-parietal attention network in distractor handling. Importantly, though, in the different- (but not same-) dimension distractor condition, fusiform gyrus and superior parietal lobule were activated more with a distractor occurring in the rare versus frequent region. This suggests that distractors defined in a different dimension to the target (namely, colour) are, in crucial respects, handled differently by the brain to same-dimension distractors (defined by orientation).

The behavioural signature of statistical distractor-location learning has been well documented recently: RT interference is reduced for distractors occurring at frequent versus rare locations, and this is associated with reduced capture of the first saccade by distractors at frequent locations (Di Caro et al. 2019; Wang et al. 2019a; Sauter et al. 2020). Together with an ERP component interpreted in terms of distractor suppression (Wang et al. 2019b), this has been taken as evidence that observers learn to proactively down-modulate the attentional priority signals (Itti and Koch 2001; Fecteau and Munoz 2006; Wolfe and Gray 2007; Kok et al. 2012; Aitken et al. 2020) generated by distractors at frequent locations, thus reducing their potential to capture attention and cause interference. In line with this, we found that early visual-cortex signalling was reduced for distractors occurring in the frequent versus rare region. Assuming that the attentional priority map is situated in some integrative brain area – such as the pulvinar of the thalamus (Bundesen et al. 2005; Kastner and Pinsk 2004), which (in its inferior and lateral parts) contains retinotopic maps that are reciprocally connected with cortical areas V1, V2, V4, and MT, while receiving ('saliency') signals from SC and (indirectly, via SC) from LIP and FEF – then the reduced distractor signalling in the early visual cortex might reflect learned top-down inhibition of feature coding in early visual areas. The fact that this is observed generally (with both types of distractor) is consistent with Won et al. (2020), who found reduced visual-cortex signalling when different-dimension distractors (i.e., colour singletons that varied in the specific colour feature) occurred with 80%, but not 25%, frequency *anywhere* in the search display, and with Adam and Serences (2021), who found distractor-related responses to be attenuated throughout the visual hierarchy, starting from V1, when the distractor colour was fixed vis-à-vis that of the target and non-distractor items compared to when it varied randomly, swapping colour with the target and non-distractor items (distractor frequency of 67% in both conditions). In contrast, the reason why Bertleff et al. (2016) did not find evidence of down-modulated distractor signalling (when comparing blocks with 100% vs. 0% distractor presence) in early visual areas may be that they varied the spatial-attentional setting (focused vs. distributed) for the *target* (rather than the *distractor*), along with the use of different-dimension (colour) distractors.

Neurally, early visual cortex is thought to constitute the first cortical stage of salience processing: the generation of local feature-contrast, or 'saliency', signals (Knierim and van Essen 1992; Nothdurft 2000; Li 2002) within the various feature dimensions, which are subsequently integrated across dimensions into an 'overall-saliency' map determining the priorities for the allocation of attention. Stimuli that contrast more strongly with their surroundings (i.e., are more bottom-up salient) generate higher peaks on the priority map and have a higher likelihood of summoning attention (Treue 2003; Töllner et al. 2011; Kamkar et al. 2018). Accordingly, if distractors are more salient than targets, they are more likely to capture attention inadvertently. Thus, our finding of reduced distractor signals in the early visual cortex (especially at frequent locations) likely indicates a general down-modulation of feature-contrast signals, broadly consistent with Gaspelin and Luck's (2019) 'signal-suppression' hypothesis. Of note, this down-modulation does not amount to complete suppression, even in the frequent region – as distractors in this region (especially those defined in the same dimension as the target) can still cause massive interference, and targets in this region can efficiently summon attention in the absence of a distractor.

Importantly, if anything, our colour distractors were more salient than our orientation distractors (see Methods), and so, on a purely bottom-up account, they should *not* have produced less interference than the orientation distractors. However, the fact that the colour distractors produced substantially less (rather than more) behavioural interference, coupled with a less marked frequent versus rare distractor-region RT effect and the absence of a correlation of early visual-cortical BOLD activity with the magnitude of RT interference, suggests that distractor-signal suppression, and particularly enhanced suppression in the frequent versus the rare region, involved some other or additional mechanism with different-dimension distractors.

According to the Dimension-Weighting Account (Found and Müller 1996; Müller et al. 2003, 2009; Liesefeld and Müller 2021; Liesefeld et al. 2021), such a mechanism is provided by dimension-based signal suppression (also referred to as 'second-order feature suppression' by Gaspelin and Luck 2018b; Won et al. 2019). That is, with distractors defined in a different dimension to the target (here: colour distractors, orientation targets), suppression might operate at the level of the distractor dimension, selectively down-modulating the contribution of colour signals to (supra-dimensional) priority computation without impacting the contribution of orientation signals. This strategy is unavailable with same-dimension distractors. Consistent with a filtering stage specific to the distractor dimension, the whole-brain analysis revealed that the left fusiform gyrus was generally involved in dealing with colour-defined different-dimension distractors (whereas it was not activated by orientation-defined same-dimension distractors). Previous neuropsychological, electrophysiological, and neuroimaging studies have revealed the (left) fusiform gyrus to play a role in colour processing (Allison et al. 1993; Chao and Martin 1999; Pollmann et al. 2000; Simmons et al. 2007). Of note, Simmons et al. (2007) considered the left fusiform gyrus to be "a high-level colour perception region" that is activated not only during colour perception (responding more strongly to colour than to greyscale stimuli), but also during the top-down-controlled retrieval of conceptual colour knowledge (i.e., during verifying whether a named colour is true of a named object). In the present study, the whole-brain results pointed to the involvement of left fusiform gyrus in dealing with different- (but not same-) dimension distractors in both regions, and especially with different-dimension distractors in the rare region. The increased activation associated with distractors in the rare region might reflect increased demands on fusiform gyrus in filtering out colour-defined distractors appearing at unlikely locations; or it might reflect increased residual colour processing due to distractors being more likely to break through the filter in the rare region. Whatever the precise explanation, this pattern is consistent with the fusiform gyrus playing a role in colour-based stimulus filtering via reducing the weight of colour-based feature-contrast signals in attentional priority computation. Previous studies have shown that colour-based distractor filtering can operate quite effectively across all display locations (e.g., Müller et al. 2009; Won et al. 2019), so tuning the filter to a region where colour distractors occur frequently might yield little extra benefits. This additional, spatially uniform filtering could explain why the correlation between distractor-generated BOLD activity in early visual areas and behavioural (RT) distractor interference was effectively abolished for colour-defined distractors (while it was robust for orientation-defined distractors). Additionally, the *dimensional* filter might be modified by statistical distractor-location learning, up-modulating the suppression weights for colour signals in the frequent, relative to the rare, distractor region. Consistent with this, the fusiform gyrus was activated less strongly by colour distractors in the frequent versus the rare region. Thus, the reduced interference from different-dimension (colour) distractors session might result from the interplay of two mechanisms: spatially tuned (as a result of distractor-location learning) suppression of (colour-) feature-contrast signals in early visual cortex, followed by a spatially global or tuned down-weighting of any residual colour-based signals in the computation of the (supra-dimensional) attentional-priority map (i.e., dimension-based filtering). In Supplementary-Materials Section S4, we present a simple, 'proof-of-principle' computational model which implements essential properties of the neural architecture envisaged here. The model predicts reduced distractor interference, a smaller distractor-location learning effect and a lower correlation between behavioural distractor interference and neural activity for different-compared to same-dimension distractors, despite there being little difference in the assumed early visual-cortex neural activity.

Given this general sketch of learnt distractor suppression, at least two questions arise: 1) How does the adaptation, in the early visual cortex, to the spatial distractor distribution come about? 2) Why was the beta-value gradient between the frequent- and rare-distractors-region VOIs not significantly reduced for different- compared to same-dimension distractors?

Concerning the first question, the reduced response to distractors in the frequent versus the rare region might reflect a form of low-level 'habituation' (e.g., Turatto et al. 2018). Of note, though, VOI activity was reduced not only to distractor signals in the frequent region but also to target signals (despite targets occurring with equal frequency in both regions). Behavioural work has demonstrated *facilitation* of locations at which *targets* appear frequently, analogous to *inhibition* of positions where *distractors* occur frequently (Ferrante et al. 2018) – suggesting that behavioural facilitation (target-location learning) is the flipside of inhibition (distractor-location learning). Thus, if inhibition involves a top-down-mediated reduction of neural responsivity in the early visual cortex, owing to the status of 'distractors' as task-irrelevant, to-be-rejected items, one would expect facilitation to be associated with *higher* beta values for targets at frequent versus rare *target* locations. This expectation is at variance with habituation accounts predicting the beta values to be *lower* (as for distractors at frequent versus rare *distractor* locations). To our knowledge, these contrasting predictions have not yet been tested for statistical *target*-location learning. However, assuming that *distractor*-location inhibition is top-down mediated (tied to the status of distractors as 'distractors'), the fact that target signals, too, were reduced in the early visual cortex would argue in favour of the inhibition at the lower level originating from some higher level. One likely source is the priority map, that is, inhibition of salient distractors that captured attention at the priority-map level feeds back to and adapts ('habituates') neuronal responsivity in feature-coding areas. Consistent with the notion of the priority map being an inherently 'feature-blind' representation, this feeding-back of inhibition appears to be feature-unspecific: it impacts not only the coding of the distractor feature but also that of the target feature, even if the latter belongs to a different dimension. Of note, though, the feedback tended to be generally weaker in the different (vs.

the same-) dimension condition, as reflected by the beta values being numerically more positive for VOIs in both the frequent and rare distractor regions (this pattern was seen both with a distractor and a target appearing in a given VOI). Weaker feedback is also consistent with a reduced target-location effect in the different- (vs. the same-) dimension condition.

A second, related question concerns why the early visual-activation difference (i.e., the gradient of the beta values) between the frequent and rare distractor regions was not noticeably reduced for the different-dimension, as compared to the same-dimension, distractor condition in the present study, given that different-dimension distractors permitted efficient, dimension-based filtering of distractor signals. One possibility is that the gradient is learnt early on during practice (e.g., in the present study, already in the three practice blocks, of 3 × 55 trials, performed outside the scanner) because initially distractors in one (i.e., the frequent) region capture attention more often than distractors in the other (the rare) region, and then persists. In contrast, the strategy of dimension-based filtering would be 'discovered' only later on during task performance , once the early-level gradient has been established (cf. Zhang et al. 2019). That is, capture prevention by dimension-based filtering does not lead to unlearning of the initially acquired gradient. Consistent with this are indications that statistical distractor-location learning effects are pretty resistant to unlearning (Turatto et al. 2018). Alternatively, even after a different-dimension distractor ceases to capture attention (due to efficient dimension-based filtering), the presence of a distractor may still be registered by the system and responded to with top-down inhibitory feedback, reinforcing the gradient at the lower level. In line with this, Liesefeld et al. (2021) have recently shown that different-dimension distractors, while not, or no longer, giving rise to an N2pc component (assumed reflect attentional capture; Luck and Hillyard 1994; Eimer 1996; Hickey et al. 2006; McDonald et al. 2013), still produce a P_D component (assumed to be indicative of reactive suppression; Hickey et al. 2009; Sawaki and Luck 2010; Gaspar and McDonald 2014; Gaspelin and Luck 2018a) – though, compared to same-dimension distractors, the P_D amplitude is reduced. Liesefeld et al. (2021) took this to mean that less reactive effort is required to fully suppress a different-dimension distractor because its saliency signal is proactively down-weighted before reaching the priority map. Weaker inhibitory feedback (reactive suppression) would also explain the generally less negative beta values in early visual cortex developed with different-dimension distractors. Thus, on this account, the beta-value gradient reflects the distractor frequency in the two regions, independently of whether or not the distractor is potent enough to capture attention. In other words, the low-level gradient represents the basic distractor-region ‘prior’.

The whole-brain analysis also revealed the right SPL to be more strongly activated by different-dimension distractors appearing in the rare versus the frequent region (an effect not seen with same-dimension distractors). The right SPL, which has long been considered critical for visual-spatial attentional control (Shapiro et al. 2002; Thakral and Slotnick 2009), is engaged not only in shifts of spatial attention (Corbetta et al. 1995; Behrmann et al. 2004) but also in shifting attention between separable dimensions of the input (Yantis and Serences 2003). The more robust SPL activation by different-dimension distractors in the rare region might reflect a higher incidence of attentional capture by such distractors, which may require combined dimensional and spatial shifting of attention to a target defined in a different dimension. Dimensional shifting would not be required with same-dimension distractors, which might explain why no distractor-region-specific SPL activation was seen in the same-dimension distractor condition.

In summary, the current results show that statistical learning of distractor locations involves (acquired) suppression down to the level of the early visual cortex. Besides, with different-dimension (colour) distractors, higher-level, dimension-specific filtering mechanisms can come into play. Colour-based filtering, involving the right fusiform gyrus and SPL, substantially reduces the interference caused by colour distractors, whether they occur in the frequent or rare region. A dimension-based filtering strategy does not seem to be available with distractors defined in the same dimension as the target (orientation), in which case interference reduction relies solely on spatially tuned lower-level signal suppression.

Although the current results support the view that the reduced distractor interference in the frequent region involves signal suppression in early visual cortex and points to differential neural mechanisms of distractor handling with different- as compared to same-dimension distractors, there are limitations in the design of the present study that require further examination in future work. One limitation is likely to arise from the (necessarily) uneven number of trials with distractors in the frequent versus rare distractor region, which may affect the statistical power to estimate the rare conditions. This could be dealt with by increasing the number of trials overall and analysing the same number of (randomly sampled) trials in the frequent distractor-location condition as in the rare condition. Another limitation derives from the target and the 'same-dimension' distractor being exclusively defined by orientation and the 'different-dimension' distractor exclusively by colour. Note that this choice of stimuli was motivated by the fact that, since Theeuwes's (1992) pioneering work, most studies investigating singleton-distractor interference (in the additional-singleton paradigm) have used form-defined targets and colour-defined distractors and generalized their findings with colour distractors to singleton-distractor interference at large. However, behavioural work from our group has challenged this assumption by showing that, when paired with a form- (or, in our case, orientation-) defined target, a colour-defined distractor produces a quantitatively and qualitatively different effect pattern to a form-defined distractor – as predicted by the 'dimension-weighting account'. However, although theoretically motivated, referring to one type of distractor as 'different-dimension' and the other as 'same-dimension' also involves a generalization, which needs to be corroborated empirically by examining other pairings of target and distractor dimensions. Starting this work in behavioural studies, we have shown that generalization is warranted, for instance, for combinations of 'orientation' and 'luminance' (e.g., Liesefeld and Müller 2021; see also Sauter 2018 for a reversal of the roles of orientation and luminance as target- and, respectively, distractor-defining). However, work on other dimensions – including reversing the roles of colour and orientation as target- and distractor-defining – remains to be done. Thus, concerning the underlying brain mechanisms, it remains to be answered whether the differential MRI results between the different- and same-dimension distractor in the current study generalize to other stimulus dimensions, in particular, colour-defined 'same-dimension' distractors and orientation-defined 'different-dimension' distractors.

Acknowledgements

This work was supported by German Research Foundation (DFG) grants MU773/16-2, awarded to HJM and ZS, and MU773/14-2, awarded to HJM, as well as a China Scholarship Council

(CSC) award to BZ.

Conflict of Interest Statement

All the authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Adam KCS, Serences JT. 2021. History modulates early sensory processing of salient distractors. J Neurosci.

Aitken F, Menelaou G, Warrington O, Koolschijn RS, Corbin N, Callaghan MF, Kok P. 2020. Prior expectations evoke stimulus-specific activity in the deep layers of the primary visual cortex. PLoS Biol. 18:e3001023.

Allenmark F, Zhang B, Liesefeld HR, Shi Z, Müller HJ. 2019. Probability cueing of singleton-distractor regions in visual search: the locus of spatial distractor suppression is determined by colour swapping. Vis cogn. 27:576–594.

Allison T, Begleiter A, McCarthy G, Roessler E, Nobre AC, Spencer DD. 1993. Electrophysiological studies of colour processing in human visual cortex. Electroencephalogr Clin Neurophysiol. 88:343–355.

Bacon WF, Egeth HE. 1994. Overriding stimulus-driven attentional capture. Percept Psychophys. 55:485–496.

Behrmann M, Geng JJ, Shomstein S. 2004. Parietal cortex and attention. Curr Opin Neurobiol. 14:212–217.

Bertleff S, Fink GR, Weidner R. 2016. The Role of Top–Down Focused Spatial Attention in Preattentive Salience Coding and Salience-based Attentional Capture. J Cogn Neurosci. 28:1152–1165.

Brainard DH. 1997. The Psychophysics Toolbox. Spat Vis. 10:433–436.

Bundesen C, Habekost T, Kyllingsbaek S. 2005. A neural theory of visual attention: bridging cognition and neurophysiology. Psychol Rev. 112:291–328.

Chao LL, Martin A. 1999. Cortical regions associated with perceiving, naming, and knowing about colors. J Cogn Neurosci. 11:25–35.

Corbetta M, Shulman GL, Miezin FM, Petersen SE. 1995. Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. Science. 270:802–805.

de Fockert J, Rees G, Frith C, Lavie N. 2004. Neural correlates of attentional capture in visual search. J Cogn Neurosci. 16:751–759.

Di Caro V, Theeuwes J, Della Libera C. 2019. Suppression history of distractor location biases attentional and oculomotor control. Vis cogn. 27:142–157.

Eimer M. 1996. The N2pc component as an indicator of attentional selectivity. Electroencephalogr Clin Neurophysiol. 99:225–234.

Eickhoff SB, Stephan KE, Mohlberg H, Grefkes C, Fink GR, Amunts K, Zilles K. 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage. 25:1325–1335.

Erdfelder E, Faul F, Buchner A. 1996. GPOWER: A general power analysis program. Behav Res Methods Instrum Comput. 28:1–11.

Failing M, Feldmann-Wüstefeld T, Wang B, Olivers C, Theeuwes J. 2019. Statistical regularities induce spatial as well as feature-specific suppression. J Exp Psychol Hum Percept Perform. 45:1291–1303.

Fecteau JH, Munoz DP. 2006. Salience, relevance, and firing: a priority map for target selection. Trends Cogn Sci. 10:382–390.

Ferrante O, Patacca A, Di Caro V, Della Libera C, Santandrea E, Chelazzi L. 2018. Altering spatial priority maps via statistical learning of target selection and distractor filtering. Cortex. 102:67–95.

Folk CL, Remington R. 1998. Selectivity in distraction by irrelevant featural singletons: evidence for two forms of attentional capture. J Exp Psychol Hum Percept Perform. 24:847–858.

Forster S, Lavie N. 2008. Attentional capture by entirely irrelevant distractors. Vis cogn. 16:200–214.

Found A, Müller HJ. 1996. Searching for unknown feature targets on more than one dimension:

Investigating a “dimension-weighting” account. Percept Psychophys. 58:88–101.

Gaspar JM, McDonald JJ. 2014. Suppression of salient objects prevents distraction in visual search. J Neurosci. 34:5658–5666.

Gaspelin N, Leonard CJ, Luck SJ. 2017. Suppression of overt attentional capture by salient-but-irrelevant color singletons. Atten Percept Psychophys. 79:45–62.

Gaspelin N, Luck SJ. 2018a. Combined Electrophysiological and Behavioral Evidence for the Suppression of Salient Distractors. J Cogn Neurosci. 30:1265–1280.

Gaspelin N, Luck SJ. 2018b. Distinguishing among potential mechanisms of singleton suppression. J Exp Psychol Hum Percept Perform. 44:626–644.

Gaspelin N, Luck SJ. 2019. Inhibition as a potential resolution to the attentional capture debate. Curr Opin Psychol. 29:12–18.

Geng JJ, Behrmann M. 2005. Spatial probability as an attentional cue in visual search. Percept Psychophys. 67:1252–1268.

Goschy H, Bakos S, Müller HJ, Zehetleitner M. 2014. Probability cueing of distractor locations: both intertrial facilitation and statistical learning mediate interference reduction. Front Psychol. 5:1195.

Henson RNA, Price CJ, Rugg MD, Turner R, Friston KJ. 2002. Detecting latency differences in event-related BOLD responses: application to words versus nonwords and initial versus repeated face presentations. Neuroimage. 15:83–97.

Hickey C, Di Lollo V, McDonald JJ. 2009. Electrophysiological indices of target and distractor processing in visual search. J Cogn Neurosci. 21:760–775.

Hickey C, McDonald JJ, Theeuwes J. 2006. Electrophysiological evidence of the capture of visual attention. J Cogn Neurosci. 18:604–613.

Itti L, Koch C. 2001. Computational modelling of visual attention. Nat Rev Neurosci. 2:194–203.

Kamkar S, Moghaddam HA, Lashgari R. 2018. Early Visual Processing of Feature Saliency Tasks: A Review of Psychophysical Experiments. Front Syst Neurosci. 12:54.

Kastner S, Pinsk MA. 2004. Visual attention as a multilevel selection process. Cogn Affect Behav Neurosci. 4:483–500.

Kelley TA, Yantis S. 2009. Learning to attend: effects of practice on information selection. J Vis. 9:16.

Knierim JJ, van Essen DC. 1992. Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. J Neurophysiol. 67:961–980.

Kok P, Jehee JFM, de Lange FP. 2012. Less is more: expectation sharpens representations in the primary visual cortex. Neuron. 75:265–270.

Kristjánsson A, Vuilleumier P, Schwartz S, Macaluso E, Driver J. 2007. Neural basis for priming of pop-out during visual search revealed with fMRI. Cereb Cortex. 17:1612–1624.

Krueger F, Fischer R, Heinecke A, Hagendorf H. 2007. An fMRI investigation into the neural mechanisms of spatial attentional selection in a location-based negative priming task. Brain Res. 1174:110–119.

Larsson J, Smith AT. 2012. fMRI repetition suppression: neuronal adaptation or stimulus expectation? Cereb Cortex. 22:567–576.

Leber AB, Egeth HE. 2006. It's under control: top-down search strategies can override attentional capture. Psychon Bull Rev. 13:132–138.

Leber AB, Gwinn RE, Hong Y, O'Toole RJ. 2016. Implicitly learned suppression of irrelevant spatial locations. Psychon Bull Rev. 23:1873–1881.

Liesefeld HR, Liesefeld AM, Müller HJ. 2021 (in press). Preparatory control against distraction is not feature-based. Cereb Cortex.

Liesefeld HR, Müller HJ. 2021. Modulations of saliency signals at two hierarchical levels of priority computation revealed by spatial statistical distractor learning. J Exp Psychol Gen. 150:710–728.

Li Z. 2002. A saliency map in primary visual cortex. Trends Cogn Sci. 6:9–16.

Luck SJ, Hillyard SA. 1994. Electrophysiological correlates of feature analysis during visual search. Psychophysiology. 31:291–308.

Lund TE, Nørgaard MD, Rostrup E, Rowe JB, Paulson OB. 2005. Motion or activity: their role in intra- and inter-subject variation in fMRI. Neuroimage. 26:960–964.

McDonald JJ, Green JJ, Jannati A, Di Lollo V. 2013. On the electrophysiological evidence for the capture of visual attention. J Exp Psychol Hum Percept Perform. 39:849–860.

Monti MM. 2011. Statistical Analysis of fMRI Time-Series: A Critical Review of the GLM Approach. Front Hum Neurosci. 5:28.

Müller HJ, Geyer T, Zehetleitner M, Krummenacher J. 2009. Attentional capture by salient color singleton distractors is modulated by top-down dimensional set. J Exp Psychol Hum Percept Perform. 35:1–16.

Müller HJ, Reimann B, Krummenacher J. 2003. Visual search for singleton feature targets across dimensions: Stimulus- and expectancy-driven effects in dimensional weighting. J Exp Psychol Hum Percept Perform. 29:1021–1035.

Munneke J, Heslenfeld DJ, Usrey WM, Theeuwes J, Mangun GR. 2011. Preparatory effects of distractor suppression: evidence from visual cortex. PLoS One. 6:e27700.

Nothdurft H. 2000. Salience from feature contrast: additivity across dimensions. Vision Res. 40:1183–1201.

Pollmann S, Weidner R, Müller HJ, von Cramon DY. 2000. A fronto-posterior network involved in visual dimension changes. J Cogn Neurosci. 12:480–494.

Ruff CC, Driver J. 2006. Attentional preparation for a lateralized visual distractor: behavioral and fMRI evidence. J Cogn Neurosci. 18:522–538.

Sawaki R, Luck SJ. 2010. Capture versus suppression of attention by salient singletons: electrophysiological evidence for an automatic attend-to-me signal. Atten Percept Psychophys. 72:1455–1470

Sauter M. 2018. Learning to shield visual search from salient distractors. Doctoral thesis, Ludwig-Maximilians-Universität München.

Sauter M, Hanning NM, Liesefeld HR, Müller HJ. 2020. Post-capture processes contribute to statistical learning of distractor locations in visual search. Cortex. 135:108–126.

Sauter M, Liesefeld HR, Müller HJ. 2019. Learning to suppress salient distractors in the target dimension: Region-based inhibition is persistent and transfers to distractors in a nontarget dimension. J Exp Psychol Learn Mem Cogn. 45:2080–2097.

Sauter M, Liesefeld HR, Zehetleitner M, Müller HJ. 2018. Region-based shielding of visual search from salient distractors: Target detection is impaired with same- but not different-dimension distractors. Atten Percept Psychophys. 80:622–642.

Serences JT, Yantis S, Culberson A, Awh E. 2004. Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. J Neurophysiol. 92:3538–3545.

Shapiro K, Hillstrom AP, Husain M. 2002. Control of visuotemporal attention by inferior parietal and superior temporal cortex. Curr Biol. 12:1320–1325.

Shaw ML, Shaw P. 1977. Optimal allocation of cognitive resources to spatial locations. J Exp Psychol Hum Percept Perform. 3:201–211.

Simmons WK, Ramjee V, Beauchamp MS, McRae K, Martin A, Barsalou LW. 2007. A common neural substrate for perceiving and knowing about color. Neuropsychologia. 45:2802–2810.

Thakral PP, Slotnick SD. 2009. The role of parietal cortex during sustained visual spatial attention. Brain Res. 1302:157–166.

Theeuwes J. 1992. Perceptual selectivity for color and form. Percept Psychophys. 51:599–60.

Töllner T, Zehetleitner M, Gramann K, Müller HJ. 2011. Stimulus saliency modulates pre-attentive processing speed in human visual cortex. PLoS One. 6:e16276.

Treue S. 2003. Visual attention: the where, what, how and why of saliency. Curr Opin Neurobiol. 13:428–432.

Turatto M, Bonetti F, Pascucci D. 2018. Filtering visual onsets via habituation: A context-specific long-term memory of irrelevant stimuli. Psychon Bull Rev. 25:1028–1034.

Wang B, Theeuwes J. 2018. Statistical regularities modulate attentional capture. J Exp Psychol Hum Percept Perform. 44:13–17.

Wang B, Samara I, Theeuwes J. 2019a. Statistical regularities bias overt attention. Atten Percept Psychophys. 81:1813–1821.

Wang B, van Driel J, Ort E, Theeuwes J. 2019b. Anticipatory Distractor Suppression Elicited by Statistical Regularities in Visual Search. J Cogn Neurosci. 31:1535–1548.

Wang L, Mruczek REB, Arcaro MJ, Kastner S. 2015. Probabilistic Maps of Visual Topography in Human Cortex. Cereb Cortex. 25:3911–3931.

Wolfe JM, Gray W. 2007. Guided search 4.0. Integrated models of cognitive systems. 99–119.

Won B-Y, Forloines M, Zhou Z, Geng JJ. 2020. Changes in visual cortical processing attenuate singleton distraction during visual search. Cortex. 132:309–321.

Won B-Y, Kosoyan M, Geng JJ. 2019. Evidence for second-order singleton suppression based on probabilistic expectations. J Exp Psychol Hum Percept Perform. 45:125–138.

Yantis S, Serences JT. 2003. Cortical mechanisms of space-based and object-based attentional control. Curr Opin Neurobiol. 13:187–193.

Zehetleitner M, Goschy H, Müller HJ. 2012. Top-down control of attention: it's gradual, practice-dependent, and hierarchically organized. J Exp Psychol Hum Percept Perform. 38:941–957.

Zehetleitner M, Koch AI, Goschy H, Müller HJ. 2013. Salience-based selection: attentional capture by distractors less salient than the target. PLoS One. 8:e52595.

Zhang B, Allenmark F, Liesefeld HR, Shi Z, Müller HJ. 2019. Probability cueing of singleton-distractor locations in visual search: Priority-map- versus dimension-based inhibition? J Exp Psychol Hum Percept Perform. 45:1146–1163.