Frontopolar Activity Carries Feature Information of Novel Stimuli During Unconscious Reweighting of Selective Attention

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Abstract

Adapting to novelty is essential for an organism's survival in an uncertain world. Neuroimaging evidence consistently links the anterior prefrontal, specifically the frontopolar cortex (FPC; BA10), to exploratory reweighting of attentional weights thereby underscoring the role of the FPC in responding to environmental changes that are often complex and may occur very rapidly. Here we report new evidence showing that the FPC serves a role in attentional reallocation even in the absence of conscious awareness. Both mass-univariate and multivariate pattern analyses of fMRI data revealed that the right FPC and other attention-related areas not only are sensitive to unaware changes in the relevant stimulus dimension, but also that unconsciously processed information of the novel stimulus was globally represented across these regions. Our results indicate that unconsciously processed information can reach a global level of representation outside the occipitotemporal cortex, and that the FPC is crucial for the reweighting of selection biases in the absence of visual awareness.

Highlights

- Frontopolar cortex (FPC) drives the exploratory reallocation of attention even in the absence of visual awareness.

- FPC signal changes in response to invisible stimulus changes.

- Successful decoding of stimulus-specific information in FPC and other attention brain areas.

1 Introduction

The frontopolar cortex (FPC) is uniquely large in the human brain and possesses a distinctive cytoarchitecture (Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 2001; Ramnani & Owen, 2004; Petrides, Tomaiuolo, Yeterian & Pandya, 2012). With its high number of spines and synapses it appears particularly suited for the integration of information (Jacobs et al., 2001; Ramnani & Owen, 2004). FPC plays a pivotal role in human cognition, where it ranks at the top of a high-level executive control system orchestrating our behavior by temporally organizing top-down strategic processing for goal-directed action (Cohen, Botvinick & Carter, 2000; Fuster, 2002; Ramnani & Miall, 2004). Only recently, frontopolar function has also been investigated in non-human primates. Bilateral FPC lesions increased conflict adaptation in a

Wisconsin Card Sorting-like task (WCST; Grant & Berg, 1948) in which the animals needed to adapt to frequently changing task rules (Mansouri, Buckley, Mahboubi & Tanaka, 2015). Importantly, FPC lesions did not affect the ability to follow the rule switches of the WCST, in contrast to frontal lesions posterior to FPC. In a human fMRI study utilizing a comparable WCST task, FPC activation signaled the presence of interfering task rules (Konishi, Chikazoe, Jimura, Asari & Miyashita, 2005). Again, FPC activation was not affected by rule changes per se, whereas this was observed more posteriorly, in the left inferior frontal cortex. These data exemplify a pattern that suggests a vital role of FPC in exploratory shifts of attentional selection, which is further supported by findings from the literature on decision making (Daw et al., 2006; Boorman, Behrens, Woolrich & Rushworth, 2009; Kovach et al., 2012; Beharelle, Polanía, Hare & Ruff 2015).

In line with this notion, studies in the visual search domain showed that attention changes between feature dimensions (Pollmann, Weidner, Müller & Cramon, 2000) or, likewise, between locations (Lepsien & Pollmann, 2002) went along with increased BOLD signal in the FPC. Importantly, exploratory attention shifts were assumed to be implicit, namely, to occur without volitional orienting of attention to the new feature. In line with this assumption, FPC activation was also observed in response to changes in target-distractor contingencies that were learned implicitly: even though distractor configurations were not remembered explicitly, the violation of contingencies between

learned target locations and specific distractor configurations activated FPC (Pollmann & Manginelli, 2009a; 2009b). Yet, the search tasks used in the above studies employed fully visible stimuli that were consciously seen and attended to on every trial. Hence it is unclear whether the role of the FPC in re-weighting of selection biases extends to changes of unconsciously processed stimuli.

To tackle this question, we developed a novel visual masking paradigm in which a Gabor patch was presented centrally followed by a backward mask to minimize the patch's visibility. The spatial orientation of the target stimulus randomly repeated or changed on a trial-by-trial basis and volunteers were obliged to distinguish between vertical and non-vertical orientations. At the end of each trial, we asked them to rate the target visibility using an adaptation of the perceptual awareness scale (PAS; Ramsøy & Overgaard, 2004). Prior to this study, we provided behavioral evidence that attentional re-selection in response to a target change occurred in the full absence of visual awareness (Güldener, Jüllig, Soto & Pollmann, 2021). However, the role of the FPC in supporting this process remained untested. Here we used functional MRI to address this question using the experimental paradigm described above.

In line with our previous findings, we expected attentional adaptation to occur as soon as a given grating possessed the same orientation as the previous one (one-trial learning; Boschin, Piekema & Buckley, 2015) resulting in a selection bias favoring the repeated orientation. Conversely, this attentional bias should be disrupted and adjusted

as soon as the novel grating´s orientation differed. Such reorienting of attentional resources in response to an orientation change in these *switch trials* was expected to result in reaction time switch costs on the behavioral level and to increase the BOLD response in FPC (Pollmann, Weidner, Müller & Cramon, 2000). Consequently, we used the RTs obtained in the orientation discrimination task as a proxy to measure attentional reorienting processes. Participants' perceptual decisions were analyzed by means of signal detection theoretic measures in combination with visibility ratings to measure visual (un)awareness and isolate unconscious information processing (Wiens, 2007; Soto, Sheikh & Rosenthal, 2019). Visual unawareness was associated here with null perceptual sensitivity in those trials subjectively rated as unaware. This approach precluded confounds arising from individual response criterion shifts in reporting subjective awareness.

Importantly, we manipulated the proportions of the two non-vertical gratings (left vs. right) presented in a single block by presenting one tilt twice as often as the other tilt. We hypothesized that the increase of the frequency at which a certain tilt (i.e., a grating tilted to the left or right) was presented will boost the attentional selection weight for this tilt, consistent with feature-based statistical learning (Turk-Browne et al., 2009; Chetverikov et al., 2017). Thus, particularly switch trials in which the prior orientation was the highly frequent tilt should show increased behavioral response latencies (e.g., Leber et al., 2009; Chetverikov et al., 2017).

Critically, we also tested whether the FPC activation pattern carried information about the grating's orientation in the non-conscious trials by using multivariate pattern analyses. Recent research has shown that consciously processed stimuli in working memory can be decoded from BOLD activity patterns from regions across the entire attention network (Corbetta, Patel & Shulman, 2008) like the left superior precentral gyrus, bilateral superior parietal lobule (Ester, Sprague & Serences, 2015), and representations of task-relevant feature dimensions can be found in the frontal eye field and left prefrontal cortex (lPFC) including FPC (Reeder, Hanke & Pollmann, 2017). Furthermore, unconscious perceptual contents (i.e. living vs non-living categories) can be decoded from brain activity patterns in prefrontal regions (Mei, Santana and Soto, 2022). Here, we tested the role of FPC in representing the relevant informational content during reorienting of attention across different states of visual (un)awareness. It has been shown that cortical representations of subjectively versus objectively invisible stimuli may differ (Stein, Kaiser, Fahrenfort & van Gaal, 2021; but see also Mei, Santana and Soto, 2022). Stein and colleagues asked participants to perform a visual discrimination task distingushing between masked houses and faces. The key finding was that the processing of objectively invisible stimuli was restricted to visual (shape-related) object properties processed in early, lower-level visual areas, while the processing of subjectively invisible stimuli reached up to more categorical levels of representation in higher-level category-selective areas. However, this pattern of results may change once the stimulus processing is affected by attentional modulation (i.e,

difference of goal relevance between stimulus types). Here we aim at testing whether feature representations of objectively unaware stimuli can reach a more global level of processing extending from occipital cortex up to frontopolar cortex if the represented object feature is associated with a higher attentional weight.

2 Methods and procedure

2.1 Participants

In total 25 native German students (11 female) from the University of Magdeburg, Germany were recruited. The volunteers were 20 to 39 years old ($M = 24.08$ years), all right-handed by self-report, and had normal or corrected-to-normal vision. They provided written consent and were either monetarily reimbursed (8 euros per hour) or received course credits for the two hours of participation. The local ethics committee gave approval for conducting this study. A total of 8 participants were excluded prior to the main fMRI experiment: 3 participants interrupted the session during the calibration or the main experiment and were thus excluded and 2 other participants were excluded as they reported insufficient correction of their impaired vision using the MR compatible lenses. Three participants did not successfully pass the calibration, i. e. even after multiple repetitions we were not able to determine a stable threshold of the stimulus' luminance contrast. Out of the 17 participants that took part in the fMRI experiment, three reported a very low number of subjectively invisible trials despite the initial

calibration (less than 5% of all trials); this was insufficient for statistical analysis and they were thus excluded. Hence, the following report is based on a final sample size of n = 14.

2.2 Apparatus & Stimuli

The stimulus display and responses were controlled with PsychoPy (Peirce, 2019). The stimuli were back-projected onto an 18-inch screen placed in the bore of the magnet behind the participant's head. The projector's resolution was 1920 × 1080 pixels with a 60 Hz refresh rate. Participants viewed the screen via a mirror placed on top of the head coil. Stimuli were Gabor gratings with an individually calibrated Michelson contrast and a spatial frequency of 3.703 cycles per degree. They were centrally presented on a grey background and subtended 3.437° visual angle. The gratings' orientation was either vertical (180°), 165°, 150° or 135° if it was a left-tilted, non-vertical Gabor patch, and 195°, 210° or 225° if it was a non-vertical patch tilted to the right. To further reduce the visibility of the Gabor patch we used a circular backward mask of black and white random dots (3.437° visual angle).

2.3 Experimental procedure

2.3.2 Threshold Determination. All experimental sessions took place in the MR scanner (Siemens Prisma, Erlangen, Germany) of the Neurology Department of the University of Magdeburg, Germany. After placing the participant inside the scanner, the session started with a 1-up:1-down adaptive staircase procedure (adopted from Jachs,

Blanco, Grantham-Hill & Soto, 2015) to determine the stimulus´ luminance contrast for the first trial of the main experiment. Gabor patches occurred centrally on the screen for 33 ms directly followed by a random-dot mask for 350 ms. If participants saw the grating´s orientations they were to respond by pressing the "2" button, while the "1" button was to be pressed if they did not see anything at all. In the following main experiment participants would rate the subjective visibility of the target at the end of each trial using the four-point perceptual awareness scale: 1: "did not see anything at all", 2: "saw a brief glimpse without seeing the orientation", 3: "had an almost clear image of the stimulus", 4: "saw the stimulus and its orientation" (Ramsøy & Overgaard, 2004). During initial calibration, participants were thus instructed to give an unaware response only if they did not see anything at all which corresponded to the "1" rating of the PAS. Conversely, they were to give an aware response, corresponding to the remaining three points of the PAS whenever a brief glimpse or a more stable percept of the Gabor grating was experienced. The Gabor's luminance contrast was increased following an unaware response and further decreased following an aware response.

Each participant completed 90 trials (30 trials for each of the three orientations) and the percentage of aware responses was calculated on a trial-by-trial basis. The subjective awareness threshold was reached when the percentage of aware responses was about 50% over the last ten trials. Then, the final threshold luminance contrast was defined as the mean luminance contrast across the last ten trials of the staircase. If the

individual threshold was not reached within the 90 trials, the staircase was repeated. Next, participants performed one block of training under experimental conditions consisting of 36 practice trials. Here, the luminance contrast obtained with the first staircase procedure was used for the contrast value of the training stimuli. The practice phase was followed by a second calibration conducted according to the same protocol as the first staircase procedure. This recalibration provided the threshold value for the luminance contrast used in the first trial of the main experiment. On later trials, this value was further adjusted. If the grating's visibility was rated with a 2, 3 or 4 on the PAS, the contrast value was decreased in the next trial. If the grating was rated as being invisible (AL1), the contrast value was increased instead.

2.3.2 Main Experiment. In the main experiment, volunteers were asked to perform an orientation categorization task based on the masked Gabor patches presented in the center of the screen. Participants had to quickly make a forced-choice response with two custom buttons, deciding if a vertical or non-vertical grating had been presented. In each trial, after the categorization response participants rated how well they perceived the orientation of the masked grating using the four-point perceptual awareness scale. As we were particularly interested in examining differences between unaware and aware trial conditions, we aimed to achieve a maximum number of trials with unaware 1-ratings respectively aware 3 or 4-ratings. Thus, the luminance contrast was adjusted on every trial after the participants rated their subjective awareness: the

luminance contrast value was further decreased following trials rated as fully aware (AL4), almost fully aware (AL3), and residually aware (AL2), and increased if the participant reported being fully unaware of the orientation (AL1).

A trial started with the brief presentation of a central fixation cross for 500 ms, followed by a blank screen for another 500 ms. Next, the target Gabor occurred at the center of the screen for 33 ms. The mask followed immediately for 350 ms. Subjects were trained to give their categorization response during the next 1500 ms following the onset of the Gabor. Following this, they had another 2.5 s to rate the subjective visibility of the Gabor using a keyboard with four keys. Figure 1 shows an example of a trial sequence, as well as a depiction of the experimental conditions.

All trials were separated by inter-trial-intervals (ITI) with varying durations (1.5 - 3.5 s) following a logarithmic distribution. All volunteers that passed the calibration process completed 10 runs of the main experiment (360 trials) in the MR scanner. However, due to the subjective awareness rating, the total number of trials for each level of awareness varied across runs and subjects and so did the number of runs that were analyzed. After completing the main experiment each participant was asked whether he or she had general comments on her experience during the task and whether they had noticed any differences in the presentation frequencies of the three orientations. A complete fMRI session including the calibration, recalibration, training, and main experiment lasted two hours.
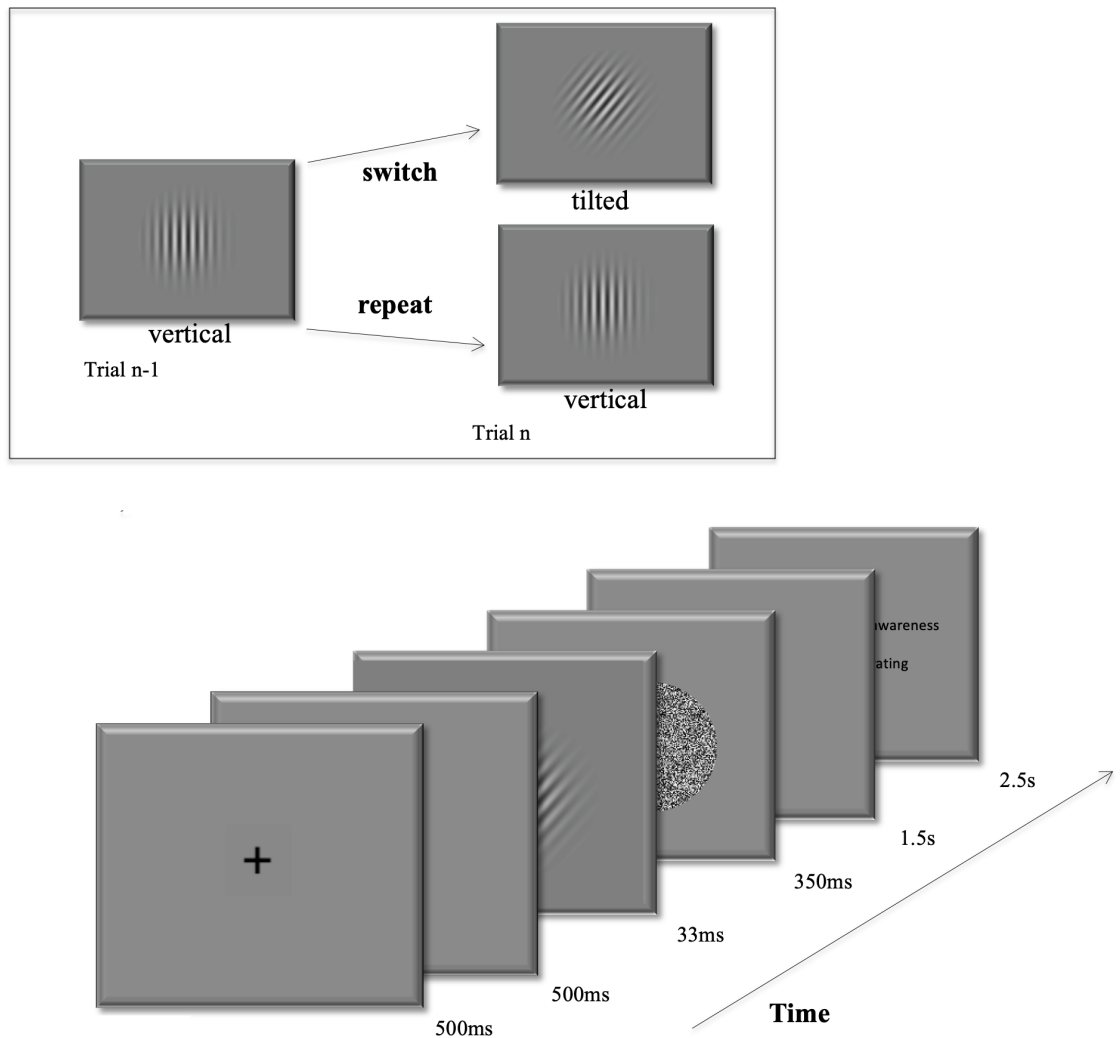
Fig. 1: The scheme on the top left shows an example of the two critical experimental conditions: a vertical target grating in the first trial is followed by another vertical grating in the second trial (repeat) versus a tilted target follows after a vertical target orientation (switch). Figure bottom: example of a trial sequence. A trial started with a central fixation presented for 500 ms followed by a blank of the same duration. Next, the target grating appeared for 33 ms followed by the backward mask with a duration of 350 ms. After the mask's offset another 1.5 s remained for the categorization response. At the end of the trial, participants were asked to rate their subjective level of awareness using the 4-point PAS.

2.4 Design

Although the categorization task demanded participants only to discriminate vertical from tilted orientations, irrespective of the specific direction of tilt, we expected attentional weighting of left versus right tilt, so that attentional resources would be allocated to discriminating the most recent tilt direction from vertical based on analogous attention weighting effects observed in visual singleton search tasks (Müller, Heller, & Ziegler, 1995). This attentional weighting was expected to lead to reduced response times when the tilt direction repeated (e.g. left following left tilt) irrespective of the exact orientation of the grating (e.g. 165°, 150° or 135°) compared to longer response times if the tilt direction changed.

To boost tilt-based attention weighting, we manipulated the likelihood of the two non-vertical gratings (left versus right): by increasing the frequency at which left or right-tilted gratings occurred, the attentional weighting of this orientation should be enhanced, while it should be reduced for the less frequent orientation (Desimone, 1996; Henson & Rugg, 2003). Thus, tilt-change costs were expected to be higher if the change occurred from the frequent to the infrequent orientation than vice versa. Additionally, if attentional weighting towards the frequent tilted orientation is used to facilitate the discrimination between a vertical and a tilted grating, this should result in higher tilt-change costs following the switch from the frequent tilt to vertical compared to the

change from infrequent tilt to vertical as in the former case more attentional weight needs to be re-weighted, while in the latter case attentional reorienting should be relatively easy because the attentional weighting for the target preceeding the orientation change should be only weak. Hence, within a single run consisting of 36 trials, the stimulus orientation was set to be vertical in 12 trials (~33%). The two non-vertical orientations, however, occurred in uneven proportions with 18 trials (50%) and six trials (~16%), respectively. Thereby we obtained either left- (75% of all non-vertical trials with a left-tilted grating) or right-weighted (75% of all non-vertical trials with a right-tilted grating) blocks, each containing frequent and infrequent non-vertical orientations in random order.

2.5 Statistical analysis

2.5.1 Sensitivity analysis. Signal detection theory (Stanislaw & Todorov, 1999; Macmillan & Creelman, 2004) was used to assess participants' ability to correctly categorize vertical and non-vertical gratings for each level of subjective awareness. We determined individual response biases (criterion location C) and sensitivities (A') using Python (version 3.6. Available at http://www.python.org) and tested these measures on group level with Bayes factor analysis (e.g. C = 0 and A' = 0.5). All statistical analyses were carried out with R (Version 3.5, R Core Team, 2012): for the Bayes factor (BF) analysis (Rouder, Speckman, Sun, Morey, & Iverson, 2009) we used the R-package

BayesFactor. False-positive rates (FPR = False alarms / (False Alarms + Correct Rejections)) and hit rates (TPR = Hits / (Hits + Misses)) were collected defining a hit as the correct report of a non-vertical orientation when the orientation truly was non-vertical. Any vertical grating reported as non-vertical was thus a false alarm. Eventually, response bias (C) and sensitivity (A') were calculated as follows (Stanislaw & Todorov, 1999):

C = - (Z(TPR) + Z(FPR))/2

A' = .5+sign(TPR−FPR) ((TPR−FPR)2+ |TPR−FPR| / (4max(TPR,FPR)−4*TPR*FPR))

Unbiased performance results in *C*-values around 0. A more liberal decision criterion favoring yes-responses (non-vertical) leads to negative values for *C*, while positive values indicate the opposite tendency. Perfect sensitivity, on the other hand, is associated with values for *A'* around 1 which decrease to 0.5 if the sensitivity is at chance level (Stanislaw & Todorov, 1999). Bayes factors were computed to assess the distributions of individual sensitivities and response biases on each awareness level (AL). Per convention a BF_{10} between 1 and 3, 3 and 10, 10 and 30, 30 and 100 and >100 provides anecdotal, moderate, strong, very strong, and extreme evidence, respectively, for H1 (Quintana & Williams, 2018).

2.5.2 Analysis of RT data. We used the packages lme4 (Bates, Mächler, Bolker & Walker, 2014b) as well as lmerTest to conduct linear mixed model (LMM) analyses. LMMs were used to analyze RT data instead of repeated measures ANOVAs due to the

unbalanced structure of the data resulting from the fluctuating subjective visual awareness ratings leading to uneven numbers of trials across the four awareness levels (see Avneon & Lamy, 2018). Cases with missing data would be dropped in an ANOVA. Therefore the LMM approach provides a better means to make use of all available data in the face of an unbalanced design (Magezi, 2015). RTs of trials in which incorrect responses had been given were discarded and each participant's individual outliers (mean RTs ± 2.5 *SD*) were removed prior to the analysis. The model was fitted using a restricted maximum likelihood estimation and the influence of the fixed effect predictors was tested with a type III ANOVA as implemented in the *lmer* and *anova* function of the *lme4* package (Version 1.1-23). The *p*-values were obtained using Satterthwaite approximations to degrees of freedom using the *anova* function of the package *lmerTest* (Version 3.1-2, Kuznetsova, Brockhoff & Christensen, 2014). Post hoc tests (least squared means of the contrasts with Bonferroni correction) were performed using the R package *emmeans* (Version 1.4.7). Prior to the statistical assessment of the factors of interest, we defined the full random effect structure of the mixed model with likelihood ratio tests (Baayen, Davidson & Bartes, 2008).

Most critical for the purpose of this study was to examine if changes in the orientation between a given and the previous trial *(switch)* affected RTs. In particular we expected a switch-related increase in RTs compared to trials without a switch between orientations *(repeat)*. Therefore we entered the switch of orientations (switch versus

repeat) as the first fixed effect predictor into the LMM. In addition, RTs should decrease with increasing visual awareness: the less the participants saw, and the poorer they performed at categorizing the stimulus orientation, the slower they were expected to be at responding to the grating's orientation. Thus, visual awareness was added as the second fixed effect predictor. To account for a possible interaction between the two fixed effects, the model also included the interaction term of the factors switch and awareness. For the interindividual baseline differences in response latencies, we entered a by-subject random intercept. We determined the full random effect structure of the model (Barr, Levy, Scheepers & Tily, 2013) via model comparisons based on likelihood ratio tests (χ^2) (Baayen, Davidson & Bartes, 2008). This method is conceptually similar to the procedure of a hierarchical regression. Yet, instead of entering relevant predictors to the regression model and keeping them if they significantly improve the model fit (changes in R^2), different by-subject random slopes were added and tested. This method is considered to be appropriate to formally define the random effect structure of a LMM even if the sample size is small (Baayen, Davidson & Bartes, 2008; Bolker et al., 2009). Based on this analysis a by-subject random slope for the factors switch and awareness was added to model potential heteroscedasticity with respect to levels of the fixed effect factors switch and awareness (i.e., allowing uneven variances between the levels (Baayen, Davidson & Bartes, 2008)). Thus, the final model was defined as *RT ~ switch + awareness + switch:awareness + (1 + awareness + switch | sub)*.

Importantly, we defined the switch condition in two different ways: in the first LMM analysis (weighted switch model) only those trials in which we expected the highest RT costs to occur were included: due to the frequency differences between the three orientations, attentional weighting was expected to be boosted for the highly frequent non-vertical orientations (either left or right). Consequently, re-weighting to the infrequent non-vertical orientation should cause higher switch costs than vice versa. Similarly, the change away from the heavily weighted to the vertical orientation should require more pronounced attentional re-weighting. Changes away from the low-frequent tilted orientation to vertical, on the other hand, should result in lower switch costs since attentional weighting for this tilted orientation is weaker, facilitating attentional reallocation, and were thus not included in the weighted dataset. For comparison, we repeated the LMM analysis using a fixed effect predictor (*switch)* that, this time, comprised all types of switch trials (exhaustive switch). Results are given separately for the LMM analyses using the weighted switch factor and the exhaustive switch factor.

2.6 fMRI analysis

2.6.1 fMRI Measurements. All participants were scanned on a 3 Tesla MAGNETOM Prisma (Siemens). fMRI data was sampled using a standard head coil and EPI-sequence (TR, 2000 ms; TE, 30 ms; flip angle, 90°; epi factor, 80; echo time, 0.49 ms; matrix size, 80 × 80; FOV, 240 mm; 36 slices with interleaved acquisition; 3 mm isotropic voxels; interslice gap). A single scanning session was split into ten runs of 246

s each. 123 volumes were sampled, of which the first three dummy scans were excluded prior to analysis. T1-weighted MPRAGE scans (TR, 2500 ms; TE, 2.82 ms; flip angle, 7°; matrix size, 256 x 256; FOV, 256 mm; 192 slices, 1 mm isotropic resolution) were additionally sampled for each participant.

2.6.2 Pre-processing. The imaging data was pre-processed and analyzed by means of tools of the FSL package (Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012). The anatomical scans underwent a non-brain removal with BET (Brain Extraction tool; Smith, 2002) in preparation for the realignment. The functional images were motion-corrected to an image in the middle of each run with a normalized correlation ratio (MCFLIRT; FMRIB's Linear Image Registration; Tool, Jenkinson, Bannister, Brady & Smith, 2002; Jenkinson & Smith, 2001) and slice time corrected (temporally aligned to the middle slice of the 3D volume). To ensure the validity of Gaussian random field theory, the functional data was spatially smoothed using a Gaussian kernel with a size matching the double of the voxel dimensions (FWHM = 6 mm). In order to remove low-frequency drifts (Smith et al. 1999), we temporally filtered the data using a highpass filter with a cutoff value of 90 s.

2.6.3. GLM-Analysis. For statistical analyses of the functional brain scans, we defined the onsets of the experimental events as explaining variables (EV) to model the BOLD response by means of a general linear model. The Gabor onsets of trials in which the orientation had changed compared to the previous trial (switch) and the Gabor onsets

of trials on which the orientation had remained unchanged (repeat) were modeled for each awareness level separately (1 − 3), as well as the onsets of the start fixation, mask, and categorization response which were also defined as regressors. These were convolved with a hemodynamic response function (double gamma HRF) and regressed against the observed fMRI-data. Collinearity was checked for the modeled time series for each voxel ensuring a variance inflation factor (VIF) smaller than 5 (Mumford, Poline & Poldrack, 2015). Each regressor was paired with a temporal derivative allowing for temporal flexibility, and motion parameter estimates were added as nuisance regressors. Serial voxel-wise autocorrelations were controlled with pre-whitening by the FSL tool FILM (Woolrich, Ripley, Brady & Smith, 2001; Monti, 2011).

In the first-level analysis, all contrasts of interest were tested for significance under mixed-effect assumptions and contrast images were processed for each participant (voxelwise Z threshold of 3.1 and a cluster significance threshold of $p = .001$, family-wise error (FWE) corrected). These images were consequently used in the second-level analysis estimating individual mean contrasts for the parameters across all runs using a fixed-effect model with the same voxelwise and cluster significance threshold ($Z = 3.1$, $p_{FWE} = .001$). In a two-step post-statistical normalization, prior to group analysis, the functional data was firstly co-registered to the individual, anatomical scan using boundary-based registration (BBR), and secondly normalized to the Montreal

Neurological Institute standard space (MNI 152 2mm). Thus, statistical modeling on the subject level was carried out in native space. The statistical modeling at the group level was performed using FLAME 1+2 (FMRIB's Local Analysis of Mixed Effects) as implemented in FSL's FEAT (Version 6.00). Results are given by means of whole-brain maps of BOLD responses thresholded using clusters determined by a voxelwise Z threshold of 3.1 and a corrected cluster-forming significance threshold of $p_{FWE} = .001$, across the whole brain (Worsley, 2001; Eklund, Nichols & Knutsson, 2016).

2.6.4. MVPA searchlight. Our goal was to test whether the involved regions convey reproducible spatial patterns of activity that differentiate between the specific orientations in the absence of awareness. Thus, we made use of multi-voxel pattern analysis (MVPA) in combination with a searchlight algorithm (Kriegeskorte, Goebel & Bandettini, 2006) in order to further examine the nature of the brain signals that we observed in response to invisible orientation changes in the GLM analysis. Therefore we carried out searchlight analyses within those brain regions that had been identified previously in the GLM analysis as to be particularly responsive to invisible orientation change. To do so we created binary masks of these regions and used them as ROI in the consequent searchlight analysis. Note that GLM results were orthogonal to the decoding analysis as we chose those clusters as ROIs for the searchlight analysis that showed increased BOLD signal in response to unaware orientation changes but not to the different orientations per se.

Prior to decoding, the individual fMRI data were motion-corrected and smoothed (FWHM Gaussian kernel = 6 mm) to reduce noise and the impact of fine-scale signal patterns (Op de Beeck, 2010; Gardumi et al., 2016). Note that the MVPA analysis was conducted for both smoothed and unsmoothed data. Both analyses led to comparable results. A rather positive effect of smoothing was previously reported for MVPA-analyses in prefrontal cortex and sensory regions (Hendriks, Daniels, Pegado & Op de Beeck, 2017), so we report the MVPA-results based on the smoothed fMRI data. After smoothing, we transformed subjects' data into MNI standard space and fitted a standard hemodynamic response function model to estimate the statistical parameters (scaling parameters, beta values) for each of the experimental conditions, resulting in one beta map for every run per experimental condition. The resulting datasets were detrended and z-scored per voxel within each run. The searchlight analysis was implemented by extracting the z-scored β-values from spheres centered on each voxel in the ROI masks. For the accuracy maps, the classification accuracy (the mean of the proportion of correctly classified targets) for each sphere was assigned to the sphere's central voxel. To test the sensitivity as a function of sphere radius, we carried out the analysis with the radii of 6 and 9 mm. If different searchlight radii reveal the same or similar overlapping clusters, it is more likely that these clusters are indeed not spurious (Etzel, Zacks & Braver, 2013). For classification within a single sphere, we chose a linear support vector machine to classify the three stimulus orientations (LIBSVM; with fixed regularization hyper-parameter C = -1). We selected this type of classifier as it

tends to perform better or at least equivalent compared to other algorithms on fMRI data, and, due to its limited complexity, it reduces the probability of over-fitting (Pereira & Botvinick, 2011; Lewis-Peacock & Norman, 2013). Eventually, an n-fold cross-validation (leave-one-run-out) was carried out, using the *PyMVPA* software package (Hanke et al., 2009); with n as the given number of runs, the training dataset comprised all unaware trials of the first run (fold) to run n-1, while the unaware trials of run n constituted the test dataset. Note the total number of runs per subject varied between four and ten depending on the number of subjectively unaware trials that were (i.e., in some subjects some runs did not include trials rated as subjectively unaware). This splitting was repeated until each of the n folds served once as the test dataset. To test if brain activity on unaware trials conveyed local information sufficient to discriminate the stimulus orientations, trials with higher levels of subjective awareness (AL2 – AL3) were omitted in this procedure. Furthermore, all unaware trials were included without differentiating between switch and no switch trials to maximize the total number of trials serving training and testing the classifier (26.88% of all trials). Likewise, we included correct as well as incorrect subjectively unaware trials (AL1) in the MVPA to maximize the chances of decoding.

In a two-step analysis with permutation tests on the subject level and bootstrapping on the group level, we aimed for finding final group-level clusters with decoding accuracies significantly exceeding the chance level (Stelzer, Chen & Turner,

2013). First, permutation tests for each subject (100 permutations) were carried out to assess chance distributions and to obtain individual chance accuracy maps (Chen et al., 2011; Golland & Fischl, 2003; Stelzer, Chen & Turner, 2013). To do so, we created a random permutation of the observation order of the orientations (labels) and applied this scheme to the data set. Next, the cross-validation was performed on the permuted data set, which was repeated 100 times. This resulted in a sampling distribution of the mean classification accuracy under the null hypothesis (i.e., no information of orientation representations present in the multivoxel activity patterns). The significance level (p value) was estimated by the fraction of the permutation samples that were greater than or equal to the classification accuracy from the data without label shuffling. This "chance" map of decoding accuracies was saved each time for each participant. Importantly, balanced partitions containing the same number of items per orientation class were initially created within each subject and each cross validation fold. At the group level, we recombined the individual null distribution maps into group accuracy maps (Stelzer, Chen & Turner, 2013). For this, we randomly drew (with replacement) one of the 100 chance accuracy maps of each subject and averaged this selection of 14 chance maps (one for each participant) voxel-wise to one permuted group accuracy map. Repeating this 10^5 times with replacement we obtained a distribution of 10^5 permuted group accuracies. For statistical testing, we next calculated the probability of the unpermuted mean decoding accuracies across all 14 volunteers in the distribution of the permuted group accuracies (one-tailed) with a voxel-wise threshold of $p < .001$. Cluster p-values

were calculated for the unpermuted accuracies that referred to the probability of observing a particular cluster size or a larger one given the Null hypothesis, controlling for multiple comparisons using false discovery rate correction (FDR, $p_{Cluster} < .01$). Group cluster brain maps containing clusters with above-chance decoding accuracies were saved as well as classification accuracy maps.

3 Behavioral results

To assess subjective awareness, we calculated the number of trials for each level of awareness for each participant using the trial-by-trial PAS-rating. In the majority of trials, participants' subjective awareness of the to-be-categorized orientation was low (AL2; 34.71%) or even fully absent (AL1; 24.97%). In 31.1% of all trials, subjects reported an almost clear perception of the grating and its orientation (AL3) and in only 9.23% they clearly saw the grating and its orientation (AL4). The mean numbers of trials for each level of awareness and trial type are summarized in Table 1. As the number of fully aware trials (AL4) was overall very low with less than 10 trials in 64% of all subjects, we excluded these trials from further analyses.

Table 1

Average Number of trials per visibility condition and trial type (switch versus no switch).

	Awareness							
	Level 1		Level 2		Level 3		Level 4	
	switch	*repeat*	*switch*	*repeat*	*switch*	*repeat*	*switch*	*repeat*
M	55.9	32.8	75.1	48.1	68.6	41.8	21.6	11.1
SD	21.9	14.2	28.0	16.8	19.2	11.6	17.4	9.3

3.1 Discrimination ability depends on subjective awareness

According to the individual reports after the experiment, some participants had noticed that non-vertical Gabors had occurred more often than the vertical Gabor. None of the participants, however, noticed a difference in the frequency between left- and right-tilted orientations. Participants' sensitivity to discriminate between a non-vertical and a vertical grating decreased with vanishing subjective awareness. On trials with almost full (AL3) and partial awareness (AL2) participants maintained considerable perceptual sensitivity regarding the Gabor's orientation: Bayes-factors provided strong evidence for the mean A' of 0.675 ± 0.056 to be greater than 0.5 in AL3 trials, $BF_{10} = 12.89$, 95% CI (0.553, 0.797) and anecdotal evidence for the mean *A'* of 0.585 ± 0.049 (*SE*) to be truly greater than 0.5 in AL2 trials , $BF_{10} = 1.671$, 95% CI (0.479, 0.690). In contrast, in unaware trials (AL1), the mean *A'* was 0.48 ± 0.030 with the Bayes factor providing moderate evidence for the H0 suggesting that volunteers' perceptual discrimination ability was at chance, $BF_{10} = 0.178$, 95% CI (0.414, 0.545), (Quintana & Williams, 2018). Comparing the sensitivity between the three awareness levels Bayes factors provided strong evidence that A' in AL1 trials was truly smaller than the mean *A'*

in AL2 trials, $BF_{10\ (AL1\ <AL2)} = 19.957$, and extreme evidence that it was smaller than the

mean A' in AL3 trials, $BF_{10\ (AL1\ <AL3)} > 100$. Comparably, there was strong evidence for

A' of AL2 trials to be smaller than A' of AL3 trials, $BF_{10\ (AL2\ <AL3)} = 34.336$. Violin plots

of the sensitivity distribution of each level of awareness are depicted in Figure 2 a).

We assumed a yes/no discrimination task set up in our paradigm and calculated

A' as the sensitivity measure. However, given the fact that volunteers were required to

map left and right tilted Gabors with differing angles to the same response (i.e.,

non-vertical), a classification scenario may be more appropriate (Snodgrass et al., 2004).

On the cognitive level, such a scenario demands volunteers to establish two rather than

one decision criteria, thereby increasing the decision uncertainty. The proportion of

correct responses (i.e., proportion correct, $p(c)$) then serves as the means to measure

perceptual sensitivity (Macmillan & Creelman, 2004, p.190-191). Hence we next

calculated $p(c)$ for each level of subjective awareness, where $p(c)$ was defined by using

the presentation probabilities of the two non-vertical targets as weights for the hit rate

and adding this to the product of the 1-false alarm rate (i.e., correct rejection rate) and

the presentation probability of the vertical target (i.e., p(c) = (8/36)*H + (16/36)*H +

(12/36)*(1-F); Macmillan and Creelman, 2004, p. 89).

In agreement with the results of the sensitivity analysis using A', we observed a

mean $p(c)$ of 0.514 ± 0.042 in AL1 trials with a Bayes factor analysis providing

moderate evidence for $p(c)$ to be equal to chance (50%), $BF_{10} = 0.310$, 95% CI (0.423,

0.605) (Quintana & Williams, 2018). In AL2 trials the $p(c)$ was 0.609 ± 0.060 and the Bayes factor gave anecdotal evidence that it was truly above the chance level, $BF_{10} = 1.885$, 95% CI (0.480, 0.739) (Quintana & Williams, 2018). In AL3 trials the mean $p(c)$ was 0.695 ± 0.272 and the Bayes factor showed moderate evidence for a $p(c)$ above chance, the $BF_{10} = 6.738$, 95% CI (0.538, 0.852) (Quintana & Williams, 2018). Group distributions of the $p(c)$ for each level of subjective awareness are depicted in Figure 2 b).

Finally, we analyzed individual response biases. On unaware trials (AL1) we observed a negative mean C of -0.471 ± 0.187 and the Bayes factor provided only anecdotal evidence in favor of a C smaller than zero, $BF_{10} = 1.720$, 95% CI (-0.821, -0.012) (Quintana & Williams, 2018), tentatively suggesting that volunteers were biased to report a non-vertical orientation more often. In trials with residual awareness (AL2) the mean C of -0.098 ± 0.147 was associated with a Bayes factor providing moderate evidence for a C truly at zero indicating unbiased responses, $BF_{10} = 0.328$, 95% CI (-0.415, 0.219), (Quintana & Williams, 2018). Similarly, in almost fully aware trials (AL3) the Bayes Factor for the mean C of 0.242 ± 0.159 provided anecdotal evidence for a C equal to zero, $BF_{10} = 0.692$, 95% CI (-0.102, 0.586) (Quintana & Williams, 2018). Next, we computed a Bayesian mixed model using the subjective measures of awareness (AL1-AL3) as fixed effect predictor and a by-subject random intercept to test for variations in C across the three levels of awareness. The analysis resulted in $BF_{10} =$

52.89 providing strong evidence for variations in C across the levels of subjective awareness. Violin plots showing the distributions for the criterion location for the three awareness levels are shown in Figure 2 c).

Together, the data show that the ability to distinguish the two types of orientations (non-vertical versus vertical) strongly depended on subjective visibility. Importantly, we found a concordance of subjective visibility and the objective measure of awareness: the lower volunteers rated their subjective awareness, the worse their ability to correctly identify the stimulus orientation, being at random when subjective unawareness was reported. Trials with higher subjective levels of awareness (AL2 - AL3) showed substantial sensitivity above chance level and were thus counted as aware. However, the variation in the response bias across the three levels of visual awareness may suggest that volunteers' perceptual decision criteria were affected by their subjective awareness reports and variations in the sensitivity measure (A') could potentially be influenced by variations in the response bias. In fact, the low sensitivity (i.e., A' or p(c), respectively) in AL1 trials could have resulted from a response bias in this condition (Macmillan & Creelman, 2004). Thus, true absence of perceptual sensitivity in the subjectively unaware trials cannot be fully ascertained.
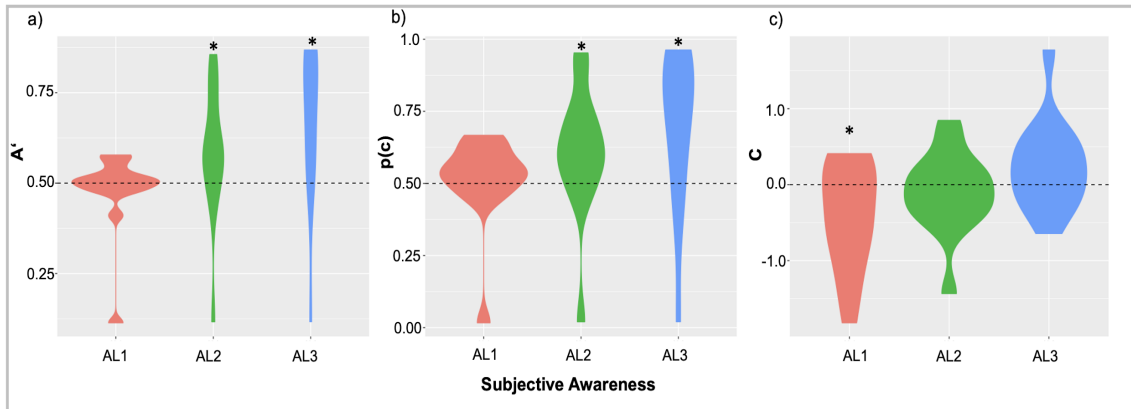
Fig.2: a) Violinplot shows the sensitivity parameter A' as a function of subjective awareness. Black dashed line shows the level of zero sensitivity. Black asterisks indicate Bayes factors providing evidence for a mean A' truly greater than 0.5. **b)** Sensitivity parameter p(c) as a function of subjective awareness. Black dashed line shows the level of zero sensitivity. Black asterisks indicate Bayes factors providing evidence for a mean p(c) truly greater than 0.5. **c)** Response bias C as a function of subjective awareness. Black dashed line appears at the level of no response bias. Black asterisk indicates a Bayes factor providing evidence for a mean C truly smaller than 0. To illustrate distributions of numeric data, violin plots make use of density curves where the width matches the approximate frequency of data points in each region. The lower and upper limits of each plot is determined by the distribution's minimum and maximum value.

Table 2

Average response bias (C) and sensitivity (A') for the categorization task on each level of subjective awareness.

	Awareness					
	Level 1		Level 2		Level 3	
	A'	*C*	*A'*	*C*	*A'*	*C*
M	0.513	-0.254	0.616	-0.060	0.685	0
SD	0.048	0.538	0.128	0.399	0.139	0.422

3.2 Reaction times – switch costs in response to unaware orientation changes

Critical for the purpose of this study was to examine if there was an effect on decision RTs in switch trials, i.e. due to changes in the orientation between a given trial and the previous trial. Descriptive mean RTs and *SE*s for switch versus repeat trials for each level of awareness are summarized in Table 3.

Table 3

Averaged reaction times (RT) in seconds for the categorization task on each level of visual awareness.

	Awareness					
	Level 1		Level 2		Level 3	
	switch	repeat	switch	repeat	switch	repeat
specific switch model						
M	1.152	1.036	0.990	0.959	0.906	0.910
SD	0.185	0.178	0.151	0.162	0.124	0.145

Exhaustive switch model

M	1.061	0.986	0.921
SD	0.158	0.125	0.140

First, we analyzed the weighted switch model containing only those trials with the highest expected switch costs. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. Here the LMM analysis showed that estimated RTs increased with decreasing visual awareness, $F(2, 13.671) = 24.1176$, $p < .001$; Post hoc tests after Bonferroni correction showed that mean RTs across both switch and repeat trials significantly slowed down about 119.7 ± 35.9 ms in AL1 trials compared to AL2, $t(12.5) = 3.335$, $p = .0169$, 95% CI (20.57, 219.0), about 186.5 ± 37.2 ms compared to AL3 trials, $t(12.0) = 5.019$, $p < .0001$, 95% CI (83.24, 290.0). Finally, mean RTs in AL2 trials were on average 66.8 ± 22.6 ms slower compared to AL3 trials, $t(15.5) = 2.961$, $p = .0284$, 95% CI (6.26, 127.0).

More importantly, the orientation change (fixed effect switch) had also impacted RTs as indicated by the significant interaction between the factors switch and subjective awareness, $F(2, 35.999) = 5.4058$, $p = .0088$. Here the post hoc tests showed that in the unaware condition (AL1) RTs in repeat trials were on average 115.35 ± 32.5 ms faster compared to switch trials $t(29.4) = -3.570$, $p = .0013$, 95% CI (-182.4, - 49.6). In trials with higher levels of visual awareness switch costs were not significant, AL2, $p = .3433$,

95% CI (-97.7, 35.1); AL3, p = .9073, 95% CI (-62.6, 70.2). There was also a statistical trend for the main effect of the fixed effect predictor switch, which was, however, not significant, $F(1, 13.278)$ = 3.8892, p = .0697. In Figure 3 a) RTs for both switch and repeat trials are plotted as a function of visual awareness for the weighted switch model. The LMM solutions for the fixed and random effects for the weighted switch model are given in Table 4 a).

Next, we calculated the same LMM analysis for the exhaustive model in which the mean of the switch condition included all possible switch trials. Residual plots did not suggest deviations from homoscedasticity or normality. Again estimated RTs appeared sensitive to changes in the level of visual awareness indicated by the significant fixed effect of awareness, $F(2, 12.575)$ = 6.0728, p = .0142. The post hoc tests with Bonferroni correction indicated that RTs in AL1 trials were on average 76.1 ± 31.0 ms slower compared to AL2 trials, but this difference was statistically not significant, $t(12.1)$ = 2.454, p = .0909, 95% CI (-10.05, 162.0). However, RTs in AL1 trials were on average 133.2 ± 40.4 ms slower compared to AL3 trials, $t(12.0)$ = 3.301, p .0190, 95% CI (21.06.49, 254.0). Finally, mean RTs in AL2 were about 57.1 ± 18.7 ms slower compared to AL3 trials, $t(12.4)$ = 3.046, p = .0294, 95% CI (5.29, 109).

The switch effect, however, did not significantly impact RTs: There was no significant main effect of switch, $F(1, 14.515)$ = 2.6334, p = .1261, nor a significant interaction $F(2, 36.00)$ = 0.2667, p = .7674. RTs for both switch and repeat trials as a

function of visual awareness for the exhaustive switch model are depicted in Figure 3 b).
The LMM solutions for the fixed and random effects for the exhaustive switch model
are given in Table 4.

Taken together the LMM analysis showed that RTs were sensitive to decreasing
visual awareness as well as to changes in the stimulus orientation. Yet, orientation
changes impacted RTs only if those switch trials were taken into account in which the
novel orientation changed away from the highly biased orientation (highly frequent tilt)
suggesting that prior visual selection had boosted behavioral switch costs. RT data were
best described by an interaction of visual awareness and changes in the stimulus
orientation with significant slowing of RTs only in unaware switch trials.

Table 4

Estimates, (β values, in seconds), standard errors, t-ratios and p-values for the fixed effect predictors in the final LMM. a) T- and P-values indicate the difference of each *factor level (and factor level combination) compared to baseline (intercept AL1 for the fixed effect awareness and switch for the fixed effect switch). The intercept is tested against zero. The model results based on the fixed effect predictor switch comprising only the changes away from the heavily weighted orientation are given in Table 4 a); Table 4 b) shows the results of the model using the fixed effect predictor switch including all types of orientation changes.*

a) Weighted Switch				
Fixed Effects	Coefficient	*SE*	*t*-value	*P*-value
(Intercept)	1.03669	0.04584	22.617	3.91e-12 ***
Awareness				
AL1 – AL2	-0.07737	0.03883	-1.916	.070276
AL1 – AL3	-0.12661	0.04202	-2.980	.008178 **
Repeat – Switch	0.11599	0.03249	3.570	.00116 **
AL2: Switch – Repeat	-0.08469	0.03746	-2.261	.016213 *
AL3: Switch – Repeat	-0.11981	0.03746	-3.198	.00288 **

Random Effects	Variance	*SE*
Subject (intercept)	0.022751	0.15084
AL1 – AL2	0.012188	0.11040
AL1 – AL3	0.013392	0.11572
Switch	0.004604	0.06754

b)   Exhaustive Switch

(Intercept)	1.036688	0.047479	21.835	2.51e-11 ***
Awareness				
AL1 – AL2	-0.077365	0.033110	-2.337	.0.03326 *
AL1 – AL3	-0.126607	0.041977	-3.016	.0.00924 **
Repeat - Switch	0.024623	0.018619	1.322	.19467
AL2: Switch - Repeat	0.002497	0.023136	0.108	.91464
AL3: Switch - Repeat	-0.013223	0.023136	-0.572	.57120

Random Effects	Variance	SE	
Subject (intercept)	0.027566	0.16603	
AL1 – AL2	0.010772	0.10379	
AL1 – AL3	0.019427	0.13938	
Switch	0.001027	0.03205	

Note: Significance codes: '***' = $p < 0.001$; '**' = $p < 0.01$; '*' = $p < 0.05$.
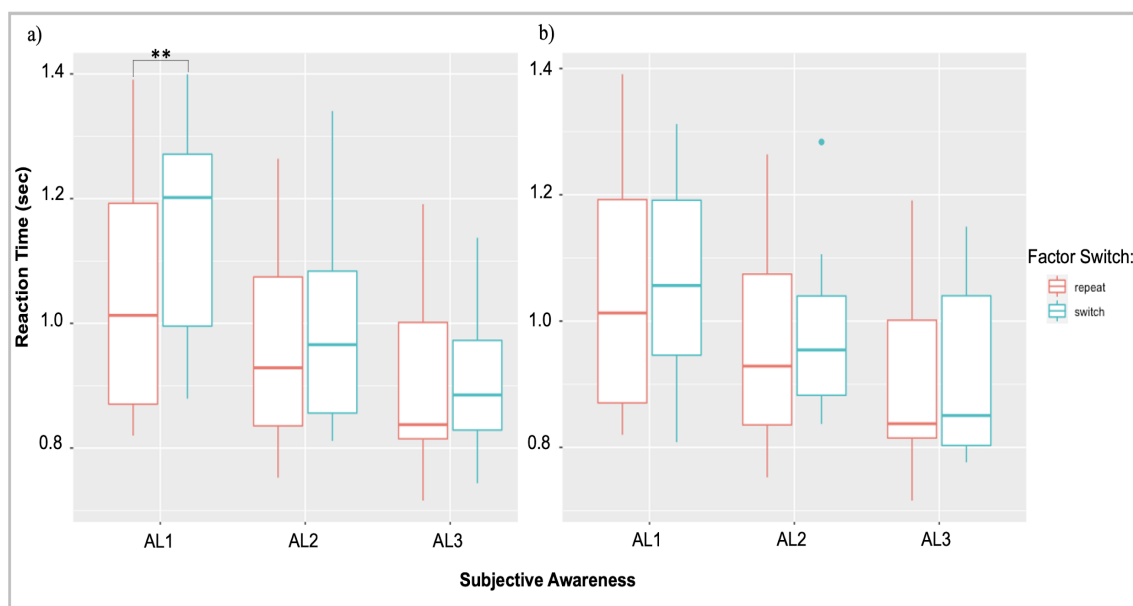
Fig. 3: Boxplots depicting RTs in seconds as a function of visual awareness plotted for switch (blue) and repeat trials (red) in the weighted model (**a**) in which the switch factor comprised only those switch trials away from the strongly weighted (frequent tilt); **b)**

average model in which all switch trials were included; black asterisks = significant difference between switch and repeat trials, $p < .01$.

5. Discussion

In this study we investigated exploratory shifts of attention in the absence of visual awareness and hypothesized, on the brain level, the right FPC to be crucially involved. At the behavioral level, we indeed observed that participants' RTs in the categorization task were prolonged when the orientation of a central bar stimulus changed away from the most frequent orientation, while both subjective and objective measures indicated the absence of conscious perception.

Thus, our participants appeared to have optimized perception by attentional weighting of the most frequent orientation although the stimuli were not consciously perceived. This, in turn, caused RT costs when less frequent orientations were presented. Previously, we had observed left lateral FPC activation when attention was reweighted following visible target changes. Here, we investigated if the same pattern would be observed for unconsciously processed stimuli. However, FPC was not more strongly activated in unconscious change trials. Thus, a specific role of the FPC for attentional

modulation of unconsciously perceived stimuli could not be confirmed. Instead, however, FPC activation represented the stimulus orientation of unconsciously perceived stimuli. Thus, the FPC would be able to send feedback to posterior regions such as the TPJ and IPS when target changes occur. Due to the lack of change-related FPC activation, we have no evidence that such change signaling occurs for unconsciously perceived target changes, but it cannot be ruled out that such change signals might have been too weak to be observed in the present experiment, or that they might occur for target dimension changes instead of feature changes (Pollmann et al., 2000, Weidner et al., 2002) or spatial attentional changes (Lepsien et al., 2002) even if these occur unconsciously.

Above-chance decoding of the invisible target's orientation was also observed in the right TPJ. This area showed a negative correlation between RTs in unaware switch trials and classification accuracies of clusters with significant searchlight centers, consistent with the idea that the feature representation in the TPJ serves to facilitate attentional weighting of the novel target orientation. Potentially, the better the orientation of the invisible stimulus was represented in the multivoxel activity patterns, the faster the participants could disengage attention (Corbetta et al., 2008) from the

previous orientation to facilitate subsequent attentional weighting of the new orientation.,

Increased activation during unconsciously perceived switch trials was observed only in the right posterior parietal cortex. This aligns well with many studies showing posterior parietal involvement in conscious attention changes (reviewed by Corbetta et al., 2008; Wager et al., 2004). Activation along the posterior, descending segment of the IPS was recently found to be increased for salient distractor stimuli rather than for equally salient targets (Jamoulle et al., 2021). Thus, posterior IPS activation was not driven by salience per se, but discriminated between the task-relevant, attended targets and the task-irrelevant, non-attended distractors. In the present experiment, we find a similar pattern in that this area was more strongly activated by the non-attended, new orientation than the attended orientation. In both cases, the underlying function may be a response to stimulus changes that may potentially require a reallocation of attention. Certainly, the visual search task used by Jamoulle et al. (2021) and our task differ in many respects. Thus, the hypothesis that both studies induced the same functional process in posterior IPS needs to be confirmed by further studies where consciousness is varied within the same paradigm.

Our findings support the distinction between attention and consciousness: the reweighting of attention in response to a change of an unconscious target is in keeping with the view that attention and consciousness can be dissociated (Lamme, 2003; Koch & Tsuchiya, 2007). Our findings tie in well with other reports, showing visual selection biases can occur in the absence of visual awareness (Kanai, Tsuchiya, Verstraten, 2006; Zhang & Fang, 2012; for a review see Mulckhuyse & Theeuwes, 2010; Pan, Lin, Zhao & Soto, 2014) and are thus in keeping with emerging evidence that higher-order cognitive control mechanisms can be deployed without conscious awareness (Van Gaal, Ridderinkhof, Scholte & Lamme, 2010; Van Gaal & Lamme, 2012; Soto & Silvanto, 2014). Previous studies provided evidence for mid-DLPFC (BA 46) to be responsive during unconscious priming of task response settings (Lau & Passingham, 2007) and for left lateral FPC to serve implicit attention guidance for visible items (Pollmann & Manginelli, 2009b), but the activity was not tested for task-relevant representational content. Frontal involvement in dorsolateral and anterior PFC has been shown during a visual short-term memory task for masked stimuli (Dutta, Shah, Silvanto & Soto, 2014), however in this study visual awareness was defined by means of a subjective measure (items reported as 'unaware') while here we used both objective and subjective measures to establish the lack of visual awareness. Critically, our multivariate pattern

analyses showed that the FPC was involved in the representation of the task-relevant feature (orientation).

Previous work demonstrated that masked stimulus information (i.e., orientation) is processed and maintained in the visual cortex (e.g., Haynes & Rees, 2005). Yet, our classification analysis provides novel evidence that the representation of an unconscious stimulus orientation was maintained across a distributed set of brain areas in the right lateral FPC, right IFG, right MTL, right parietal and visual cortex. This pattern of results aligns with recent evidence showing that unconscious perceptual content can be decoded from activity patterns in a distributed set of brain regions, including parieto-frontal areas (Mei, Santana and Soto, 2022) and further elaborates on recent evidence showing that the frontoparietal cortex is implicated in the maintenance of conscious feature information during visual working memory and search tasks (Ester, Sprague & Serences, 2015; Lee & Baker, 2016; Reeder, Hanke & Pollmann, 2017). Importantly, our results foster the notion that unconscious information processing implicates supra-modal areas typically linked to conscious processing such as the pre-frontal cortex (for reviews see van Gaal & Lamme, 2012; Soto & Silvanto, 2014). The present results align with the view that engagement of prefrontal areas is not restricted to conscious processing.

A somewhat unexpected result was the absence of significant switch costs in trials in which the target was consciously perceived (AL2-AL3), a pattern that we already observed in a previous behavioral study (Güldener, Jüllig, Soto & Pollmann, 2021). It should be noted that consciousness levels 2 and 3, at which no switch costs were observed, were perceptually more demanding than classical task-switching studies with clear stimulus visibility. Thus, our participants' responses at AL 2-3 were putatively more effortful for both switch and remain trials, thereby potentially minimizing switch costs. *Moreover, in line with Bundesen's theory of visual attention (1990), goal-relevant information (i.e., statistical knowledge about orientation likelihood) may gain increased influence on sensory processing whenever the sensory evidence of the to-be-processed stimulus is low, i.e, in trials rated as subjectively unaware. In these trials, stimulus information that could form the attentional selection weight in a "bottom-up" fashion is scarce. Thus, the knowledge of orientation frequencies, obtained in the visible trials, may have dominantly driven responses during invisible trials. Nevertheless, the switch costs in invisible trials showed that stimulus change was processed, though not consciously.*

It is possible that the information about the target orientation decoded from the MVPs of brain activity may be related to participants' expectations regarding the target's orientation in addition to the actual stimulus orientation. Further studies are needed to

test this hypothesis by using MVPA for decoding participants' predictions regarding the incoming perceptual input (e.g. based on the categorization response given to each stimulus orientation). As we did not specify different responses for the left versus right tilt, our study was not designed to pinpoint this issue. Note, however, that, since correct and incorrect responses were used for the MVPA in the unconscious trials, and volunteers performed at chance (A' = 0.5) in these trials, it is unlikely that the results presented here were driven by categorization responses or participants' expectations driving their responses rather than the actual stimulus orientation.

Our methodological approach in which we combined subjects' perceptual sensitivity as the objective measure of the stimulus visibility with subjects' awareness ratings may potentially be criticized because there is only a single distribution of vertical and tilt responses that we arbitrarily divided into the four levels of subjective awareness. Thus, the sensitivity measure (A') is biased if the response bias differs across the levels of subjective visual awareness (AL1-4). The analysis of subjects' response bias (C) indeed revealed variations and we therefore cannot rule out that the A' was biased which may have led to an under-estimation of A' in subjectively unaware trials (AL1) (Stein, Kaiser & Hesselmann, 2016). Hence, even if combining subjective and objective

measures to determine the stimulus visibility appears conceptually appealing, we cannot fully rule out that there is some variance in sensitivity across conditions.

Could other mechanisms than attentional reweighting explain our results? It might be argued that a simple repetition effect (Bertelson, 1961; 1963), leading to neural repetition suppression (Henson & Rugg, 2003), could alternatively explain the observed response facilitation and lower activation in unaware repeat trials compared to unaware switch trials. In previous work, we have demonstrated modulation of activity in visual areas processing color and motion in support of attentional weighting of the target dimension (Pollmann et al., 2006). In the present experiment, such a proof is difficult because stimulus changes occured between features of the same stimulus dimension, which are neurophysiologically represented in neural columns within the same brain areas (Hubel & Wiesel, 1962). However, our central claims, that orientation changes can be processed in invisible stimuli and that orientation was represented in several brain areas up to FPC are valid both for attentional weighting or repetition suppression accounts.

5.1 Conclusions

Orientation changes in unconscious e stimuli induced both behavioral and neural effects. Behaviorally, we observed switch -costs that went along with increased

activation in the posterior parietal cortex. In addition, the orientation of invisible targets was represented in a number of brain areas, reaching anteriorly up to the frontopolar cortex. We conclude that while change-related activation was restricted to the posterior cortex, the information about target feature changes was available in a network of brain areas including prefrontal cortex.

6 Author contributions

LG, DS, and SP designed the study. LG and AJ collected and managed data. LG analysed the behavioral data. LG wrote all formal analysis scripts and analysed the fMRI data. LG wrote the manuscript. All authors commented on the final version.

7 Acknowledgements

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