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Dynamic causal interactions between occipital and parietal cortex explain how endogenous spatial attention and stimulus-driven salience jointly shape the distribution of processing priorities in 2D visual space



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ABSTRACT

Visuo-spatial attention prioritizes the processing of relevant inputs via different types of signals, including current goals and stimulus salience. Complex mixtures of these signals engage in everyday life situations, but little is known about how these signals jointly modulate distributed patterns of activity across the occipital regions that represent visual space. Here, we measured spatio-topic, quadrant-specific occipital activity during the processing of visual displays containing both task-relevant targets and salient color-singletons. We computed spatial bias vectors indexing the effect of attention in 2D space, as coded by distributed activity in the occipital cortex. We found that goal-directed spatial attention biased activity towards the target and that salience further modulated this endogenous effect: salient distractors decreased the spatial bias, while salient targets increased it. Analyses of effective connectivity revealed that the processing of salient distractors relied on the modulation of the bidirectional connectivity between the occipital and the posterior parietal cortex, as well as the modulation of the lateral interactions within the occipital cortex. These findings demonstrate that goal-directed attention and salience jointly contribute to shaping processing priorities in the occipital cortex and highlight that multiple functional paths determine how spatial information about these signals is distributed across occipital regions.

1. Introduction

Visual scenes often contain more information than the brain can process at any given moment (Dukas, 2004). Visual selective attention allows prioritization of a subset of the incoming sensory signals and plays a key role in guiding overt behavior (Dukas, 2004; Chelazzi et al., 2011). Attention can be controlled via goal-directed mechanisms that account for the participant's goals (endogenous control), as well as via stimulus-driven mechanisms that relate to the physical characteristics of the external signals (exogenous control) (Desimone & Duncan, 1995; Egeth & Yantis, 1997). These two types of control mechanisms are traditionally associated with separate networks in the dorsal (associated to the control of endogenous attention) and ventral (associated to the control of exogenous attention) frontal and parietal areas (Corbetta et al., 2000; Corbetta & Shulman, 2002). However, any real-life situation involves a complex mixture of signals likely to call upon both goal-directed and exogenous control (Itti & Koch, 2001; Chelazzi et al., 2011; Macaluso & Doricchi, 2013). Many different paradigms have been developed to study these interactions, including spatial cueing tasks combining central and peripheral cues (Berger et al., 2005), search tasks with singleton distractors (Theeuwes, 1994; Belopolsky et al., 2007) and more ecological approaches using naturalistic stimuli (Nardo et al., 2016). At the behavioral level, performance improves when both endogenous and exogenous signals coherently prioritize the same location (i.e. salient targets, see Desimone & Duncan, 1995), while salient distractor stimuli presented away from the target location can hamper performance by exogenously pulling attention away from the target (Proulx & Egeth, 2007, but see Gaspelin & Luck, 2018 for the suppression of exogenous capture and Luck et al., 2021, for a recent opinion paper on this issue). At the neural level, imaging studies found little impact of fully irrelevant salient distractors either in the dorsal or the ventral fronto-parietal network (Kincade et al., 2005; Indovina & Macaluso, 2007; Natale et al., 2009; but see Thomsen et al., 2005), showing instead that the activation of the ventral attentional

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system requires some combination of task-relevance and stimulus-driven salience (cf. "contingent capture of attention", Folk et al., 1992; Natale et al., 2010). These effects are consistent with the view that the ventral system acts as a "circuit-breaker", interacting with the dorsal system when attention needs to be re-oriented in a stimulus-driven manner towards a new relevant location (Corbetta & Shulman, 2002; Corbetta et al., 2008; Vossel et al., 2012, but see Chica et al., 2013; DiQuattro et al., 2014; and Vossel et al., 2014; for reviews).

Together with the fronto-parietal systems, attention control also entails the modulation of activity in the occipital visual cortex that represents the external visual space (Heinze et al., 1994; Martínez et al., 1999; Li, 2002; Seymour et al., 2009; Awh et al., 2012). The biased competition model of attention (Desimone & Duncan, 1995) proposes that the simultaneous presentation of multiple stimuli triggers competitive interactions suppressing activity in the visual cortex and that attention can counteract this effect by enhancing activity for the attended stimulus and suppressing distractor-related responses. The theory was derived from single-cell data showing that both endogenous attention (Luck et al., 1997; Reynolds et al., 1999) and stimulus salience (Reynolds & Desimone, 2003) can reduce competitive interactions between two stimuli located within a neuron's receptive field. Using functional Magnetic Resonance Imaging (fMRI), Kastner and colleagues reported related effects in the human visual cortex (Kastner et al., 1998; Kastner et al., 2001; Beck & Kastner, 2005). Competitive interactions were evidenced by comparing the simultaneous vs. sequential presentation of four stimuli briefly flashed in the same visual quadrant. In different studies, the authors demonstrated that both endogenous attention (Kastner et al., 1998) and exogenous factors (Beck & Kastner, 2005, using displays with/without singleton distractors) can reduce suppressive effects associated with the simultaneous presentation of the stimuli.

While highlighting the impact of both endogenous and exogenous attention on visual representations, these studies did not address the interaction between the two mechanisms of attention control. Only a few previous neuroimaging studies directly investigated how the presence of concurrent goal-directed and stimulus-driven signals affects the representation of visual space in the occipital cortex (Melloni et al., 2012; Sprague et al., 2018; Won et al., 2020). These three studies utilized similar experimental approaches. First, a fMRI localizer was used to identify voxels in the occipital cortex that represent specific locations in the visual field (e.g. the four visual quadrants, in Melloni et al., 2012). During the attention task, stimuli were presented simultaneously at multiple locations (the four quadrants, in Melloni et al., 2012), but only one location was task-relevant and included the target to be judged. Across conditions, changes of the task-relevant location allowed us to map the spatial effects of endogenous attention orienting. At the same time, the physical characteristics of the stimuli (e.g. color or luminance) either at the task-relevant location or in one of the other locations (distractor locations) were also manipulated. The latter enabled studying how the endogenous and exogenous spatial attention control jointly influence activity in the visual cortex, as a function of the location of the two signals.

Overall, these three studies revealed a convergent pattern of results, including: i) increased activation in the occipital regions representing the target location (Melloni et al., 2012; Sprague et al., 2018; Won et al., 2020), ii) increased activation in the occipital regions representing the location of salient compared with non-salient distractors (Sprague et al., 2018; Won et al., 2020), and iii) larger differences between target- and distractor-related activation, when the target was also the salient stimulus (Melloni et al., 2012; Sprague et al., 2018). The three studies thus confirmed that both endogenous and exogenous attention can modulate the visual cortex activity in a spatially-specific manner and that the two types of control signals are combined in the occipital cortex. Yet, these studies did not explicitly assess how attention shapes processing priorities across the whole visual field (but see Sprague et al., 2018, and the Discussion section). For example, is target priority also shaped by the activity in a non-target visual region laying within the same hemifield (i.e. yielding an overall hemifield bias)? More generally, can the joint effects of endogenous and exogenous attention be determined just by changes of activity in the region that represents the target, or is it the overall distribution of activity across the representation of the whole visual space that best accounts for visual selective attention?

Moreover, extensive evidence indicates that the modulation of activity in the visual cortex by endogenous attention arises from feed-back signals originating from the dorsal fronto-parietal network (Kastner et al., 1999; Moore & Armstrong, 2003). Exogenous effects in visual areas may also be mediated via dorsal regions that, following the initial detection of salient stimuli in the ventral system, would bias visual representations via feed-back connectivity (Corbetta & Shulman, 2002; Vossel et al., 2012). However, exogenous attention may also be instantiated via direct interactions within visual cortex, including local competitive mechanisms (Chelazzi et al., 1998; Reynolds et al., 1999; Kastner et al., 2001), as well as via intra-areal lateral connectivity (Martínez et al., 1999, see also Turova & Rolls, 2019, for a computational model of spatial competition comprising inter-areal forward/feedback connectivity). These different mechanisms emphasize again the importance of considering the overall distribution of attentional influence across the visual field (cf. also "priority maps", Ptak, 2012; Bisley & Mirpour, 2019) and raise the question of whether/how the fronto-parietal attention control network simultaneously modulates processing priorities at multiple locations of the visual field. In particular, this would relate to attention signaling from the posterior parietal cortex (PPC) to the visual occipital areas (e.g. see Buchel, 1997; Desseilles et al., 2011; Vossel et al., 2012).

To address these questions, we computed *spatial bias vectors* that combine fMRI activity across the occipital regions that represent the visual field, providing us with a measure of how spatial attention affects processing priorities in 2D space; and we used analyses of effective connectivity to test hypotheses about the mechanisms generating these distributed patterns of activity. During fMRI scanning, the participants were presented with 4 stimuli, one in each quadrant. On a trial-by-trial basis, a fully predictive central cue indicated the task-relevant quadrant, where the target was presented shortly thereafter. In three different display-conditions, the 4 stimuli were either all of the same color (homogeneous display, HD), the target was a salient color-singleton (salient target display, STD), or the distractor in the quadrant opposite to the target was a color-singleton (salient distractor display, SDD). The spatial bias vector for the HD-condition provides us with a measure of the spatial distribution of processing priority generated by endogenous attention, while changes of the vector's magnitude and/or direction during STD and SDD index any further modulation by exogenous spatial attention. Dynamic Causal Models (Friston et al., 2003; Stephan et al., 2010) tested how the local connectivity within the occipital cortex and/or the connectivity between the occipital cortex and the PPC contribute to generating these distributed patterns of activity.

2. Material & methods

2.1. Participants

Twenty-four right-handed healthy adults were recruited for the study. They had normal or corrected-to-normal vision, no neurological, psychiatric or cognitive impairments and gave their written informed consent to participate in the study. The study was approved by a national ethics committee in biomedical research (Comité de Protection des Personnes: Sud-Méditerranée II, authorization ID: 2019-A00713-54). A total of nineteen participants were included in the final analyses (mean age: 27, range 20-39; 12 females). Five participants were excluded because: 1 participant asked to stop the experiment, for 1 participant we had technical problems with the eye-tracking, 1 participant had excessive head movements (> 3 mm), 1 participant moved the eyes towards the stimulus location during the localizer task (preventing us from obtaining the quadrant-specific ROIs) and 1 participant did not understand

the task instructions (performance below chance level). While the final sample size (N=19) was not very large, a power analysis based on effect sizes reported in Won et al. (Won et al., 2020) (who employed a similar paradigm) permitted confirming that our study had sufficient statistical power. Specifically, we considered the effect of "salient vs. non-salient distractors" that was the weakest fMRI effect in our current dataset (cf. Results section, below). Using the G*Power software, we estimated the number of participants required to attain the power of 0.8, with alpha = 0.05 and Won et al. (Won et al., 2020) effect size (Cohen's d' = 0.757). The resulting sample size was 16 participants, indicating that our study had sufficient power to detect this effect in the occipital cortex.

2.2. Experimental design

Each participant underwent a total of 7 functional imaging runs (6 runs of the main attention task, 7 min each; plus 1 localizer run, 10 min) and one anatomical scan (6 min). Visual stimuli were presented using Cogent Graphics, developed by John Romaya at the Wellcome Department of Imaging Neuroscience, running under MATLAB (The MathWorks, Natick, MA). The stimuli were projected on a screen placed at 90 cm from the participant's eyes (1024 × 768 pixels; projected image size: 31.5 cm height x 42 cm width).

2.2.1. Localizer task

The aim of the localizer was to identify the regions of the occipital cortex that represent the different locations of the visual field, where we then presented the stimuli during the main attention task (i.e. quadrant-specific ROIs). In order to maximize quadrant-specific activation, we employed high-contrast moving stimuli and asked the participants to perform a subtle discrimination of targets presented among distractors, employing a highly efficient blocked-design. The localizer stimuli consisted in a dynamic array of small bars (size = 0.5 × 0.1°) moving at a speed of 28°/s behind an aperture located in one of the four screen quadrants. The aperture was a 3 × 3° square centered at 7° of eccentricity from the display center (see Fig. 1, for an illustration; and *online-video* [insert video link here] for an example of the localizer stimuli). The moving bars were seen through the aperture and were oriented horizontally or vertically, with the exception of the target-bars that were titled of 45° to the right or to the left. The target-bars appeared at unpredictable times (range 1.08-3.24 sec) and the participants had to report the tilt orientation (right/left) by pressing a response-button with the index/middle finger of the right hand. At any one moment there were approximately 9 bars visible through the aperture. This procedure maximized both exogenous (densely packed moving stimuli) and endogenous (target discrimination among distractors) contributions in defining quadrant-specific activations and allowed us to identify the relevant spatial representations at the level of the individual participant (see Fig. 2A-B). The stimuli were presented in each screen quadrant for blocks of 14 seconds, interleaved with 12 seconds of central fixation without any visual stimulation. Each quadrant was stimulated 6 times, in a randomized order. The participants had to maintain central fixation throughout the localizer run.

2.2.2. Main attentional task

There were 6 fMRI runs comprising the main attention task. Each run included 84 trials. Each trial started with the presentation of a central cue signaling the task-relevant quadrant, where the target would appear shortly thereafter. The cue was a multi-colored circle in the style of a pie-chart. The cue was divided in 4 quarters, each with a unique color (blue, cyan, yellow and magenta; see Fig. 1). Before the experiment, each participant was assigned one specific color and was instructed to direct (endogenous) attention towards the quadrant indicated by the corresponding color. This procedure minimized any possible contribution of exogenous attention during the cueing phase. The cue (diameter = 0.5°) was presented for 1000ms and was followed by the presentation of the stimulus display. The display comprised 4 bars presented one in each quadrant (eccentricity = 7°, size = 2.0 × 0.5°, see Fig. 1). The bar in the cued quadrant (target) was tilted to the left or the right side (45°) and the participant had to report the left/right tilt by pressing a response-button with the index/middle finger of the right hand. The bars in the other three quadrants (distractors) were oriented either horizontally or vertically and were fully task-irrelevant. The stimulus display was presented for 300ms and the participant had up to 3000ms to respond. The inter-trial interval was between 3000 and 4000ms (uniform distribution). The participants had to maintain central fixation throughout the trial.

In different trials, the 4 bar-stimuli were either all of the same color (green or red, counterbalanced across participants) or included a color singleton (one green bar among three red bars, or vice-versa). Because of technical difficulties to accurately measure luminance inside the MR bore, we adjusted the luminance of the green and red stimuli outside the scanner (luminance of both colors = 13.5cd/m^2). Most likely, the absolute luminance values of the stimuli projected in the scanner were quite different, but the relative luminance of the green and red stimuli - which was the relevant parameter here - should remain relatively unaffected. The presence/absence and the location of the color singleton yielded three display-conditions (see Fig. 1; "Main task", in the gray inset): *Homogeneous Display* (**HD**, all stimuli of the same color), *Salient Target Display* (**STD**, when the target was the color singleton) and *Salient Distractor Display* (**SDD**, when the distractor stimulus in the quadrant opposite the target was the color singleton). The three display-conditions were presented with equal probability.

The combination of the 4 target-locations and 3 display-conditions led to a total of 12 experimental conditions that were presented in an unpredictable order and that, across the 6 runs, were repeated 42 times each. These 12 conditions conform to a 4 × 3 full factorial design manipulating in an orthogonal manner the endogenously attended location (4 cued/target quadrants: TL, top-left; TR, top-right; BR, bottom-right; BL, bottom-left) and exogenous attention (3 display-conditions: HD, no exogenous signals; STD, exogenous signal at the same location as endogenous attention; SDD exogenous signal at the opposite location compared to the target); see also Fig. S1 [insert Fig. S1 ISM link here].

2.3. Eye tracking

Participants' gaze-direction was tracked during the whole imaging session using a MR-compatible EyeLink 1000 (SR Research Ltd., Mississauga, Ontario, Canada) at a sampling rate of 500Hz. At the start of the session, the system was calibrated with a 5-point procedure. The calibration points were located in the four quadrants at 7° eccentricity, plus the center of the screen. The analyses of the eye-tracking data were carried out with custom scripts in MATLAB. Eye-tracking data were down-sampled to 100Hz. For each trial, the gaze-data were extracted in a 2500ms window, starting 500ms before cue onset. The data were baseline-adjusted using the median of the vertical and horizontal position during a 500ms pre-cue period. We evaluated the quality of each trace considering the percentage of data-points with values larger than 10° or smaller than -10°, typically caused by blinks or poor/noisy signal. Trials with more than 50% of reliable data-points (86% of the total) underwent further analyses to detect any loss of central fixation. We first identified new fixations as any displacement of the gaze-position larger than 0.5° and lasting for at least 100ms. Trials containing any fixation outside a central box (± 2° from the center of the screen) were classified as "fixation-loss". These trials (5% of the trials with reliable data) were excluded from the behavioral analyses and were modeled in a separate regressor of no-interest in the fMRI analyses.

2.4. Behavioral analyses

The analysis of the reaction times (RT) for the attention task made use of a linear mixed model analysis using log-transformed RTs

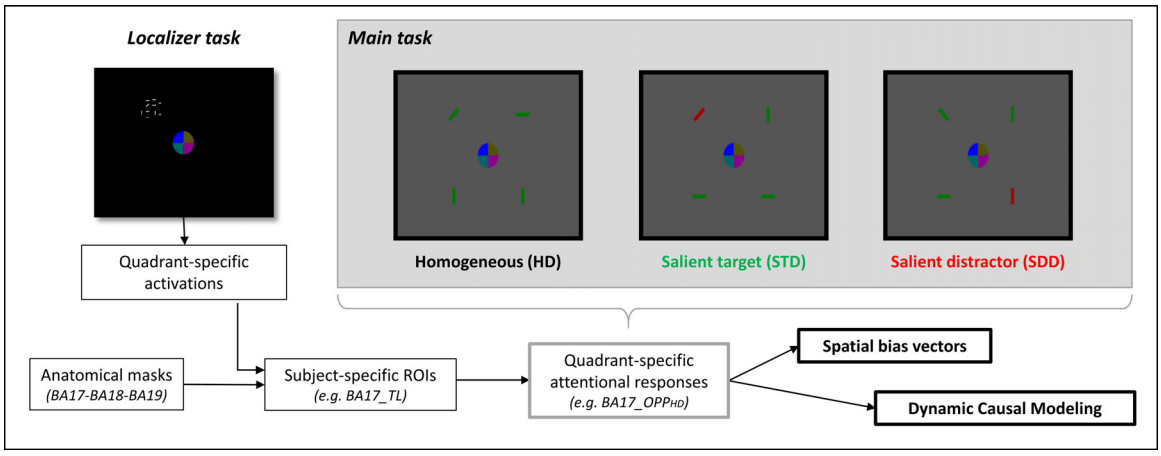


Fig. 1. Main steps of the data analysis and the three display conditions. First, subject-specific functional ROIs were generated by combining the fMRI responses during the localizer task with anatomically defined areas, using the AAL atlas. This resulted in 12 ROIs for each participant, corresponding to occipital regions in areas BA17, BA18, and BA19 that responded to stimuli in one visual quadrant (see also Fig. 2A-B). During the main attention task, the participant attended to one of the 4 quadrants, in 3 different display-conditions (see gray inset, and below). Activity for the resulting 12 conditions were averaged across ROIs, as a function of the represented quadrant and the attended location (see also Fig. 2B, panels on the right). This permitted assessing the effect of endogenous and exogenous attention at the level of the local activity in the three BA-areas (see Fig. 4 and Fig. S1B). In our main analyses, the ROIs activity was used to compute the "spatial bias vectors" (Figs. 3 and 5) and to test "Dynamic Causal Models" of effective connectivity (Figs. 6-7). The gray inset ("main task") shows the three display-conditions that allowed us to investigate the interplay between endogenous and exogenous spatial attention; see also Fig. S1A, panels on the left. Each trial began with the presentation of a central cue that informed the participant in which quadrant the target would appear (100% validity, endogenous attention). The cue comprised four colored sectors. Before the experiment, each participant was instructed to direct attention towards the quadrant indicated by one specific color (blue, in the example). One second after the cue, the stimulus display was presented. This included 4 bars, one of which was the target (here, top-left) that required a left/right orientation discrimination. The other three distractor-stimuli were either vertically- or horizontally-oriented bars and were fully task-irrelevant. In different trials, one of the stimuli could be a color singleton (exogenous attention). This yielded to the three display-conditions: Homogeneous Display (HD), no singleton; Salient Target Display (STD), the target was the singleton; Salient Distractor Display (SDD), the distractor in the quadrant opposite to the target was the singleton. The three display-conditions were randomized and presented with equal probability. Note: the size of the cue is magnified for illustration purposes.

implemented in R-studio (Bates et al., 2015). Trials with wrong/no/late responses and/or including losses of fixation (cf. above) were discarded from the analysis. The model included the log-transformed RTs as the dependent variable and the display-condition as the explanatory variable (with 3 levels: HD, STD & SDD). Because of the repeated measures, the model also included subject-specific intercepts. It is important to note that in the current design, all trials included 100% valid cues and the manipulation of endogenous attention concerned solely the position of the target (cf. Fig. S1A [insert Fig. S1 ISM link here], panels on the left). Accordingly, we did not expect any behavioral correlate of endogenous attention and averaged the RTs associated with targets in the 4 quadrants before submitting the behavioral data to the statistical models. Concerning the effect of exogenous attention (i.e. display-condition), salient target (STD) may speed up RTs compared to HD (no salient signals), while salient distractors (SDD) may slow down responses. Nonetheless, it should be anticipated that the use of 100% valid cues (highly focused endogenous spatial attention) is likely to reduce/suppress the impact of exogenous salience on behavioral performance (see Luck et al., 2021; Rashal et al., 2022; and Discussion section). The accuracy data were not analyzed, because the orientation-discrimination performance was at ceiling (> 95%, in all conditions) most likely reflecting the use of fully-predictive 100% valid cues.

2.5. Image acquisition and preprocessing

T2*-weighted echoplanar images (EPI) with blood oxygen level-dependent (BOLD) contrast (interleaved multiband sequence, multi-band factor = 2, 50 slices covering the entire brain, field of view = 220 × 210.4mm, repetition time = 1.72s, echo time = 30ms, phase encoding direction = antero-posterior, slice orientation = approx. axial, voxel size = 2.4 × 2.4 × 2.4mm^3) were obtained using a 3T MRI System (Trio, Siemens). A high-resolution anatomical scan was acquired using a standard T1-weighted 3D MP-RAGE sequence (repetition time = 3s, echo time = 3.8ms, inversion time = 1.1s, sagittal 3D volume with a field of view of 224 × 256 × 192mm, voxel size = 1 × 1 × 1mm^3).

The functional data were preprocessed and analyzed with Statistical Parametric Mapping software SPM12 (Wellcome Department of Imaging Neuroscience, University College London, UK; http://www.fil.ion.ucl.ac.uk/spm). After discarding the first four volumes of each imaging run, images were corrected for head movements. Slice-acquisition delays were corrected using the middle slice as reference. All images were normalized to the SPM12 Tissue Probability Map and re-sampled to 2mm isotropic voxel size. Unsmoothed data were used in all the analyses.

2.6. Single-subject analyses

2.6.1. Localizer and individual Regions Of Interest (ROIs)

The localizer data served to identify, for each participant, the voxels in the occipital visual cortex that responded preferentially to stimuli presented in each quadrant (Figs. 1 and 2A-B). The single-subject general linear model (GLM) included the 4 conditions of interest related to the location of the visual stimuli (top-left: "TL", top-right: "TR", bottom-right: "BR" and bottom-left: "BL") modeled as blocks of 14 seconds and convolved with the canonical Hemodynamic Response Function in SPM12, plus the 6 movements parameters resulting from the realignment procedure, as regressors of non-interest.

We used a combination of functional contrasts and the Automated Anatomical Labeling atlas (AAL, Tzourio-Mazoyer et al., 2002) to identify quadrant-specific responses in anatomically-defined occipital areas BA17, BA18 and BA19. Please note that here we refer to these spatially-specific responses as "quadrant-specific", because only four positions were tested (as opposed to the entire visual field), and that these should be considered in retino-centered coordinates, because eye-position was held fix and carefully controlled during both the localizer and the main experiment. For each participant, using the functional localizer data we tested for the main effects of side at the whole-brain level (e.g.: "TL+BL >

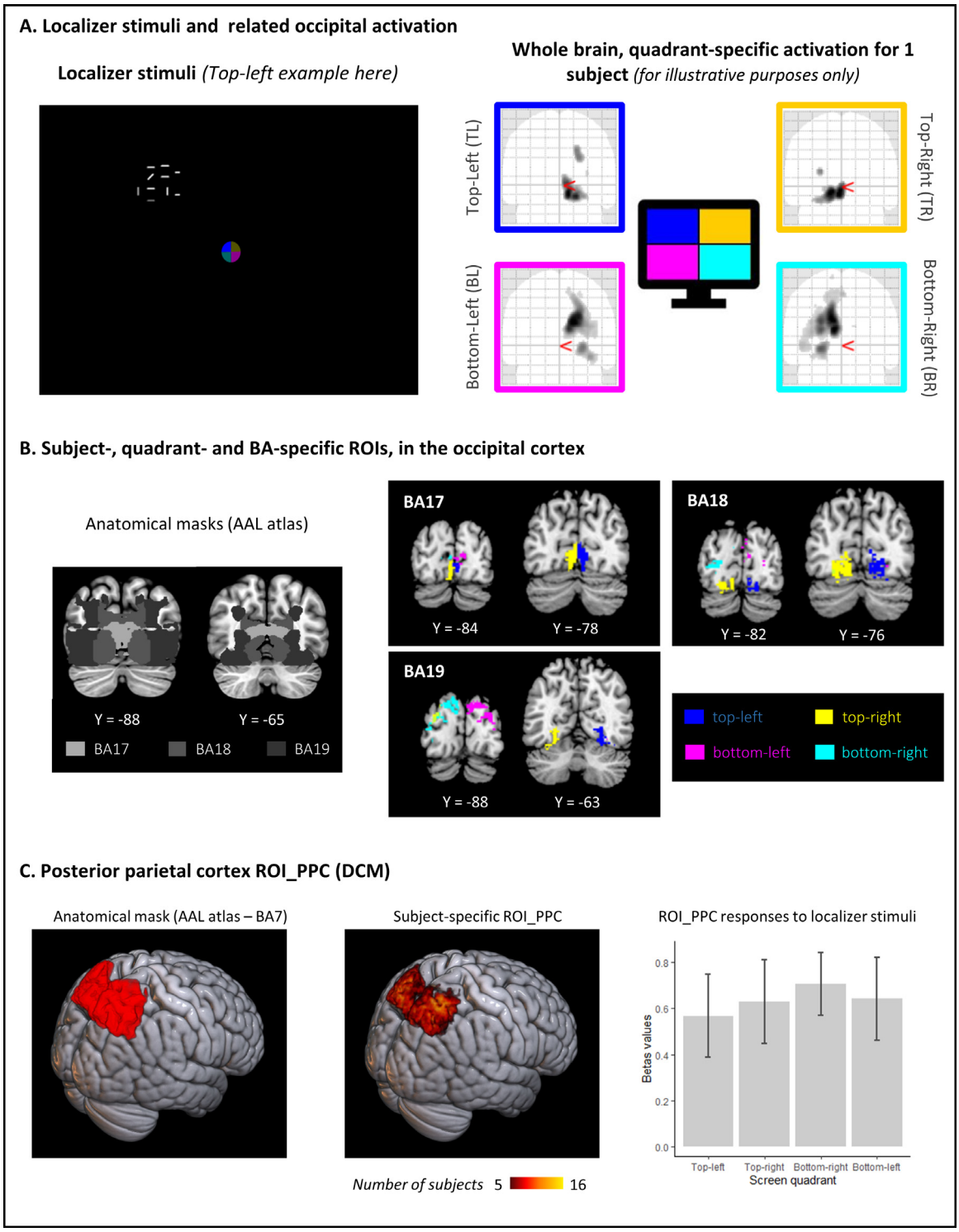


Fig. 2. Localizer task and ROIs definition. A. Localizer stimuli and the corresponding quadrant-specific activation in the occipital cortex. The left panel shows an example of the localizer stimuli (see also online-video). Localizer stimuli were presented using a blocked-stimulation protocol. For each block, a set of small white moving bars appeared in only one of the 4 quadrants of the screen (here in the top-left quadrant). The right panel shows an example of the whole brain results for one participant. Using a combination of functional contrasts (see Methods section), we identified voxels showing quadrant-specific responses during the localizer task. The 4 maximum intensity projections highlight multiple clusters associated with stimulation of each visual quadrant (cf. color coding). B. Subject-, quadrant- and BA-specific ROIs in the occipital cortex. The left panel show the anatomical masks (from the Automated Anatomical Labeling atlas) used to partition the functionally defined quadrant-specific responses (see panel A) into anatomically-defined BA17, BA18 and BA19. For each participant this enabled us to define 12 separate ROIs, corresponding the 4 quadrant-representations in the 3 BA areas. The right panels show the localization of the final ROIs, highlighting voxels where there was an overlap of at least 3 participants. C. The ROI in the posterior parietal cortex. The leftmost panel shows the anatomical mask (also from the Automated Anatomical Labeling atlas) used to define the ROI_PPC. Individual ROI_PPC were created by combining functional data (activation irrespective of stimulated quadrant, during the localizer task) and this anatomical mask. The central panel shows the localization the ROI_PPC across participants. The rightmost panel shows the mean ± SEM beta values of the ROI_PPC separately for each four quadrant-specific stimulations during the localizer.

TR+BR", for left hemifield quadrants) and separated voxels responding to the upper or the lower quadrant using inclusive masking with the relevant simple main effect (i.e. top-left quadrant: "TL > BL", and bottom-left quadrant: "BL>TR"). All contrasts were thresholded at p-unc. = 0.005, which was the sole decision parameter finally determining the number of voxels in each ROI (see table S1 [insert table S1 ISM link here] for the average number of voxels comprised in each occipital ROIs). This initial whole-brain threshold typically resulted in multiple activation clusters in the hemisphere contralateral to the simulated quadrant, comprising both dorsal and ventral extrastriate visual cortex, as well as the calcarine fissure; see Fig. 2A, for an example. These subject-specific activation clusters where then split based on anatomical criteria using the AAL atlas, finally yielding to 12 ROIs for each participant (4 visual-quadrants x 3 BA-areas), see Fig. 2B. We labelled these ROIs on the basis of their spatial selectivity and BA-area. For example, "ROI18_TL" refer to the ROI in area BA18 responding to stimuli in the top-left quadrant, which includes voxels located in the right ventral occipital cortex. The average size of the quadrant-specific ROIs (mean number of voxels ± s.e.m.) was: 82.24 ± 6.33 for BA17, 220.03 ± 15.67 for BA18 and 187.92 ± 15.24 for BA19 (see also table S1 [insert table S1 ISM link here]).

In addition, for each participant, we identified voxels in the PPC that activated during the localizer task irrespective of the stimulated quadrant ("ROI_PPC"). For this we considered the omnibus F-test at p-unc. = 0.001 and retained voxels belonging to area BA7 using the AAL atlas (Tzourio-Mazoyer et al., 2002). The parietal ROI comprised voxels in both hemispheres and, on average across voxels, it responded to stimulation of all the four visual quadrants (see Fig. 2C, and table S1 [insert table S1 ISM link here] for the number of voxels in the ROI_PPC; see also Discussion section concerning the possible differential role of the left and right PPC). The ROI_PPC was used for the analyses of effective connectivity.

2.6.2. Main task

The single-subject GLMs for the main task comprised 12 conditions of interest corresponding to the initial 4 × 3 factorial design: 4 target-quadrants x 3 display-conditions (HD, STD, SDD; see also Fig. S1A [insert Fig. S1 ISM link here], panels on the left), plus one predictor including trials to be excluded from the group analyses (no response, incorrect orientation-discrimination, reaction time out of the 200-3000ms response window and fixation-loss trials, cf. above), and 6 regressors with the realignment parameters. The GLMs included the 6 fMRI runs, with separate predictors for each run. Each trial was modeled using the canonical Hemodynamic Response Function in SPM12. The event-onsets were time locked to the presentation of the stimulus display and the event-duration was 300ms. We made this choice, rather than time locking to the cue-onset, in order to maximize the likelihood of capturing the combined effects of both the endogenous cue and the stimulus-array. Only the parameter estimates of the 12 conditions of interest were used for the subsequent group-level analyses.

2.7. Group-level analyses

2.7.1. Target- and salience-related local activation

The first question that we asked was how endogenous and exogenous attention jointly affect local activation in the occipital visual cortex. For this, we examined the activity in the ROIs representing the target quadrant and the opposite quadrant, where the salient distractors were presented in the SDD display-condition (see Fig. S1B [insert Fig. S1 ISM link here], panel on the left). First, separately for each subject and the 12 ROIs, we averaged the parameter estimates across sessions and voxels, separately for the 12 conditions of interest. Next, for each BA-area, we averaged the data across the 4 quadrant-specific ROIs as a function of the target-location (Fig. S1A [insert Fig. S1 ISM link here], panels on the right). Separately for the 3 display-conditions, we computed the activity associated with the presentation of the target in the visual quadrant represented by the ROI (**ROI_IN** responses) and activity when the target was in the opposite quadrant (**ROI_OPP**). For example, to obtain the "ROI_OPP" responses in area BA17, we averaged the activity of the ROI17_TL when the target was in bottom-right quadrant, ROI17_TR when the target was bottom-left, ROI17_BR when the target was top-left, and ROI17_BL when the target was top-right. This produced a single value per subject for each condition (IN/OPP), BA-areas and display-condition. It is important to stress that this averaging procedure preserved the orthogonality between the endogenous factor (cued/target location) and exogenous factor (salience) of the experimental design; see Fig. S1B [insert Fig. S1 ISM link here], rightmost panel.

It should be noticed that for the salient-distractor display (SDD), the response in ROI_OPP corresponds to the activity when a salient distractor is presented in the quadrant represented by the ROI. By contrast, the ROI_IN responses in the salient-target display (STD) correspond to the activation associated with a salient target (cf. Fig. S1B [insert Fig. S1 ISM link here], panel on the left). Accordingly, using the ROI_IN and ROI_OPP responses in the SDD and STD display-conditions we could test for the effect of endogenous attention (ROI_IN_{STD} + ROI_IN_{SDD} > ROI_OPP_{STD} + ROI_OPP_{SDD}), the effect of exogenous attention (ROI_IN_{STD} + ROI_OPP_{SDD} > ROI_IN_{SDD} + ROI_OPP_{STD}) and their interaction, as fully independent factors. A 2 × 2 × 3 repeated-measure ANOVA with the factors: quadrant-type (spatial endogenous attention: ROI_IN, ROI_OPP) x display-condition (spatial exogenous attention: STD, SDD) x BA-area (BA17, BA18, B19) was employed to assess these effects. It should be noticed that because the salient-singleton was presented in the ROI_IN during STD, but in the ROI_OPP during SDD, the effect of exogenous attention corresponds to the interaction between the factors "quadrant-type" and "display-condition" (i.e.: ROI_IN_{STD} + ROI_OPP_{SDD} > ROI_IN_{SDD} + ROI_OPP_{STD}).

2.7.2. Spatial bias vectors and gain/cost indexes

The analyses described in the previous section allowed us to test whether the response of quadrant-specific occipital ROIs increased when the represented quadrant contained a target compared to when the target was in the opposite quadrant (ROI_IN vs. ROI_OUT, i.e. a spatially-specific effect of endogenous attention), and whether this was modulated by the location of the salient singleton (STD vs. SDD, corresponding to the spatial interaction between endogenous and exogenous attention). However, these analyses do not fully capture the spatial distribution of the attentional effects, because they discard information about the activity in the ROIs that represent visual locations without any target or salient distractor (i.e. activity in the contralateral hemifield, but in the same upper/lower quadrant as the target: "ROI_CONTRA", and activity in the same hemifield as the target, but in the other upper/lower quadrant: "ROI_IPSI"). For example, directing endogenous attention to the top-left quadrant may generate a spatial bias across the entire left hemifield rather than specifically boosting activity in the ventral occipital cortex that represents the top-left quadrant.

In order to capture these effects, we computed *spatial bias vectors* that combine the activity of all four quadrant-specific ROIs (IN, OPP, CONTRA and IPSI, separately for each BA-area) and that represent the direction and the strength of the attentional bias in 2D visual space (see Fig. 3). First, we calculated condition-specific biases as the Euclidian sum of 4 vectors, each representing the activity of one ROI ("attention top-left", in Fig. 3A). All vectors originated at the (0,0) coordinates, i.e. the center of the visual field (no bias), but with different directions corresponding to the quadrant represented by the ROI (e.g. (-1,1) for the ROI_TL) and a magnitude corresponding to the activity of the ROI. The Euclidian sum of the 4 vectors quantified the direction and the strength of the attentional bias for one condition, in the relevant occipital representation (i.e. BA17, BA18 and BA19). Next, for each subject and display-condition, we computed the *spatial bias vectors* by averaging the data across the four target-quadrants (see Fig. 3B). For this, the condition-specific vectors were first projected into the top-left quadrant and then averaged to obtain the final *spatial bias vectors* associated with

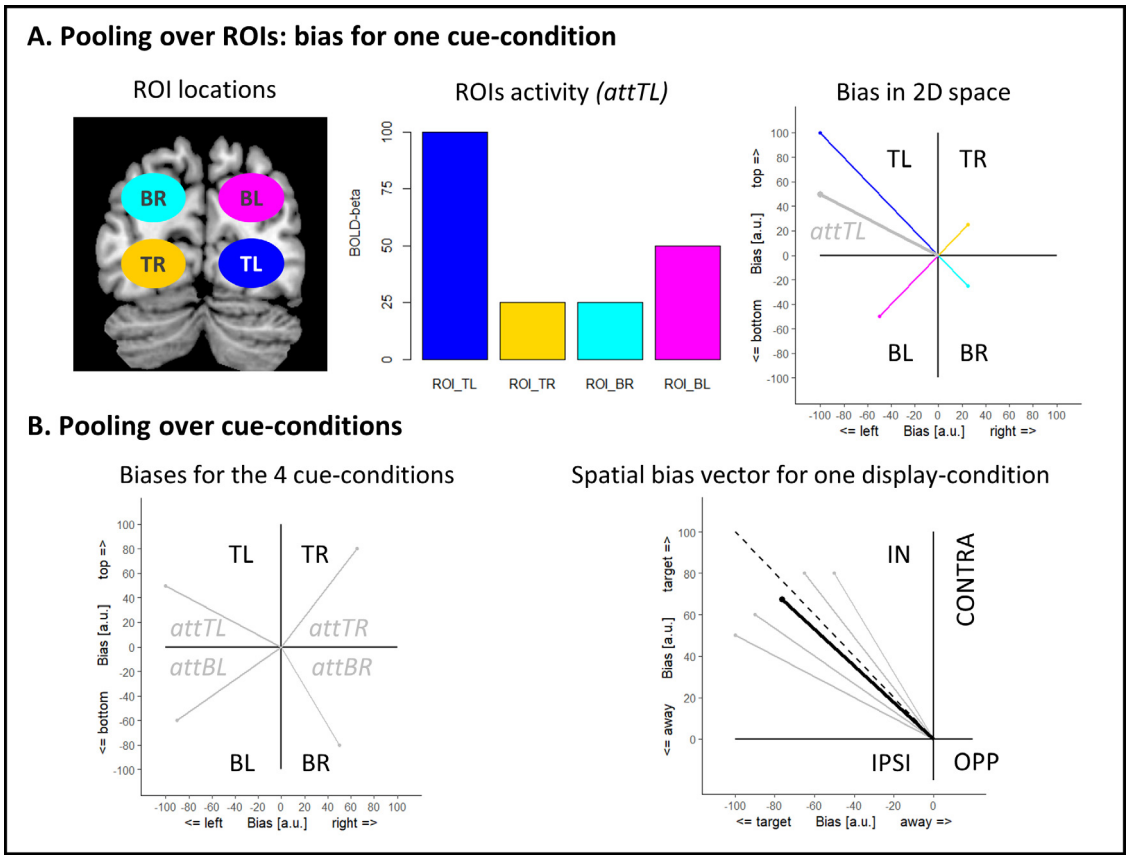


Fig. 3. [1.5-column fitting image | Color Figure]. Illustration of the procedure for the computation of the spatial bias vectors. A. Computation of the 2D bias-vector for one condition (here attention top-left, HD), considering the BOLD activity in the 4 ROIs that represent the 4 quadrants in one BA-area. The leftmost panel illustrates the ROIs location (BR = ROI representing the bottom-right quadrant, etc. cf. also Fig. 2B). The central panel displays the activity in the 4 ROIs, during the relevant condition (attTL). The rightmost panel shows the projection of the activity of the 4 ROIs in 2D space (cf. colored vectors) and their sum that yields the bias-vector for this condition (in light gray). In this illustrative example, attention to the top-left quadrant generates a bias towards the attended quadrant (TL), but also a more general left-hemifield bias due to the high activity in the ROI that represent the bottom-left quadrant (cf. magenta bar in the central panel). B. Illustration of the bias-vectors (computed as in panel A) for the four cue-conditions: attTL, attTR, attBR, attBL. The panel on the right shows the final spatial-bias vector. The 4 condition-specific vectors are projected to a new frame of reference, where the top-left locations represent the quadrant of the target (IN), bottom-right locations represent the quadrant opposite to the target (OPP), and the other two quadrants represent IPSI and CONTRA, with respect to the target position. The dotted line indicates the direction of the target, in this frame of reference. The 4 condition-specific vectors (light gray) are averaged yielding the final spatial-bias vector for this display condition (in black). In this example, the vector lies below the diagonal (dotted line) signifying the presence of an overall bias towards the target hemifield, which comprises both the “IN” (target) quadrant and the “IPSI” quadrant. The spatial-bias vectors were computed for each subject and BA-area, separately for the 3 display-conditions (see Fig. 5). L/R: left/right; T/B: top/bottom. OPP/CONTRA/IPSI: opposite/contralateral/ipsilateral with respect to the target quadrant (IN).

each display condition: $\overline{bias\text{HD}}$, $\overline{bias\text{STD}}$ and $\overline{bias\text{SDD}}$. In this frame of reference, negative x-values indicate a bias towards the hemifield of the target, and positive y-values indicate a bias towards the upper/lower target location. Please note that, in these displays/frames of reference, the IPSI and CONTRA labels refer to the location of the target and not some anatomical location in the occipital cortex (vectors are computed using the signal of the 4 ROIs, in both hemispheres). For example, if a hypothetical spatial bias vector has direction (-1, 0), i.e. lying on the x-axis and pointing leftward without any difference between "IN" and "IPSI" quadrants, this would mean that the BA-area is modulated according to the target hemifield, but not the up/down direction of attention.

We examined the geometrical characteristics of the *spatial bias vectors* to assess the impact of the display-condition on the spatial distribution of attention, as represented in BA17, BA18 and BA19. First, for the HD condition we tested whether the magnitude of the bias vector was larger than zero ($||\overline{bias\text{HD}}|| > 0$), indicating the presence of an endogenous spatial bias; and whether the vector-direction corresponded to the target location (i.e. 45° top-left, cf. dotted-line in Fig. 5, plots on the right: angle($\overline{bias\text{HD}}$) - 45, different from 0).

Next, we investigated the influence of exogenous attention by testing for changes of magnitudes and directions for "STD vs HD" (effect of salient targets) and "SDD vs HD" (effect of salient distractors). We expected that salient targets would strengthen the bias towards the target location ("Gain_indexes"), while salient distractors would weaken this bias ("Cost_indexes"). For magnitudes, we considered the magnitude difference of the two vectors (Gain_mag = $||\overline{bias\text{STD}}|| - ||\overline{bias\text{HD}}||$; and Cost_mag = $||\overline{bias\text{SDD}}|| - ||\overline{bias\text{HD}}||$). We expected positive values for Gain_mag and negative values for Cost_mag, corresponding to stronger/weaker spatial biases for STD/SDD compared with HD. For the vector directions, we assessed whether the salient stimuli modified the pointing direction of the spatial bias vector. This was tested as the difference between the deviation of the bias vectors with respect to the target location, in "STD vs HD" and "SDD vs HD" (Gain_dir = (angle($\overline{bias\text{STD}}$) - 45) - (angle($\overline{bias\text{HD}}$) - 45); and Cost_dir = (angle($\overline{bias\text{SDD}}$) - 45) - (angle($\overline{bias\text{HD}}$) - 45)). All the indexes were calculated at the single-subject level, separately for BA17, BA18 and BA19, and submitted to a series of one-tailed one-sample t-tests.

We then assessed the behavioral relevance of the measured effects using two separate multiple regression models that included the participants’ RT as the dependent measure (Gain-regression: RT_{STD} - RT_{HD}; Cost-regression: RT_{SDD} - RT_{HD}) and the Gain_mag/Cost_mag fMRI indexes computed in the 3 BA-areas as predictors. The analyses were im-

plemented using the fitlm-function in MATLAB, with "robust" estimation option.

2.8. Dynamic causal modeling (DCM)

The aim of the DCM analysis was to test specific hypotheses about the effect of attention on the effective connectivity of the occipital cortex and the PPC (see "model space", below). In order to constrain the number of nodes in the dynamic causal models, the models included the 4 quadrant-specific ROIs in BA18 (which showed the most robust effects in the vector analyses described above) and one region in the PPC (ROI_PPC). The PPC was selected because of the extensive literature pointing to this region as the main source of attention signals that modulate activity in the occipital cortex (see Introduction and Discussion sections). The ROI_PPC comprised the voxels in area BA7 that activated during the localizer scan irrespective of the stimulated quadrant.

For the DCM analyses of effective connectivity, a new set of single-subject GLMs was constructed. The 6 fMRI runs of the main attention task were concatenated and the GLM now contained 17 regressors of interest: the 12 experimental conditions (3 display-conditions x 4 target-quadrants, correct trials only), four regressors modeling the salient color-singleton separately for each quadrant, but irrespective of whether the singleton was a target or a distractor, plus one regressor that included all trials of the experiment. This GLM enabled us to then define the driving input to the DCMs (i.e. the regressor including all trials/display-onsets, and regressors coding for the position of the singleton) and the modulatory parameters of the DCMs (i.e. the 3 display-conditions, see also below). Additional regressors were added to model the main effect of fMRI run, error/fixation-loss trials and the realignment parameters.

2.8.1. Specification of the DCM and the model space

In DCM, three sets of parameters (A, B, C) characterize the connectivity of the network (Zeidman et al., 2019). The A-parameters specify the intrinsic connections between the nodes, regardless of the experimental condition. Here, we allowed all possible connections between the 5 ROIs. The C-parameters specify the driving inputs to the model. Here, the driving input affected only the 4 quadrant-specific occipital ROIs. All four ROIs were driven by the regressor coding for "all trials", because each trial included visual stimuli in the 4 quadrants, plus one singleton-regressor accounting for the presence of a salient stimulus in the ROI's quadrant (see also Stephan et al., 2007, who used an analogous approach when addressing the effect of endogenous attention on the connectivity between the occipital cortex and the posterior parietal cortex).

The B-parameters specify which experimental conditions can modulate the directional influence of one region onto another and constitute the main parameters of interest in the current DCM analysis. To test our hypotheses concerning the role of the connectivity between occipital regions and between the occipital cortex and the PPC, we constructed 6 models. The models were partitioned in two families (Stephan et al., 2010). In family F1, all the 12 attention conditions modulated feed-forward and feed-back connections between the PPC and all 4 occipital ROIs. By contrast, in family F2 the experimental conditions could affect only the connectivity between the PPC and the occipital ROI representing the location of the target (ROI_IN), and did so only when endogenous attention was directed towards that quadrant. For example, the connectivity between ROI_PPC and ROI18_TL was modulated only when endogenous attention was directed top-left, with 3 separate B-parameters accounting for the effect of display-condition (i.e. presence and location of the salient singleton). Within each family, 3 models embodied our hypotheses about the role of occipital-occipital connections. In particular, we sought to test alternative/complementary explanations to the changes of activity in the 4 occipital ROIs, beside their interactions with the ROI_PPC. Because our main interest was to understand how the brain selects pertinent information in the target-quadrant (plus how salience affects this), the model space put emphasis on the connectivity of the relevant ROI_IN. Accordingly, the first model comprised the modulation of all the connections between the occipital ROIs by all 12 experimental conditions. In the second model, attention could modulate only the connections "from" and "to" the ROI_IN that represents the current target location, and only conditions with endogenous attention directed towards the ROI quadrant could modulate these connections (three B-parameters corresponding to the 3 display-conditions). Finally, in the third model attention did not modulate any of the lateral connections between the occipital ROIs.

This model space can be seen as a 2 × 3 design: the 2 families tested whether the effect of attention on the occipital-PPC connectivity was "spatially diffused" (i.e. involving the occipital representation of the entire visual field, F1) or "spatially focused" (i.e. related only to the representation of the currently relevant quadrant, F2), and the 3 models within each family tested an analogous effect related to quadrant-specificity, but now considering the lateral connectivity within the occipital cortex. The full DCM model space is illustrated in Fig. 6.

2.8.2. Model selection and parameter inference

Given that our participants pool was sampled from a homogeneous population of young healthy adults and that the task involved simple visual judgments, we assumed that the optimal model structure would be the same across participants. Thus, a fixed-effects Bayesian model selection (BMS-FFX) was conducted to identify the most probable family and the most probable model (Stephan et al., 2010). The selection procedure takes into account the models' complexity (here the number of B-parameters that enable changes of connectivity as a function of the experimental conditions), penalizing more complex models, and selecting the best compromise between accuracy and complexity (Penny et al., 2004; Friston et al., 2007). We then used fixed-effect Bayesian Parameter Averaging (BPA) (Stephan et al., 2010) on the winning model to test for condition-specific changes of the connectivity B-parameters. Specifically, we implemented an averaging strategy analogous to that described above for the effects of conditions on the ROI activity (cf. Fig. S1, [insert Fig. S1 ISM link here]). Briefly, we averaged the B-parameters as a function of the target position/endogenous attention (ROI_IN, ROI_OPP, ROI_CONTRA and ROI_IPSI) and assessed the effect of exogenous attention by comparing "STD vs HD" (salient targets) and "SDD vs HD" (salient distractors). We discuss attentional modulations with posterior probabilities > 95%.

2.9. Data availability statement

Processed imaging data are available on the EBRAINS platform: https://search.kg.ebrains.eu/instances/cd4c0231-f9d6-4964-9763-54347029dd00.

3. Results

3.1. Behavioral data

The target orientation-discrimination task was very easy, with an average accuracy > 95%, in all three display conditions. Because of this the behavioral analyses considered only the response times (RTs). The average RTs numerically matched the expected pattern, with the fastest RTs for salient targets (STD; mean ± SEM = 584 ± 26ms), intermediate RTs for the homogeneous display (HD; 589 ± 30ms) and the slowest responses when the display included a salient distractor (SDD; 596 ± 31ms). Based on this qualitative pattern, we carried out a linear mixed model analysis using log-transformed RTs that revealed a significant effect of display condition ($F(2, 8804) = 3.68$, $p = 0.033$). We should stress that, albeit statistically significant, the effect of salient item's location was small (12ms, for STD vs. SDD; fixed-effect Cohen's $d = 0.03$) and should not be over-interpreted. This behavioral effect may reflect some combination of exogenous capture and distractor suppression (cf.

Luck et al., 2021, and Discussion section); but please note that our aim here was to investigate how quadrant-specific occipital ROIs and the posterior parietal cortex jointly process endogenous and exogenous spatial signals, rather than assessing the specific constraints that might determine any residual distractor-effects at the behavioral level.

3.2. Target- and salience-related local activation

We first aimed to assess the effects of endogenous and exogenous spatial attention considering activity in the ROIs representing the target quadrant and the opposite quadrant, as a function of display-condition (see also Fig. S1B [insert Fig. S1 ISM link here], on the left) and BA-areas. The corresponding 2 × 2 × 3 (ROI_IN/ROI_OPP x STD/SDD x BA17/18/19) ANOVA revealed a significant main effect of quadrant ($F(1,198) = 111.9$, $p < 0.001$, $\eta^2p = 0.36$), with larger activity in ROI_IN compared to ROI_OPP, corresponding to the effect of endogenous spatial attention. The analysis revealed also an interaction between quadrant and display-condition ($F(1,198) = 5.3$; $p = 0.021$; $\eta^2p = 0.03$), with larger activity in ROI_IN_{STD} compared to ROI_IN_{SDD} and in ROI_OPP_{SDD} compared to ROI_OPP_{STD}. This corresponds to the spatial effect of salience/exogenous attention, because the singleton item was presented in the ROI_IN in STD, while it was presented in the ROI_OPP in SDD, see also Methods section above and Fig. S1B [insert Fig. S1 ISM link here]. There was a main effect of BA-area ($F(2,198) = 35.4$; $p < 0.001$; $\eta^2p = 0.26$, with BA19 showing the highest activation), but no other main effects or interactions (all p-values > 0.5, all $\eta^2p < 0.01$). The results thus indicate that while both endogenous and exogenous attention affected activity in the three occipital visual areas, the two types of attention signals did not significantly interact (see Discussion section).

Fig. 4 shows the averaged parameters estimates in the ROIs representing the target quadrant (ROI_IN) and the opposite quadrant (ROI_OPP), as a function of display-conditions and BA-areas. The larger activity in ROI_IN (bars 1-3) compared with ROI_OPP (bars 4-6) highlights the effect of endogenous spatial attention. The main effect of salience, which by design is orthogonal to the effect of endogenous spatial attention (cf. Fig. S1 [insert Fig. S1 ISM link here]), is expressed by maximal activity for the STD condition in the ROI_IN (i.e. when the represented target was also the salient color-singleton, see bar 2 in each plot) and for the SDD condition in the ROI_OPP (i.e. when a salient distractor was shown in the represented quadrant, see bar 6 in each plot).

3.3. Spatial-bias vectors and gain/cost indexes

The data of the ROI_IN and ROI_OPP highlighted that both endogenous and exogenous attention affect the distribution of processing priorities towards/away from these two locations. However, these analyses do not consider the contribution of the occipital regions representing other locations of the visual field (ROI_CONTRA and ROI _IPSI). In order to take these into account, we computed spatial bias vectors using the distributed activity across all 4 ROIs and tested how endogenous and exogenous attention affect the magnitude and the direction of these vectors (Fig. 5; see also Fig. 3 for a detailed illustration of how the bias vectors were computed).

First, we assessed the effect of endogenous attention by testing whether the vectors' magnitudes in the HD condition were different from zero ($||\overline{bias}HD||>0$). This revealed highly significant effects in the 3 BA-areas (all p-values < 0.001, all Cohen's d > 3.02). The direction of the vectors provides us with the additional information about how each area implements the endogenous bias in 2D space. In our arbitrary frame of reference, the location of the target was set to [-1 1], that is, top-left along the 45° diagonal (see Fig. 3, plots on the right). Accordingly, we tested whether the angle ($\overline{bias}HD$) was different from 45°. The results showed that in ROI17 and ROI18, the directions were not significantly different from 45° (p = 0.45 in ROI17, Cohen's d = -0.18 and p = 0.33 in ROI18, Cohen's d = -0.23), highlighting that the distributed activity in these two BA-areas coded for the specific direction of the target. By contrast, the direction of the ($\overline{bias}HD$) in ROI19 was significantly different from 45° (two-tailed one-sample t-test: $T(18) = -7.6$, $p < 0.001$, Cohen's d = -1.75). The angle was smaller than 45° highlighting that, together with the selectivity for the target quadrant, the distributed activity in area BA19 also coded for an overall bias toward the hemifield containing the target. These effects can be seen in Fig. 5, plots on the right. In BA17 and BA18, the bias vectors for the HD condition (black) lie on the 45° diagonal (dotted line). In BA19, the HD vector also points to the top-

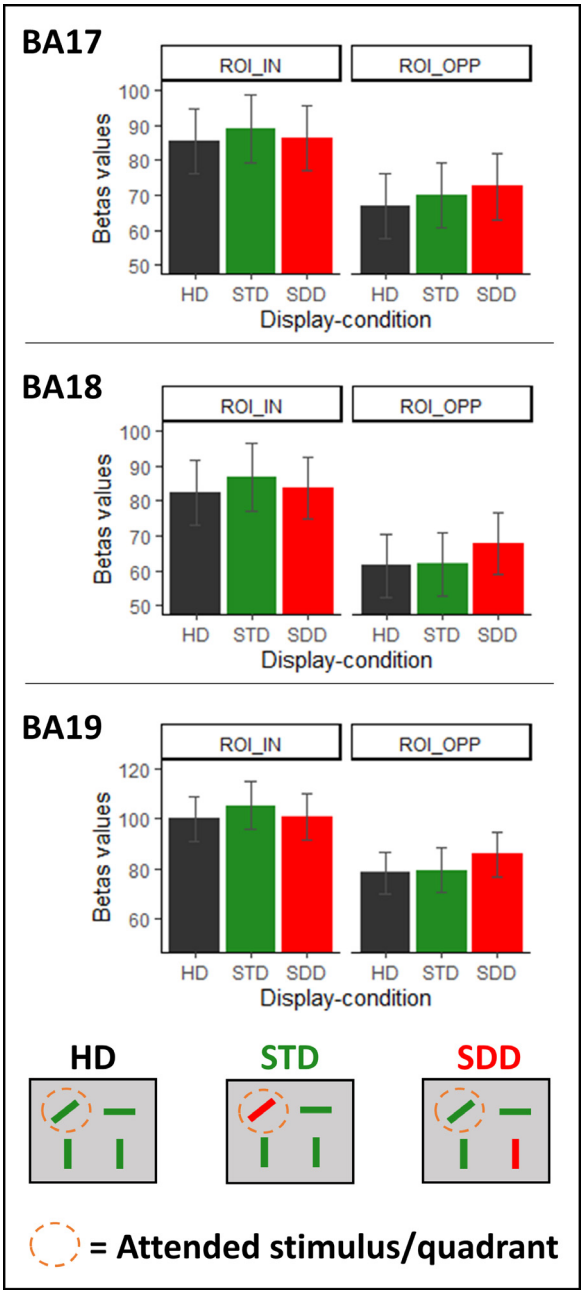


Fig. 4. Attentional effects in BA17-BA18-BA19 [1-column fitting image | Color Figure]. Local activity during the main attention task averaged across the 4 ROIs belonging to each BA-area, as a function of the represented quadrant (ROI_IN, ROI_OPP) separately for the 3 display-condition (HD, STD and SDD), see also Fig. S1 [insert Fig. S1 ISM link here]. The data analysis revealed an effect of endogenous spatial attention, an effect of exogenous attention, but no significant interaction between the two types of attention control signals. Plots show mean beta values ± SEM. See also Fig. 2 for the anatomical localization of these regions.

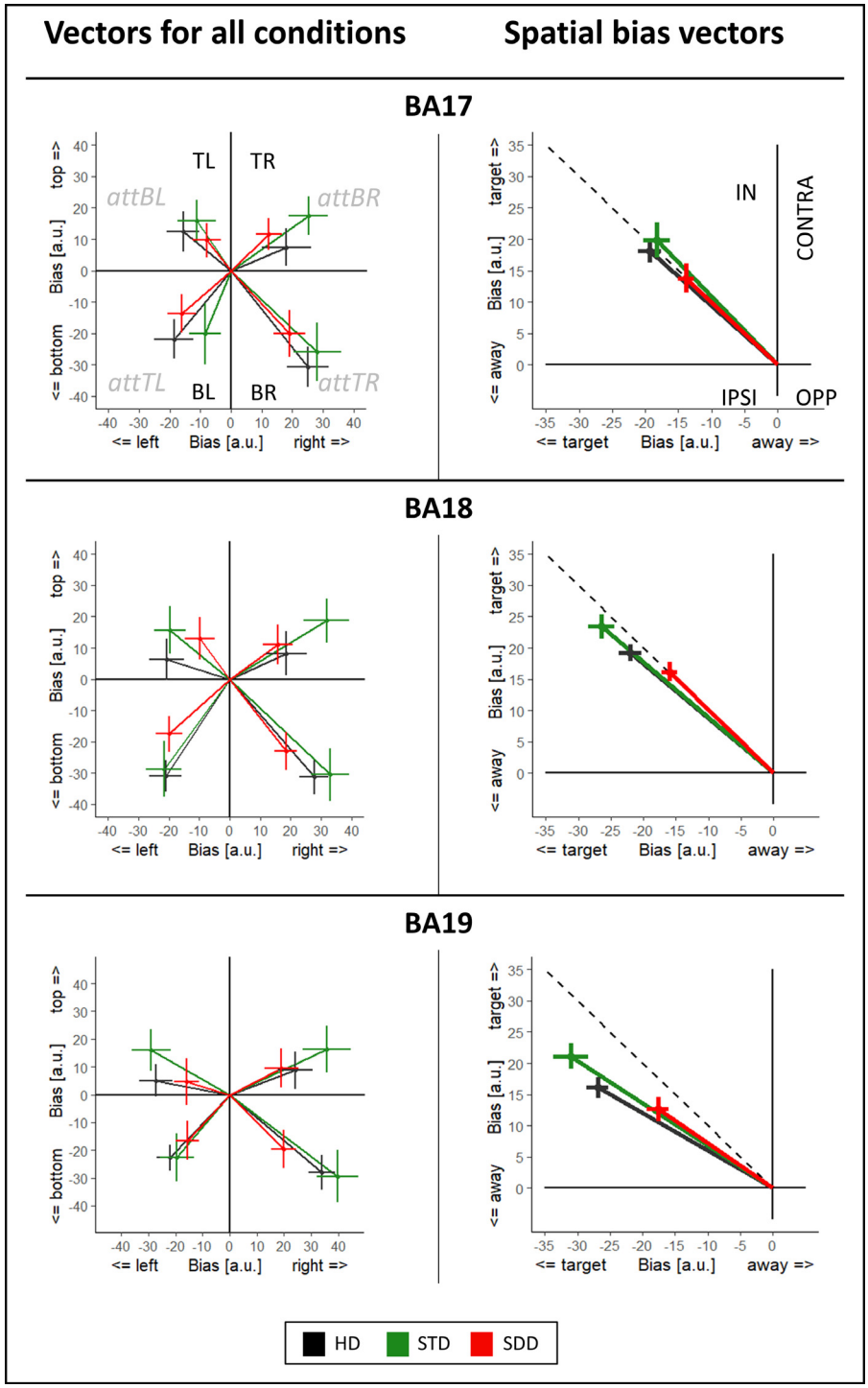


Fig. 5. Spatial biases elicited by endogenous and exogenous attention [1-column fitting image | Color Figure]. The plots on the left show the condition-specific 2D vectors plotted separately for the four attended quadrants (attTL, attTR, attBR, attBL) and display-condition (HD, STD, SDD). In all 3 display-conditions, the bias vectors were directed towards the target quadrant, reflecting the main effect of endogenous attention. The plots on the right show the final spatial bias vectors comprising the magnitude and the direction of the attentional effects in the three BA-areas, as a function of display-condition. The analysis of the vector-magnitudes showed that salient distractors reduced the spatial bias in all BA-areas (compare SDD-red vs. HD-black vectors) and that salient targets strengthened the bias in BA18 and BA19 (STD-green vs. HD-black). The vector-direction analysis highlighted that in BA19 attention also triggered an overall bias towards the target hemifield (in the rightmost plot, compare the direction of the bias vectors with the dotted-line that indicates the direction of the target). This was unaffected by the display-condition. Please note that in these plots the IPSI/CONTRA labels refer to the location of the target, not to some anatomical location in the brain. Crosses represent standard errors of the mean of the horizontal and vertical coordinates. L/R: left/right; T/B: top/bottom. OPP/CONTRA/IPSI: opposite/contralateral /ipsilateral with respect to the target quadrant (IN).

left quadrant, highlighting the endogenous attentional bias towards the target quadrant. However, the BA19 vector's direction is offset from the diagonal (toward the y-axis) also indicating the presence of an overall bias toward the hemifield containing the target (i.e. the "IPSI" quadrant, corresponding to the other quadrant within the same hemifield where the target was presented).

Next we turned to our main question concerning the joint effects of endogenous and exogenous spatial attention in the occipital cortex. In order to assess the modulatory effect of exogenous attention on the spatial bias elicited by endogenous attention (cf. above), we tested for changes of the vector magnitudes and directions as a function of display-condition. Specifically, we tested for "Gains" related to salient target (STD vs. HD) and for "Costs" related to salient distractors (SDD vs. HD).

The results highlighted that salient targets lead to an increase of the magnitude of spatial bias coded in BA18 (one-tailed one-sample t-test, $T(18) = 4.2$, $p < 0.001$, Cohen's $d = 0.96$) and in BA19 ($T(18) = 4.4$, $p < 0.001$, Cohen's $d = 1$), while there was no significant magnitude gain in BA17 ($p = 0.71$, Cohen's $d = 0.09$). The vectors' directions were unaffected by the salient targets (i.e. no significant change of the vectors' angles; all p-values > 0.14, all Cohen's d comprised between -0.06 and 0.35), including in BA19. The latter indicates that salient targets did not augment the spatial selectivity of the attentional bias in BA19. The

comparison of the vectors in the SDD vs. HD display-conditions revealed that salient distractors reduced the magnitude of the bias in all 3 areas: BA17 ($T(18) = -3.8$, $p < 0.001$, Cohen's $d = -0.84$), BA18 ($T(18) = -4.0$, $p < 0.001$, Cohen's $d = -0.92$) and BA19 ($T(18) = -4.6$, $p < 0.001$, Cohen's $d = -1.06$). Again, the vectors' direction did not change significantly between HD and SDD (all p-values > 0.11, all Cohen's d comprised between -0.19 and 0.09). Overall, the analyses of the bias vectors indicated that spatially-congruent exogenous signals boosted the spatial bias (salient targets), while incongruent signals reduced the bias (salient distractors). This was observed in all BA-areas, except for BA17 where the effect of salient targets was not significant. The analysis of the vectors' directions highlighted that distributed activity in BA19 coded for an overall bias towards the target hemifield and that exogenous signals did not modify this global effect of endogenous spatial attention.

We sought to establish the behavioral relevance of the spatial bias vectors by correlating the changes of the vector's magnitude (Gain_mag, Cost_mag) with the corresponding gains/costs at the behavioral level. Two separate multiple regressions analyses included reaction times differences (STD vs. HD, or SDD vs. HD) as the dependent variable and the Gain_mag (or Cost_mag) indexes of the 3 BA-areas as predictors. The Gain-regression yielded a non-significant model contribution compared to the "constant only" model (R-squared = 0.075, $F(3,15) = 0.41$, $p = 0.75$), while the Cost-regression model highlighted a significant relationship between behavior and the imaging Cost_mag indexes (R-squared = 0.432, $F(3,15) = 3.8$, $p = 0.033$). The regression coefficients highlighted the expected negative relationship between vector magnitude and RTs in BA18 (parameter estimate = -1.6, $p = 0.018$), with more negative Cost_mag values (i.e. larger costs) associated with larger increases of reaction times (RTs_{SDD} vs. RTs_{HD}). By contrast the coefficient in BA17 was unexpectedly positive (parameter estimate = 1.19, $p = 0.041$) and the coefficient in BA19 was not significant (parameter estimate = 0.14, $p = 0.78$). Control multiple regression analyses that considered only activity in the ROI representing the target and the salient-distractor did not reach statistical significance for the relationship between brain activity and reaction times costs (ROI_IN: R-squared = 0.29, $F(3,15) = 2$, $p = 0.16$; ROI_OPP: R-squared = 0.34, $F(3,15) = 2.55$, $p = 0.09$).

3.4. Dynamic causal modeling (DCM)

A central aim of the current study was to investigate the mechanisms governing the generation of the attentional biases on the representation of visual space in the occipital cortex. Specifically, we evaluated the contribution of feed-forward/feedback connectivity between the occipital cortex and the dorsal attention control network, and of the lateral connectivity within the occipital cortex. In order to assess these different mechanisms, we constructed six dynamic causal models and used Bayesian Model Selection (BMS) to identify the model most likely to explain our data. Because our aim here was to test specific hypotheses about attentional biases in the occipital cortex, rather than exploring the full dynamics of all the brain areas engaging in the current task, the dynamic causal models included only 5 areas: the 4 occipital ROI18 providing us with a representation of the visual space and one area in the PPC belonging to the dorsal fronto-parietal attention network (BA7, ROI_PPC). The visual area BA18 was chosen based on the bias vector results (see above), and the PPC because it has been consistently considered a main source of the attention biases in the occipital cortex (e.g. Kastner et al., 1999; Vossel et al., 2012, see also Discussion section). Each ROI was connected bi-directionally with all other ROIs and the models differed in terms of what connections could be modulated by the 12 attention conditions. The six dynamic causal models were organized into two families: the "diffuse PPC-BA18" family, where attention could modulate the connections between the ROI_PPC and all 4 ROI18; and the "focused PPC-BA18" family, where attention could modulate only the connections between the ROI_PPC and the occipital region representing the target quadrant (ROI18_IN). In each family, three DCMs embodied different patterns of attentional modulations between the occipital ROI18: modulation of all lateral connections, modulation of the connections from/to ROI18_IN only, or no modulation of the lateral connectivity (see Fig. 6, illustrating the whole DCM model space).

At the family level, BMS showed that the "diffuse PPC-BA18" family was most probable (> 99% posterior probability). This indicates that endogenous attention and visual salience most likely influence occipital activity *via* interactions between PPC and the full representation of the visual space coded by the 4 occipital ROIs, rather than selectively via modulation of the connectivity of the region representing the target quadrant (i.e. ROI18_IN, also cf. the bias vector results above).

At the model level, BMS showed that the dynamic causal model with the highest posterior probability included the modulation of the lateral connections between the ROI18_IN and the other 3 ROI18, in addition to the "diffuse" PPC-BA18 effects (see model in Fig. 6; > 99% posterior probability). Accordingly, endogenous spatial attention and visual salience operate not only by modulating top-down and bottom-up connectivity between the occipital cortex and the PPC, but also via the modulation of the lateral connectivity between the occipital region representing the attended quadrant (ROI18_IN) and the occipital regions representing the other parts of the visual field.

The choice of performing FFX-BMS rather than random effect (RFX) BMS was based on the fact that here the optimal model structure was expected to be the same across participants (Stephan et al., 2010). However, for completeness, we also performed the complementary RFX-BMS, which confirmed our FFX-BMS results: at the family level the "diffuse PPC-BA18" family was the most probable (exceedance probability = 94%) and at the model level, the Model 2 (diffuse PPC-BA18, plus occipito-occipital connectivity involving ROI18_IN only) was again selected as the most probable model (exceedance probability = 45%, with the second best model at exceedance probability = 27%). This indicates that our FFX-BMS results were not due to outliers in our pool of participants.

Finally, we used Bayesian Parameter Averaging (BPA) to explore how the experimental conditions affected the different connections of the winning dynamic causal model. The connectivity parameters related to each ROI18 were averaged as a function of the target location and compared across the display-conditions (HD, STD and SDD). The results showed that salient targets (STD vs HD) led to an increase of the bottom-up connectivity from the ROI18_IPSI to the ROI_PPC (posterior probability = 96.3%) and to a decrease of the connectivity between the ROI18_OPP and the ROI_PPC (posterior probability = 99.6%); see Fig. 7, on the left. The presentation of salient distractors (SDD vs. HD) lead to a more complex pattern of attentional modulations, affecting both the occipital-parietal connectivity and the lateral connectivity within BA18 (Fig. 7, on the right). Salient distractors lead to an increase of the top-down influence of the ROI_PPC on the target ROI_IN (posterior probability = 97.2%), as well as a decrease of the bottom-up signaling from the ROI_OPP (representing the salient distractor) to the ROI_PPC (posterior probability = 98.1%). This may correspond to a mechanism, mediated by the parietal cortex, seeking to maintain the processing priorities at the target location in spite of the salient distractor flashed in the opposite quadrant (see Discussion section). The analysis also showed that the presentation of the salient distractor yielded an increased lateral connectivity between the occipital ROIs. This included an augmented influence of ROI18_OPP to ROI18_IN (posterior probability = 99.7%), as well as a modulation of the connectivity between the ROI18_IN and the two ROIs representing visual locations without any target or salient distractors (ROI18_IPSI, posterior probability = 98.0%; ROI18_CONTRA, posterior probability = 96.9%, see Discussion section).

In sum, the DCM analyses demonstrated that both changes of the occipito-parietal connectivity and changes of the lateral connectivity between the occipital regions that represent the different visual locations contribute to shaping the attentional bias in the visual cortex. The PPC was found to interact not only with the occipital region that represents the target location (ROI18_IN), but also with the regions rep-

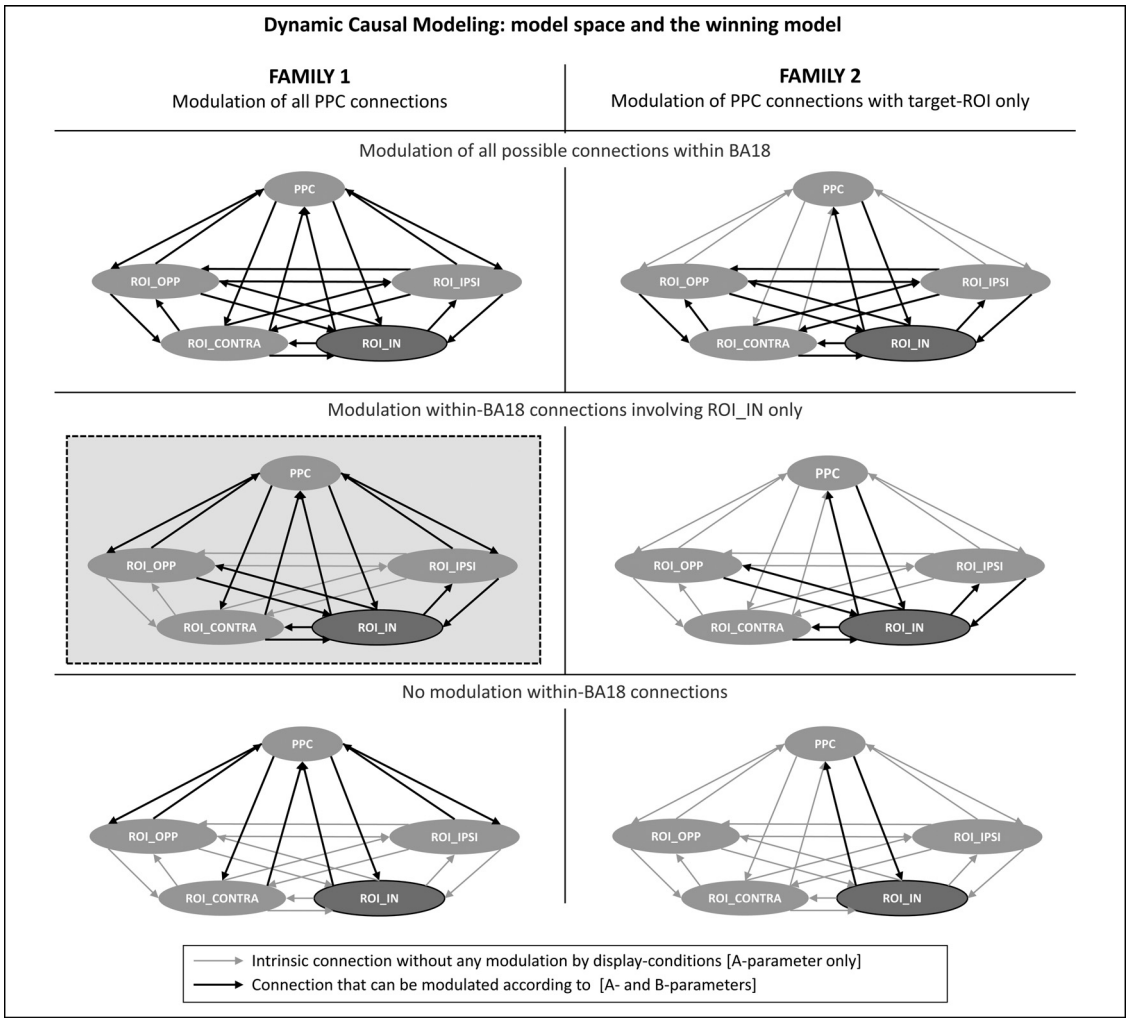


Fig. 6. Dynamic Causal Modeling: model space and the winning model [2-column fitting image | Grayscale Figure]. The model space served to test hypotheses concerning the attentional modulation of the connectivity between the posterior parietal cortex (PPC) and the four regions in BA18 that represent the visual field. All models comprised the same set of intrinsic connections [A-parameters] that reciprocally linked all 5 nodes. The models differed in terms of the connections that could be further modulated according to the 3 display-conditions [B-parameters]. The 6 models were partitioned in two families: Family 1 considers diffused interactions between PPC and all the occipital BA18 regions, while Family 2 considers that attention modulates only the connectivity between PPC and the occipital region that represent the target location (ROI_IN). In each family, 3 different models account for different patterns of effective connectivity within BA18: one model includes modulation of all connections between the 4 BA18 ROIs; the second model includes only the modulation of the connections involving the region that represents the target (ROI_IN); the third model does not allow for any attentional modulation of the intra-areal connectivity between the 4 BA18 ROIs. Black arrows highlight what connections can be modulated by the display-conditions, grey arrows represent connections that cannot be modulated by attention. Bayesian Model Selection revealed that the model most likely to explain the data included modulation of all the connections between PPC and BA18 and within-BA18 connectivity including only the region that represent the current target location (family 1, model 2: highlighted with dotted-line). PPC: Posterior parietal cortex; ROI_OPP/CONTRA/IPSI: ROIs opposite/contralateral/ipsilateral with respect to the ROI representing the target quadrant (ROI_IN).

resenting unattended locations of the visual field. Together with these diffused interactions between the parietal and the occipital cortex, the DCM analyses revealed significant changes of the connectivity between the region representing the target and the other occipital regions, in particular when the visual display included a salient distractor.

4. Discussion

We tested the joint influence of endogenous and exogenous spatial attention when participants were asked to judge a visual target presented among distractor stimuli. Our analyses focused on the modulation of activity in quadrant-specific occipital ROIs and on the effective connectivity between these areas and the PPC. We introduced a novel metric that, by using activity across regions representing different parts of the visual field, enabled us to index the direction and magnitude of the attentional bias in 2D space (*spatial bias vectors*) and we quantified the impact of endogenous and exogenous signals on this. The results revealed that both types of signals contribute to modulating the representation of 2D space in BA17, BA18 and BA19. Spatial endogenous attention was associated with a bias towards the target location and exogenous salience (color singletons) further modulated this spatial effect. Salience strengthened the spatial bias when the target was the color singleton, while it reduced the bias when a salient distractor was presented in the quadrant opposite to the target (Fig. 5). We found a significant correlation between these BOLD effects and the participants' reaction times, highlighting the behavioral relevance of the spatial bias vectors. The effective connectivity analyses revealed that the processing of salient signals involved both the modulation of lateral connectivity within the occipital cortex, as well as the bi-directional interactions between the occipital cortex and the PPC (Fig. 7). These findings demonstrate that the integration of endogenous and exogenous signals goes beyond the joint modulation of local activity, comprising instead the

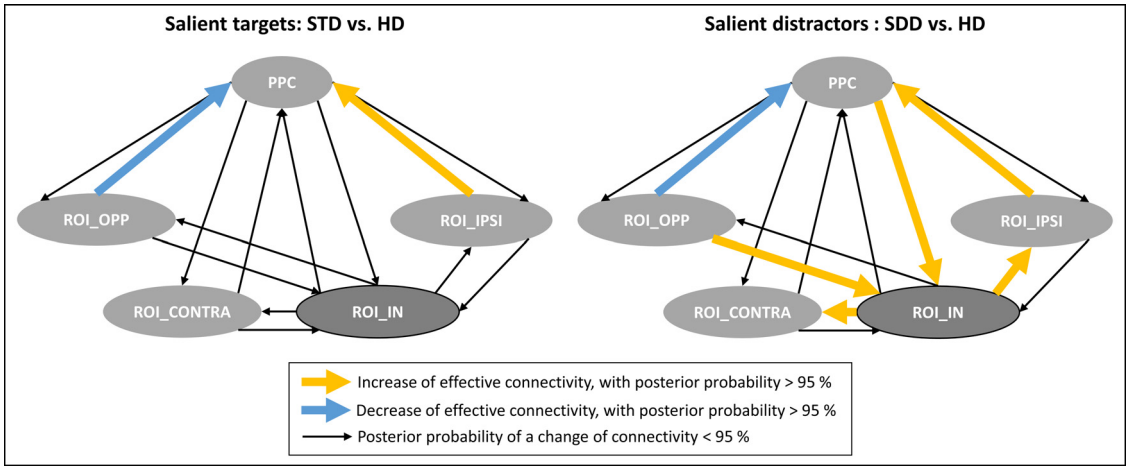


Fig. 7. Dynamic Causal Modeling: connectivity parameters of the winning model [1.5-column fitting image | Color Figure]. The wining model included diffused interactions between PPC and all the occipital BA18 regions. Bayesian Parameter Averaging of the winning model tested for the effect of "salient targets" (STD vs. HD, shown on the left) and the effect of "salient distractors" (SDD vs. HD, shown on the right). For each comparison, the thick-colored arrows highlight changes of connection strength with posterior probabilities equal or larger than 95%. ROI_OPP/CONTRA/IPSI: ROIs opposite/contralateral/ipsilateral with respect to the ROI representing the target quadrant (ROI_IN). Please note that the figure shows only the connections of the winning model that could be modulated by the experimental conditions [B-parameters], while the intrinsic connections that linked all 5 nodes of the model [A-parameters] are not shown here (cf., winning model highlighted in Fig. 6).

combination of bottom-up, top-down and lateral connections that governs competitive interactions and shapes the representation of space in the occipital visual cortex.

4.1. Endogenous spatial biases in the occipital cortex

A large body of previous work comprising both human neuroimaging and electrophysiology in non-human primates highlighted that endogenous spatial attention can modulate visual processing in the occipital cortex (Heinze et al., 1994; Desimone, 1998; Reynolds et al., 1999). Here, we used an independent localizer to map quadrant-specific ROIs in areas BA17, BA18 and BA19, and compared activity when endogenous attention was directed towards the location represented by the ROI (ROI_IN) versus activity in the opposite quadrant (ROI_OPP, i.e. the main effect of endogenous spatial attention). This showed that endogenous attention modulates occipital activity through the visual hierarchy, including quadrant-specific responses in anatomically-defined BA17, BA18 and BA19 (see Fig. 4). Of note, we found a robust modulation of activity in BA17 that corresponds to functional area V1. Attentional modulation in area V1 has been reported in several previous studies (e.g. Tootell et al., 1998; Martínez et al., 1999; Somers et al., 1999), typically using displays containing dense arrays of stimuli (Brefczynski & DeYoe, 1999; Martínez et al., 1999). Under these conditions, multiple items can fall inside the small receptive fields of V1 neurons and the attentional effects have been most often interpreted in the framework of the biased competition model (Desimone & Duncan, 1995; Kastner et al., 1999, 2001; Bles et al., 2006, also cf. the Introduction section). By contrast, the visual display in the current study comprised simple and isolated stimuli that were located too far apart from each other to activate the same neuron in V1 (see also Gandhi et al., 1999). Accordingly, mechanisms based on re-entrant feedback (Martínez et al., 1999; Martin et al., 2019), rather than the modulation of competitive interactions arising from feed-forward processing, are most likely to mediate the attentional effects in early visual areas that we observed in the present study, see also DCM results.

Besides highlighting the influence of endogenous attention in striate and extra-striate cortex, we characterized the spatial distribution of attention in 2D space. Previous studies demonstrated that spatial attention not only boosts responses in the occipital representation of the attended visual location (Kastner et al., 1999), but can also suppress activity associated with stimuli presented in other locations of the visual field (Smith et al., 2000; Heinemann et al., 2009). Thus, any comprehensive index of attentional selection should not rely only on changes of local activity. Several previous studies used multivariate approaches to characterize selective attention to visual categories (Reddy et al., 2009) and, in the context of spatial attention, Melloni et al. (Melloni et al., 2012) proposed an index based on the numerical difference between activity in the occipital regions representing target vs. activity in regions that represent the distractor stimuli. The latter accounts for any suppressive effect at the non-attended locations, but averages activity in regions that may play different roles in spatial selection (e.g. representations of within- vs. between-hemifields locations; Scalf & Beck, 2010). The vector analysis that we propose here takes into account the level of activity in the four regions that represent other regions of visual field and provide us with both "strength" and "direction" information, as jointly coded by the four regions.

Considering the HD condition only (i.e. displays without any exogenous signal), the analysis of the vectors magnitude confirmed the effect of endogenous spatial attention in BA17, BA18 and BA19. The analysis of the vectors direction added to this that the bias in BA19 entailed a significant deviation from the target direction (cf. Fig. 5). Specifically, the attentional bias was directed towards the target quadrant, but also included an overall hemifield effect. The latter would be consistent with increased attentional priority for stimuli presented in the same hemifield as the cued-target, compared with stimuli in the opposite hemifield. Here we could not directly probe such hemifield advantage, because all the targets were presented at the cued location (i.e. 100% cue validity). Moreover, due to the short cue-to-target interval, we could not separate cue-related preparatory activity vs. attentional modulation of target-related activity. Assessing these effects would require several additional conditions (e.g. targets presented at uncued locations, within vs. between hemifields conditions) and longer cue-to-target intervals. This was not possible in the current study that aimed to investigate the spatial interactions between endogenous and exogenous attention and already comprised a large number of experimental conditions, see also Fig. S1A [insert Fig. S1 ISM link here]. However, this issue has been addressed in a recent electroencephalography study that used the same target discrimination task as here (Rashal et al., 2022). Using both fully-predictive cues (as here) and no-cue trials, they showed that target selection (as captured by the "N2pc" component of the ERP) was observed

in the no-cue condition, but not following fully-predictive cues. From these results, we suggest that the effects of endogenous attention we observed here (main effect of ROI-type/endogenous attention in Fig. 4) most likely reflects early attentional selection of the cued quadrant than later target selection processes.

Further, the use of a larger set of functional localizers (e.g. color, motion) and including retino-topic mapping for each participant would enable studying how the different functional areas belonging to the anatomically-defined BA19 (i.e. V3, hV4, V5) contribute to generating the deviation of the bias from the target location. The latter is a limitation of the current study that used only anatomical constraints to categorize functionally-defined quadrant-specific responses to different levels of the visual hierarchy (cf. Fig. 2A-B). Nonetheless, the current results in BA19 highlight the relevance of the spatial bias vectors in capturing the distribution of spatial attention in 2D space; see also below for additional findings linking the vectors' characteristics with behavioral performance.

4.2. Joint influence of endogenous attention and exogenous salience

The main objective of the study was to investigate how endogenous and exogenous spatial signals jointly contribute to modulating activity in the visual cortex. For this, the current experimental design manipulated orthogonally the endogenously attended location (cued/target quadrant) and exogenous salience (display-condition). Standard analyses of local activity showed that visual salience led to quadrant-specific activation in all 3 BA-areas. The impact of salience was the same at the target location and at the distractor location, suggesting independent effects of the two types of control signals in the visual cortex (see also Sprague et al., 2018). Importantly, it should be noticed that here salience was not confounded with luminance, as the latter was matched for salient and non-salient stimuli and the red/green color of the salient singleton was counterbalanced across participants (cf. Betz et al., 2013 who reported contrast- rather than salience-dependent responses in V1-to-V3). The previous studies that assessed the interplay between endogenous attention and salience in the visual cortex provided us with mixed results (Melloni et al., 2012; Sprague et al., 2018; Won et al., 2020, see also Hopf et al., 2004, but using dense stimuli arrays). Melloni et al. (Melloni et al. 2012) reported a significant interaction between endogenous attention and the presence of salient distractors in area hV4, but not in areas V1, V2 and V3. By contrast, Sprague et al. (Sprague et al., 2018) reported significant effects of endogenous attention and stimulus salience throughout the visual hierarchy (V1, V2, V3A, hV4), but none of these areas showed a significant interaction (see also Poltoratski et al., 2017). Finally, a recent study by Won and colleagues (Won et al., 2020) demonstrated that prior knowledge about the presence of distractors modulates the representation of salience in a single ROI that included areas V1, V2 and V3. Many different methodological aspects may explain these inconsistencies, including how endogenous attention was operationalized (blocked vs. mixed condition-order in Melloni et al., 2012; fully-predictive central cues in Sprague et al., 2018; distractor frequency in Won et al., 2020), the manipulation of stimulus salience (color singletons in 4-items displays in Melloni et al., 2012 and Won et al., 2020; stimulus contrast in a 2-moving-items display in Sprague et al., 2018) as well as the different analysis approaches (target minus distractor activity in Melloni et al., 2012; reconstruction of spatial maps using an encoding model in Sprague et al., 2018; MVP classification accuracy in Won et al., 2020).

The one aspect likely to play a key role in determining the level of interaction between endogenous attention and salience concerns whether endogenous attention was fully focused at the target location or not, see also below. Melloni et al. (Melloni et al., 2012) and Won et al. (Won et al., 2020) employed search tasks entailing some uncertainty about the location of the target, while Sprague et al. (Sprague et al., 2018) and the current study used 100% valid spatial cues and thus endogenous attention was fully focused at the target location. The two studies that used search tasks (Melloni et al., 2012; Won et al., 2020) revealed significant interactions between endogenous attention and salience, both at the behavioral level and in the imaging data. By contrast, the behavioral data collected under fully-predictive cues did not demonstrate any significant effect of salience (here and in Sprague et al., 2018), in agreement with previous behavioral studies indicating that endogenous control can abolish interference by salient distractors (e.g. Leber & Egeth, 2006; Leber et al., 2016; see also Luck et al., 2021; see also Rashal et al., 2022).

Nonetheless, at the imaging level both the current study and Sprague et al. (Sprague et al., 2018) found a robust activation of the visual cortex associated with the presentation of salient distractors. Further both studies computed spatial indexes in 2D space. Sprague et al. (Sprague et al., 2018) utilized an encoding model to reconstruct detailed 2D spatial maps indexing BOLD activity across the whole visual space, while here we used a simpler vector representation. Sprague et al. (Sprague et al., 2018) approach provides us with a detailed view of the representation of visual space, but the subsequent analyses relied on comparing activity in the reconstructed maps, without directly testing for possible changes in the geometrical characteristics of the 2D maps. By contrast, the spatial bias vectors used here comprise magnitude and direction information allowing us to assess separately the impact of salience on the strength of the attentional bias and its direction with respect to the target location. The analyses of vector magnitude demonstrated that salience modulated the spatial bias in all three BA-areas. In BA18 and BA19, we found that salient targets strengthened the attentional bias, while salient distractors reduced the bias. In BA17, the effect of singleton-distractors was also highly significant, but salient targets did not lead to any significant change of the bias magnitude compared with the no-salience condition (HD). The vector analyses did not reveal any significant change of the bias direction in any of the three BA-areas. However, it should be noticed that the salient distractors were always presented in the quadrant opposite to the target. This was done to restrict the total number of experimental conditions, but prevented us from testing the prediction that salient distractors in the contralateral - or the ipsilateral - quadrant would yield not only a reduction of the vector magnitude but also shifts of the vector direction. Nonetheless, additional analyses highlighted that the change of magnitude of the spatial vectors upon the presentation of salient distractors correlated with the corresponding reaction times costs, supporting the relevance of the 2D vectors' metrics.

These results, together with the robust response to salience in all tested visual areas, indicate that salient signals were not entirely suppressed despite the lack of any overall (mean) effects at the behavioral level. This adds to the long-lasting debate concerning the suppression of irrelevant salient distractors (Folk et al., 1992; Theeuwes, 1994b; Luck et al., 2021). Specifically, there has been recent discussion about whether fully irrelevant salient items generate "attend-to-me" signals in the brain even though they do not imply behavioral costs (Geng, 2014; Geng & Duarte, 2021; Luck et al., 2021). Sprague and colleagues (Sprague et al., 2018) found systematic salience signatures in the visual cortex without any behavioral gain (salient target) or cost (salient distractor), but did not provide any model of the suppression mechanisms that may explain the so-called discrepancy between brain-level and behavioral-level results. Here, we performed analyses of effective connectivity that allowed us to study the fate of exogenous signals, as a function of whether they were presented at the endogenously attended (STD condition) or unattended (SDD) location, and we discuss this in relation to recent accounts of distractor suppression (Geng, 2014; Anderson, 2021;Geng & Duarte, 2021; Luck et al., 2021), see next section.

4.3. Effective connectivity underlying the processing of salient signals in the visual cortex

Mechanisms of distractor processing have been most often associated with high-level regions in the frontal and parietal cortex

(Melloni et al., 2012; Suzuki & Gottlieb, 2013; Won et al., 2020). The PPC is thought to play a central role, as the strength of its top-down influences on visual areas has been proposed to determine the fate of irrelevant distractors (Won et al., 2020, and see Geng, 2014 for a review). Further, competitive interactions between relevant targets and irrelevant distractors can take place locally within the PPC, where priority maps would enable attentional selection by enhancing relevant signals and suppressing distractor signals at irrelevant locations (Gottlieb, 2007; Ptak, 2012; Geng, 2014; Zelinsky & Bisley, 2015; Bisley & Mirpour, 2019). Concurrently, competition at the level of the occipital sensory areas has been shown to contribute to attentional selection and distractor suppression (Luck et al., 1997; Reynolds et al., 1999; Reynolds & Desimone, 2003), leading to the proposal that also the occipital cortex comprises attentional priority maps (Mazer & Gallant, 2003, but see Betz et al., 2013).

Here, we assessed the role of the occipital-parietal connectivity and of the lateral interactions within the occipital cortex using DCM (Friston et al., 2003). We compared a set of models that differed in terms of how attention modulates these patterns of connectivity. The model space was designed with the aim to evaluate: 1) whether attention affects the occipital-parietal connectivity selectively for the target quadrant (ROI_IN), or it modulates also the connectivity between the parietal cortex and the other occipital ROIs; and 2) whether attention modulates the lateral connectivity between all the 4 occipital regions, the connectivity of the target-quadrant ROI only, or none of the lateral connections. In order to limit the number of nodes in the model, the DCM analysis considered only the 4 occipital ROIs belonging to BA18, where we found the most reliable correlation between the spatial vector magnitude and reaction times. Bayesian Model Selection (Stephan et al., 2010) showed that the most likely model to explain the data comprised attentional modulation of all the occipital-parietal connections, plus the modulation of the lateral connectivity of the ROI_IN only.

These results indicate that multiple mechanisms can mediate the effect of attention on the representation of 2D space in the occipital cortex. Specifically, our activation data demonstrated that endogenous attention and salience jointly modulate the representation of 2D visual space, beyond just affecting the activity of the regions that represent the target and the salient distractors (cf. above). The DCM results indicate that the spread of attentional effects across the different occipital regions can take place via multiple routes. First, the finding that attention modulates the connectivity between the PPC and all 4 visual ROIs provide us with an "indirect route" that would allow salient signals to be first transmitted to the PPC via feed-forward connectivity, and subsequently affect processing in all the visual areas via feed-back from PPC to the occipital cortex. In line with this, previous studies showed that attentional effects in the occipital cortex follow in time the activation of higher-level control regions in the parietal cortex (Martínez et al., 1999; Martin et al., 2019). Using high-temporal resolution intracranial electroencephalography, Martin et al. (Martin et al., 2019) showed that after the initial feed-forward response to the stimulus-onset in the occipital cortex, spatially-specific modulatory feedback spread sequentially from parietal cortex back into the visual hierarchy, with increasing latencies from higher to lower areas (see also Lauritzen et al., 2009). In the current study, convergent projections from the occipital regions that represent the different quadrants to the PPC would enable target and salient-distractors to interact, despite the large spatial separation between target and distractors. Feed-back connectivity from the PPC to the occipital cortex would then carry information about stimuli at far-apart locations, allowing such signals to affect activity also in visual areas that contain neurons with small receptive fields (e.g. BA17/V1 and BA18/V2).

Consistent with a role of PPC in the processing of salient distractors, Bayesian parameter averaging that tested for attention-related changes of effective connectivity revealed both a reduction of the feed-forward connectivity between the visual region activated by the salient distractor (ROI_OPP) and an increase of the parietal feed-back on the occipital region representing the target (ROI_IN; cf. Fig. 7, panel on the right). The strengthened top-down effect is consistent with the mechanism described above and may reflect the "choice" of the currently relevant location, following competitive interactions between endogenous attention and salience at the level of the parietal cortex. Concurrently, the reduction of feed-forward connectivity from ROI_OPP to the PPC suggests that attention can counteract the augmented occipital activity generated by the salient distractors. Specifically, unlike previous studies reporting that endogenous attention results in a suppression of activity at unattended locations (Smith et al., 2000; Heinemann et al., 2009), here we found no reduction of salient-distractors activity (cf. main effect of salience, Fig. 4). Instead, the DCM results showed a decrease in the efficiency with which these signals propagate from the occipital to the parietal cortex. The latter may constitute an additional mechanism that reduces the impact of salient irrelevant stimuli on any parietal mechanism that integrates attentional signals at the local level (cf. priority maps, Gottlieb, 2007; Ptak, 2012; Zelinsky & Bisley, 2015; Bisley & Mirpour, 2019). These results come in support of theoretical views that attentional priority processing emerges from computations taking place in different brain areas (Corbetta & Shulman, 2002; Vossel et al., 2012, 2014 Geng, 2014; Anderson, 2021). In other words, the presence of the neural signature of an irrelevant salient item does not imply that the output behavioral response will be substantially affected by this item: other regions of the fronto-parietal attentional network (here the PPC) can suppress the bottom-up signal generated by the irrelevant salient item so that attentional priority is reorganized and focused on the target item (Geng, 2014; Geng & Duarte, 2021; Anderson, 2021).

It should be noticed that our DCM analyses included a single node belonging to the fronto-parietal attention control networks (i.e. the ROI_PPC). The reason for this was that our hypotheses targeted the role of lateral connectivity within occipital cortex vs. the connectivity between these quadrant-specific regions and higher-order regions. The choice of the PPC was dictated by extensive evidence pointing to this region as the source of attentional modulation on the visual cortex (e.g. Buchel, 1997; Vossel et al., 2012, see also Desseilles et al., 2011 for modulation of V1). Nonetheless, it should be acknowledged that many other areas - and paths - are likely to be involved in the current task. These include dorsal premotor regions that have been found to exert top-down influences on the occipital cortex (Buchel, 1997; Melloni et al., 2012, and see Moore & Armstrong, 2003 for single-cell electrophysiology) and that, together with the PPC, contribute to the integration of bottom-up and top-down signals for visuo-spatial attention control (Brázdil et al., 2007; Buschman & Miller, 2007; Ibos et al., 2013; Suzuki & Gottlieb, 2013; Bowling et al., 2020). In addition, the PPC is often identified as a spatially-specific map of the environment responding to both goals and salience (Gottlieb, 2007; Ptak, 2012, see also spatial mapping of the PPC, Silver & Kastner, 2009; Mackey et al., 2017) and has been shown to respond bilaterally to salient distractors (Won et al., 2020). However, there is also evidence supporting that the left and right PPC are associated with different aspects of salience processing. Using transcranial magnetic stimulation, Mevorach et al. (Mevorach et al., 2006) and Hodsoll et al. (Hodsoll et al., 2009) showed that the right PPC was associated with the selection of salient stimuli, while left PPC was associated with the ability to ignore salient stimuli. Accordingly, future work should seek to examine the spatial specificity of target/distractor effects - at the same time - in the occipital cortex and in the posterior parietal cortex (plus possibly other regions of the dorsal fronto-parietal network, e.g. FEF: frontal eye-field). This would help to better understand the relationship between mechanisms of spatial attention in the occipital cortex (as in the present study, and see also Melloni et al., 2012; Sprague et al., 2018; Won et al., 2020) and in hierarchically higher areas related to attentional control. Moreover, our model did not include any node belonging to the ventral attention system (TPJ: temporal-parietal junction, and IFG: inferior frontal gyrus). These regions are typically associated with re-orienting towards salient task-relevant stimuli (Corbetta et al., 2000) or irrelevant stimuli that share some feature with

the target (Natale et al., 2010). Dorsal and ventral fronto-parietal regions are thought to work together during visuo-spatial attention control (Corbetta & Shulman, 2002; Corbetta et al., 2008; Vossel et al., 2012; DiQuattro et al., 2014) and, most likely, participated to the current attention task together with the PPC.

Most important here, our DCM results showed that beside any interaction between the occipital cortex and higher-order fronto-parietal regions, attention modulated the effective connectivity within the occipital cortex. The winning model included modulation of the connections of only the region representing the current target location (ROI_IN). As noted above, the role of attention in modulating competitive interactions in the visual cortex is well understood in the framework of the biased competition model (Desimone, 1998; Beck & Kastner, 2005; Yantis, 2005), but such interactions require target and distractor stimuli to fall within the receptive field of the same neuron. This was most likely not the case for area BA18 in the current study, which included stimuli presented at a distance of 10° and across the visual quadrants. One previous study directly addressed the influence of attention on the pattern of connectivity between occipital regions representing locations further apart in the visual field (Haynes et al., 2005). The study targeted the integration of information across distant locations, when attention was divided between two quadrants while the other two quadrants contained unattended distractors. The analyses of effective connectivity considered the 4 ROIs representing the 4 quadrants, in V1, V2 and V4. Attention was found to modulate the connectivity between the different levels of the visual hierarchy (feed-forward and feed-back), as well as to increase the lateral connectivity between the 2 ROIs representing the two attended quadrants within the same area.

Unlike this previous study, here the attention task implied selecting the stimulus at the target location, while ignoring the stimuli in all the other quadrants. Bayesian parameter averaging that tested for changes of lateral connectivity in the salient distractor condition (SDD vs. HD, see Fig. 7, right panel) showed that the color-singleton augmented the influence of the ROI_OPP (i.e. the region receiving the salient input) on the target-quadrant ROI_IN, as well as the outgoing connectivity from ROI_IN to both ROI_CONTRA and ROI_IPSI. We propose that these effects reflect fast exogenous influences signaling the presence of salient stimulus (see also Martin et al., 2019, reporting fast attentional effects in the early visual cortex that are inconsistent with parietal feed-back mechanisms). Here the spreading of salience-related signals through all the occipital regions, including the ROIs representing locations contralateral and ipsilateral to the target location (ROI_CONTRA and ROI_IPSI), seems consistent with the results of the bias vector analysis showing that, in terms of correlation with reaction times, the impact of salient distractors correlated with the bias vectors computed using the combined activity of the 4 occipital ROIs (cf. above). Also, the finding of significant changes between the ROI_IN and both CONTRA and IPSI ROIs fits with the observation that salient distractors impacted on the vector's amplitude but not on direction. Indeed, any differential effect over the two ROIs - with the resulting unbalance of the local activities - would result in a shift of the bias vector direction towards the quadrant represented by the most active ROI.

In the framework of DCM analyses, it is important to stress that the attentional modulation of the lateral occipital-to-occipital connectivity does not imply the existence of any direct, mono-synaptic anatomical connection between the occipital ROIs. Instead, signaling via subcortical regions (Martin et al., 2019) and/or reentrant circuits involving higher-order areas (Haynes et al., 2005; Turova & Rolls, 2019) may mediate the observed changes of effective connectivity. Furthermore, it should be noted that here we compared a restricted set of DCM models, but a large number of alternative models could also be tested by combining the presence or absence of specific intrinsic connections (A-parameters, which were not manipulated here) and/or more specific combinations of the modulatory effect of the experimental conditions (B-parameters). Nonetheless, the current finding that intra-occipital connectivity operates in addition to any interactions between the occipital and the parietal cortex supports the notion that attentional selection should be understood in terms of distributed representations of space, rather than just the modulatory influence that the fronto-parietal control network exerts on the visual cortex. Future studies could address this further, for example, by interfering (e.g. via transcranial magnetic stimulation) with attentional control via stimulation of occipital regions that represent spatial locations other than those containing the target or the salient distractor. Based on the current results, we anticipate that this would contribute to biasing the 2D representation of space within the occipital cortex, also affecting the processing of target/distractors presented at different locations in the visual field.

5. Conclusions

We investigated how endogenous spatial attention and stimulus salience contribute to quadrant-specific activations in the occipital cortex. We quantified the impact of attention on the representation of visual space by using a vectorial index that provided us with both magnitude and direction of the attentional bias in 2D space. We found significant effects of endogenous spatial attention in anatomically-defined BA17, BA18 and BA19, including an overall hemifield bias in BA19. Salient target-singletons enhanced the attentional bias magnitude, while salient distractors reduced it. The latter was found to correlate with the corresponding reaction times costs. Analyses of effective connectivity revealed that both occipito-parietal connectivity and lateral influences within the occipital cortex explain these distributed attentional effects. These findings demonstrate that endogenous and exogenous attention jointly contribute to shaping processing priorities in the occipital cortex and highlight that multiple functional paths determine how information about these two types of signals is distributed across the different regions that represent visual space.

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Data availability statement

Processed imaging data are available on the EBRAINS platform: https://search.kg.ebrains.eu/instances/cd4c0231-f9d6-4964-9763-54347029dd00.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2022.119206.

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