# Top-Down Biasing of Visual Cortical Activity Encodes Attended Information and Facilitates Behavioral Performance in Visual Spatial Attention

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**Key words:** Top-down control, visual hierarchy, spatial attention, fMRI, MVPA, MVPA-behavior.

## Abstract

Top-down attention plays a vital role in selecting relevant stimuli and suppressing distracting information. During top-down visual-spatial attention, control signals from the dorsal attention network modulate the baseline neuronal activity in the visual cortex in favor of task-relevant stimuli. While several studies have demonstrated that baseline shift during anticipatory attention occurs in multiple visual areas, such effects have not been systematically investigated across the visual hierarchy, especially when different attention conditions are matched for stimulus and task factors. In this fMRI study, we investigated anticipatory attention signals using univariate and multivariate (MVPA) analysis in multiple visual cortical areas. First, the univariate analysis yielded significant activation differences in higher-order visual areas, with the effect weaker in early visual areas. Second, however, in contrast, MVPA decoding was significant in predicting attention conditions in all visual areas and IPS, with lower-order visual areas (e.g., V1) having greater decoding accuracy than higher-order visual areas (e.g., LO1). Third, the strength of decoding accuracy predicted the behavioral performance in the discrimination task. All the results were highly replicable and consistent across two datasets with same experimental paradigms but recorded at two research sites, and two experimental conditions where the direction of spatial attention was driven either by external instructions (cue-instructed attention) or from internal decisions (free-choice attention). Our results provide clear evidence, not available in past univariate investigations, that top-down attentional control signals selectively bias neuronal processing throughout the visual hierarchy, and that this biasing is correlated with the task performance.

## Introduction

The visual environment is highly complex and changes dynamically. Attention enables the successful navigation of the complex visual environment by selecting task-relevant information for in-depth analysis and suppressing distraction (Posner, 1980). When attention is activated by salient environmental events it is called exogenous or involuntary attention; when it is activated by behavioral goals it is called endogenous or voluntary attention.

Extensive neuroimaging and lesion evidence suggests that the dorsal attention network (DAN), comprising the frontal eye fields (FEF) in dorsal frontal cortex, and the intraparietal sulcus (IPS) in the posterior parietal cortex, is the neural substrate underlying the control of voluntary attention (Bichot *et al.*, 2015; Bisley and Goldberg, 2003; Bressler *et al.*, 2008; Corbetta and Shulman, 2002; Hopfinger *et al.*, 2000; Meehan *et al.*, 2017). According to the prevailing theory, in addition to maintaining the attention set, the DAN issues top-down signals to modulate sensory neurons in a goal-directed fashion in advance of target processing (Bressler *et al.*, 2008; Chawla *et al.*, 1999; Giesbrecht *et al.*, 2006; Hopfinger *et al.*, 2000; Kastner *et al.*, 1999; Kastner and Ungerleider, 2000; Luck *et al.*, 1997; Park and Serences, 2022; Sylvester *et al.*, 2007).

In both humans and non-human primates, attention-related neural activations <u>independent</u> of bottom-up sensory processing have been observed in visual cortex during voluntary spatial attention. In non-human primates, Luck et al. (Luck *et al.*, 1997) reported increased baseline neuronal firing rates in V2 and V4 (but not V1) that encode the attended information. In human EEG studies, a highly replicable finding is that the alpha-band (8-12 Hz) activity is modulated by the attention-directing cues (Thut *et al.*,

2006; Worden *et al.*, 2000), and the patterns of alpha modulation depend on the locus of spatial attention. Similarly, in ERP studies of spatial attention, slow potential shifts that accord with attended locations have been observed over visual cortex in the cue-to-target interval (Harter *et al.*, 1989; Hong *et al.*, 2015; Hopf and Mangun, 2000; Yamaguchi *et al.*, 1994). In human fMRI studies, spatial attention-directing cues result in increases in background BOLD activity in thalamus (Woldorff *et al.*, 2004) and retinotopic visual cortex prior to target stimulus appearance, including in V1 (Giesbrecht *et al.*, 2006; Hopfinger *et al.*, 2000; Kastner *et al.*, 1999; McMains *et al.*, 2007; Ress *et al.*, 2000; Serences *et al.*, 2004; Silver *et al.*, 2007; Woldorff *et al.*, 2004). Applying multivariate fMRI analysis techniques, a recent study by Park and Serences (Park and Serences, 2022) found differences in multivoxel patterns evoked by different attention-directing cues in several retinotopic visual areas (but not V1).

A pattern that is generally consistent across the foregoing studies in humans and animals is that the baseline shifts induced by top-down attention in visual cortex are small or undetectable in early visual cortex (V1), but grow in amplitude in subsequent visual areas (i.e., V2, V3, VP, V4). Understanding the potentially differential effects of top-down attention on visual cortical excitability at different stages of the visual hierarchy is key to understanding how spatial attention biases visual processing. One goal of the present research is to investigate top-down biasing of BOLD activity in multiple areas in the ventral and dorsal streams of visual processing.

What is the role of baseline activity shifts in visual cortex during anticipatory visual attention? It is commonly thought that the stronger the top-down attentional modulation of sensory cortex, the more effective would be the processing of the

attended stimulus, which should result in enhanced behavioral performance. Ress *et al.* (2000) found that cue-related baseline BOLD increases in V1 through V3 were positively associated with task performance in a visual spatial attention task. Giesbrecht *et al.* (2006) reported similar findings for both spatial and feature attention. Fannon *et al.* (2008), however, found that cue-related pre-stimulus neural activity did not predict the stimulus-evoked activity or the subsequent behavioral performance. McMains et al.(2007) also reported that the post-stimulus effects of attentional selection observed in feature-selective regions were not accompanied by increased background activity during the anticipatory (pre-stimulus) period. The discrepancy across studies may lie in differences in the tasks and stimuli used, or in the way in which the analyses were performed, such as for example, how the regions of interest in each visual area were identified.

Another possibility is that the anticipatory activity was confounded with sensory evoked responses elicited by the attention-directing cues themselves, although some studies used auditory cues in the visual-spatial tasks, which would reduce the likelihood of any such confound (Fannon *et al.*, 2008; Silver *et al.*, 2007). Hence here, in addition to a traditional cuing paradigm where different physical cues instructed (instructed trials) participants to covertly attend either the left or the right visual hemifield with different cue prompts, in another condition the participants were required to choose which hemifield (left or right) to attend prompted by the same choice cue. When the subjects chose which hemifield to attend, there could be no interference from differences in the physical features of the cues, because the cue (choice cue) was the same whether the subjects chose to attend left or right. This provides a strong test of the nature of top-

down control over baseline activity in visual cortex in a fashion that has not been possible previously.

Analyzing the cue-evoked activity on a trial-by-trial basis we tested two hypotheses using both univariate and multivariate analysis methods: (1) in line with the extant literature, the representation of spatial attention conditions within the visual cortical hierarchy should be stronger as one ascends the hierarchy, and (2) the strength of the attentional biasing, represented by MVPA decoding accuracy, will be positively associated with behavioral performance. fMRI recordings from two separate datasets utilizing similar experimental setups were used to test these hypotheses.

## Methods

### Overview

Two datasets from studies conducted at the University of Florida (UF dataset) and the University of California, Davis (UCD dataset) were analyzed. By design, both datasets used the same stimuli and experimental conditions. By comparing and contrasting the two datasets we could provide test-retest reliability. These studies have been analyzed and published before addressing different questions (Bengson *et al.*, 2015; Bengson *et al.*, 2014; Liu *et al.*, 2016; Liu *et al.*, 2017; Rajan *et al.*, 2019).

*UF Dataset:* The Institutional Review Board at the University of Florida approved the experimental procedure. Eighteen healthy participants provided written informed consent and took part in the experiment. fMRI data were collected from the participants while they performed a cued visual spatial attention task. Two participants were excluded from the analysis: one failed to follow the experimental instructions and another did not achieve a behavioral accuracy above 70%. Three additional participants were removed due to excessive head/body movements. Data from the remaining

thirteen participants were analyzed and reported here (n=13; 5 females). EEG data were recorded along with the fMRI but not considered here.

*UCD Dataset:* The Institutional Review Board at the University of California Davis approved the experimental procedure. Nineteen healthy participants provided written informed consent and took part in the experiment. fMRI data were recorded while the participants performed the visual spatial attention task. One participant was removed owing to inconsistent behavioral performance. Data from the remaining eighteen participants were analyzed and reported here (n=18; 2 females).

**Experimental Paradigm**

As shown in Figure 1, a fixation point was placed at the center of the monitor, and the participants were instructed to maintain eye fixation on the dot during the experiment. Two white dots in the lower left and lower right visual fields marked the two peripheral spatial locations where stimuli would be presented.

At the beginning of each trial, one of three symbolic cues (cross, diamond, and circle) was presented above the fixation dot for 200 ms, with two of them explicitly instructing the participants to direct their attention covertly either to the left or right hemifield location (instructed trials) and the third prompting them to freely choose one of the two hemifields to covertly attend (choice trials). The choice condition, which was introduced in the original study to investigate willed attention (Bengson *et al.*, 2015; Liu *et al.*, 2016; Liu *et al.*, 2017; Rajan *et al.*, 2019), was significant to include for the purpose of this study in that it elicited the two attentional states (attend left vs. attend right) by using the same visual cue (the choice cue), thereby eliminating the influence of different visual cues on neural patterns in visual cortex and allowing the cross-validation of the findings from the instructional cue trials. The three cue conditions occurred with equal probability, and the three symbols used as cues were counterbalanced as to their meanings across participants, i.e., cue-left, cue-right, and freely-choose.

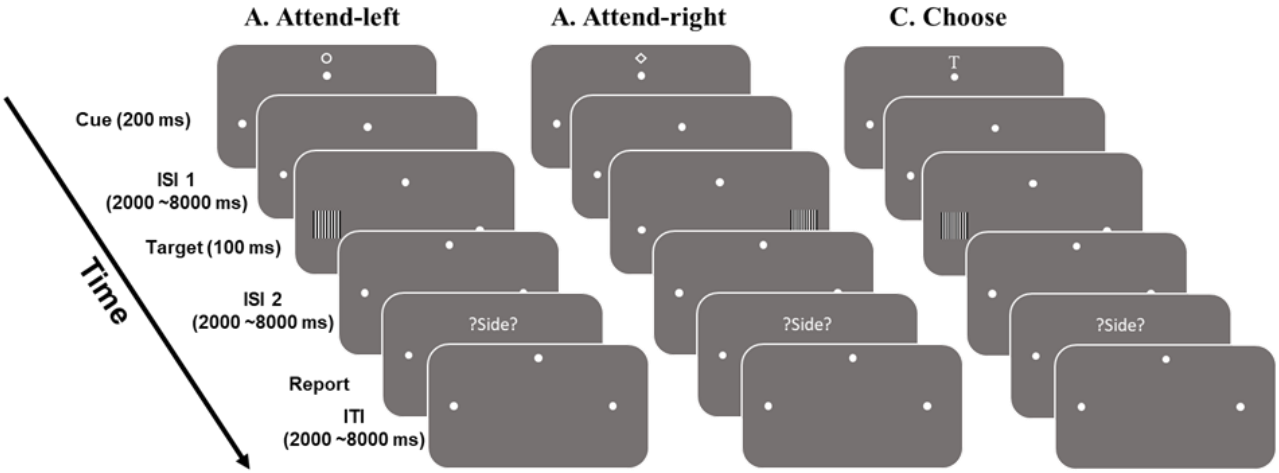


*Figure 1. Experimental paradigm. Each trial started with one of three visual cues (200ms), two of them instructing subjects to covertly attend either left (A) or right (B) hemifields, indicated by the two white dots. A third cue, the choice cue (C), prompted the participants to choose either left or right visual field to attend. Following a variable cue-to-target delay (2000-8000ms), a target in the form of a grating patch appeared briefly for 100ms with equal probability in the left or the right hemifield. Participants were asked to discriminate the spatial frequency of the grating displayed in the cued or chosen location and ignore the un-attended side. After a second variable ISI (2000-8000ms), participants were presented with a '?SIDE?' screen and were asked to report the hemi-field they paid attention to in that trial. An inter-trial interval, varied randomly from 8000-12800ms, elapsed before the start of the next trial.*

Following a random cue-target interval ranging from 2000 to 8000 ms, a black-and-white grating pattern (100% contrast; 5 x 5 deg visual angle) appeared at one of the two peripheral spatial locations for 100 ms, and participants discriminated between two possible spatial frequencies of the target grating (5.0 vs 5.5 cycles/degree) appearing in the attended hemifield via a button-press and ignored the grating appearing in the unattended hemifield. The grating occurred in either the left or right visual hemifields with equal probability, and were presented in the lower visual field. After the target stimulus, following a variable inter-stimulus interval (ISI) ranging from 2000 to 8000 ms, participants were prompted by the visual cue “?SIDE?” to report the spatial location that they attended on that trial. This reporting was needed to track the participant’s direction of attention in the choice attention condition and was also included in instructed trials to maintain consistency across conditions.

Reporting of the side attended was highly accurate across the group of participants, with the accuracy being 98.4% averaged across conditions. While side-reporting accuracy could be determined by comparing self-reports with the cue during instructed attention trials, the accuracy for choice attention trials was further determined by examining the consistency between participants’ responses to targets and the self-reports (e.g., responded to the target in the left visual field and reported choosing left). A variable inter-trial interval (ITI; 2000-8000 ms) was inserted after the subject reported the side attended.

All participants went through a training session prior to scanning to familiarize them with the task and to ensure adequate performance (above 70% correct) and compliance with procedures. The experiment was divided into blocks of trials with the

duration of each block approximately six minutes. All participants completed at least eight blocks of trials for the experiment.

**Data Acquisition**

*UF Dataset:* MR images were acquired at the University of Florida using a 3T Philips Achieve scanner equipped with a 32-channel head coil. The stimuli were presented using a 30-inch MR-compatible LCD monitor with a viewing distance maintained at 230 cm. The target was presented at spatial locations 5º lateral to the vertical meridian and 1.2º below the horizontal meridian. Functional magnetic resonance images (fMRI) were obtained using an echo-planar sequence (EPI) with parameters as follows: repetition time (TR) = 1980ms; echo time (TE) = 30ms; matrix = 64 x 64 field of view= 224 mm, slice thickness = 3.5 mm. Thirty-six transverse slices parallel to the plane connecting anterior to posterior commissure were obtained in ascending order with a voxel resolution of 3.5x3.5x3.5mm.

*UCD Dataset:* MR images were collected at the Imaging Research Centre of the University of California at Davis using a 3-T Siemens Skyra scanner with a 32-channel head coil. Functional magnetic resonance images were obtained using an echo-planar sequence with parameters as follows: TR = 2100ms; TE = 29ms, matrix= 64 x 64, field of view= 216mm, slice thickness=3.4mm. Thirty-four transverse slices were obtained within an interleaved acquisition order and slices were oriented parallel to the plane connecting the anterior-posterior commissure.

**Data Preprocessing**

The fMRI data were preprocessed in SPM with custom-created MATLAB scripts. The slice timing differences were corrected with a *sinc* interpolation to account for the acquisition delay. Motion realignment was performed by co-registering all images with

the first scan of each session. Six motion parameters (3 translational and 3 rotational) were calculated and regressed from the fMRI data. All images were spatially co-registered to the standard MNI space and resampled to a voxel resolution of 3x3x3mm. Finally, the spatially normalized images were smoothed using a Gaussian kernel of 8mm full width at half maximum. A high-pass filter with a cutoff frequency of 1/128Hz was used to remove any low-frequency noise, and global signals were removed by adjusting the intensities of each voxel.

**Estimation of Single-Trial BOLD Activity**

The MVPA approach is applied at the single trial level. The trial-by-trial BOLD estimate was obtained using the beta series regression approach (Rissman *et al.*, 2004). This method involves modeling each trial event, the cue (instructed and choose) in our case, using a separate regressor in the GLM technique. In the current investigation, all trials with correct responses were used and cue-evoked BOLD activity was modeled using separate regressors for instructed (attend left and right) and choose (choose left and right) conditions. One regressor was used for target onsets to account for the target-evoked activity and to remove its influence on the estimation of cue-evoked activity. The resulting trial-by-trial beta coefficient for each attention condition was then analyzed using the MVPA analysis technique (see below).

**Region of Interest (ROI) Selection**

Fifteen retinotopic visual regions from a recently published probabilistic visual topography map by Wang et al. (2015) were used as regions of interests (ROIs) ,

including V1v, V1d, V2v, V2d, V3v, V3d, V3a, V3b, LO1, Hv4, VO1, VO2, PHC1, PHC2, and IPS (Figure 2) .

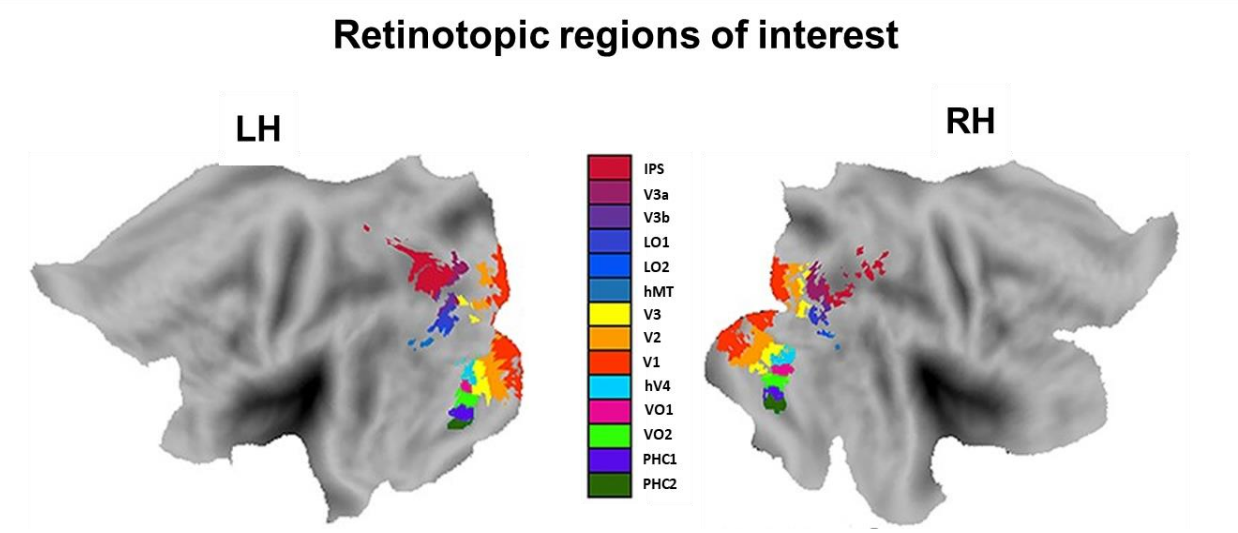


*Figure 2. Retinotopic ROIs from Wang et al., 2015 visualized on a flattened brain map.*

**Multivoxel Pattern Analysis (MVPA)**

The MVPA method uses pattern classification algorithms to distinguish between two brain states based on distributed BOLD activities across multiple voxels in a given ROI. In this study, we used support vector machine (SVM) in the MATLAB Statistics and Machine Learning Toolbox as the classifier for the MVPA. A 10-fold cross-validation approach was applied to minimize the effects of overfitting. The classifier performance was measured in terms of decoding accuracy which serves as a measure of the distinctness between two BOLD activation patterns corresponding to two attention conditions. The higher the decoding accuracy, the more distinct the multivoxel patterns between the two attention conditions (e.g., attend left vs. attend right), and we hypothesized, the stronger the strength of the top-down biasing signals.

A non-parametric permutation-based technique was used to determine whether the decoding accuracy is above the chance level of 50% (Stelzer *et al.*, 2013). In this approach, the class labels were shuffled 100 times within each subject. After each

shuffling, the classifier performance was obtained. On a group level, one of the 100 chance accuracies was chosen randomly from each subject and then averaged across subjects as the null hypothesis population-level accuracy. Repeating the procedure $10^5$ times yielded an empirical distribution of the chance level decoding accuracy. The actual decoding accuracy was compared against this distribution and p=0.0001 was used as a threshold accuracy for statistical significance.

**Relating Decoding Accuracy with Behavior**

To understand the functional significance of higher decoding accuracy in classifying  the top-down biasing of visual cortex during anticipatory attention, the relationship between this decoding accuracy in the visual cortex and behavioral performance in the target discrimination task was analyzed. Here behavioral performance was characterized by the efficiency score (ES), which is the ratio of accuracy over reaction time (accuracy/RT), with a higher scores indicating better behavioral performance. Prior work has used inverse efficiency score (Bruyer and Brysbaert, 2011), which is the ratio of reaction time over accuracy, with a lower score indicating better behavioral performance. We note that in our design, the instruction to the participants was to respond *as fast as they could* while also being *as accurate as they could*, the speed-accuracy tradeoff may prevent the use of RT or accuracy singly as the appropriate behavioral measure. Computing the ratio of accuracy and RT eliminates the speed-accuracy trade-off effect while retaining the main task effect (Bruyer and Brysbaert, 2011; Liesefeld and Janczyk, 2019; Vandierendonck, 2017).

**Combining Datasets Using Meta-Analysis**

Analysis was done first on the UF and UCD datasets separately, and then a meta-analysis combining the two datasets was performed where appropriate using the

Lipták-Stouffer method (Lipták, 1958). This method has been used commonly to combine results from different datasets (Cheng *et al.*, 2015; Huang and Ding, 2016). It involves converting the p-value of each dataset to its corresponding Z value using the formula:

$$\mathrm{Z_i} = \Phi^{-1}(1 - p_i) \tag{1}$$

Here Φ denotes the standard normal distributive function. The Z values of different datasets is then combined using the Liptak- Stouffer formula:

$$\mathrm{Z} = \frac{\sum_{\mathrm{i}=1}^{\mathrm{k}}(\mathrm{w_i z_i})}{\sqrt{\sum_{\mathrm{i}=1}^{\mathrm{k}}(\mathrm{w_i})^2}} \tag{2}$$

Here Z is the combined z score of k datasets (for the present study k=2), i refers to the $i^{th}$ dataset or site, $w_i$ is the weight $i^{th}$ dataset which is equal to $\sqrt{N_i}$, where $N_i$ is the number of samples in $i^{th}$ dataset. From the combined z score, the corresponding p value can then be assessed.

## Results

### Behavioral Analysis

***UF dataset:*** For instructed trials, target discrimination accuracy for cue-left and cue-right was 75.2 ± 4.2% and 76.2 ± 2.1%, respectively (Figure 3A); there was no statistically significant difference between the two conditions (p = 0.77, d = - 0.07). Reaction time to valid targets for cue-left trials was 927.94 ± 28.06, and for cue-right trials was 911.38 ± 23.00 ms (Figure 3B); there are not statistically significant difference between the two conditions (p = 0.38, d = 0.17). For choice trials, accuracy was 78.1% ± 3.6% for choose-left and 81.4% ± 3.1% for choose-right trials (Figure 3A), and the reaction time was 942.27 ± 47.75 ms for choose-left and 938.25 ± 29.04 ms for choose-

right (Figure 3B). There was no statistically significant difference between choose left and choose right for either accuracy or reaction time ($p_{acc}$= 0.43,$d_{acc}$= - 0.26 ; $p_{RT}$ = 0.92, $d_{RT}$ = 0.02). A one-way main effects ANOVA further confirmed that there were no significant differences in behavioral performance between instructed and choice trials [$F_{acc}$ (3,76) = 0.69, p = 0.56; $F_{RT}$ (3,48) = 0.17, p = 0.91; Figure 3A and 3B].

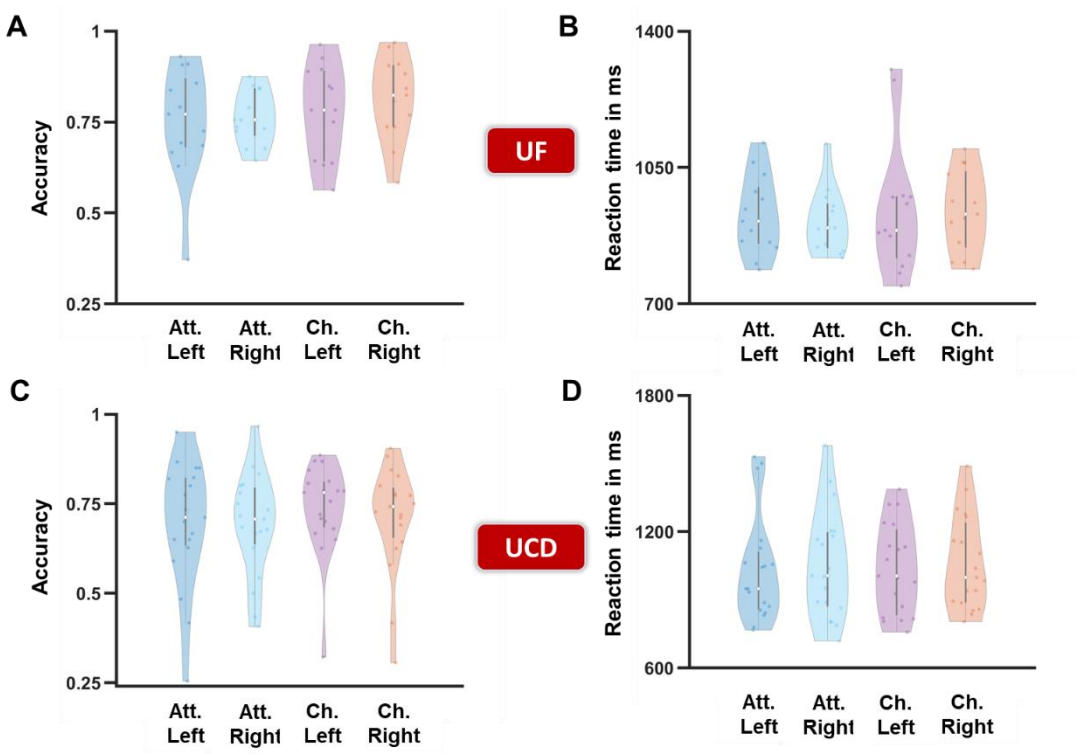


*Figure 3. Behavioral results from instructed/choice trials. (A & C): Comparison of accuracy (ratio of correct trials and total number of valid trials) between different attention conditions for UF (A) and UCD (C) datasets. (B & D): Comparison of reaction times (RT) between different attention conditions for UF dataset (B) and UCD dataset (D).*

***UCD dataset:*** For instructed trials, response accuracy for cue-left and cue-right was 70.0 ± 4.0% and 69 ± 3.2% (Figure 3C); there was no statistically significant difference between the two conditions (p = 0.84, d = 0.02). Reaction time for cue-left was 1030.41 ± 57.13 ms and cue-right 1046.23 ± 56.77 ms (Figure 3D); there was no statistically significantly difference between the two conditions (p = 0.42, d = -.07). For

choice trials, the accuracy was 74.0% ± 13% for choose-left and 71%±15% for choose-right trials, and the reaction time was 1034.52 ± 48.06 ms for choose-left and 1043.43 ± 45.84 ms for choose-right trials. There was no statistically significant difference between choose-left and choose-right in either accuracy or reaction time ($p_{acc} = 0.33$, $d_{acc} = 0.20$ ; $p_{RT} = 0.42$, $d_{RT} = -0.10$). A one-way ANOVA further confirmed that there were no significant differences in behavioral performance between instructed and choice trials [$F_{RT}$ (3,72) = 0.06, p = 0.98; $F_{acc}$ (3,76) = 0.4, p = 0.75; Figure 3C and 3D].

**Univariate Analysis of Cue-Evoked BOLD Activation:**

For instructed trials, BOLD activity in the hemisphere ipsilateral to the cued direction was subtracted from that in the hemisphere contralateral to the cued direction (i.e., cue-left minus cue-right for right hemisphere, and cue-right minus cue-left for left hemisphere) and the difference was averaged across the two hemispheres and within each ROI. As shown in Figure 4A and 4B, for higher-order visual cortex such as LO and

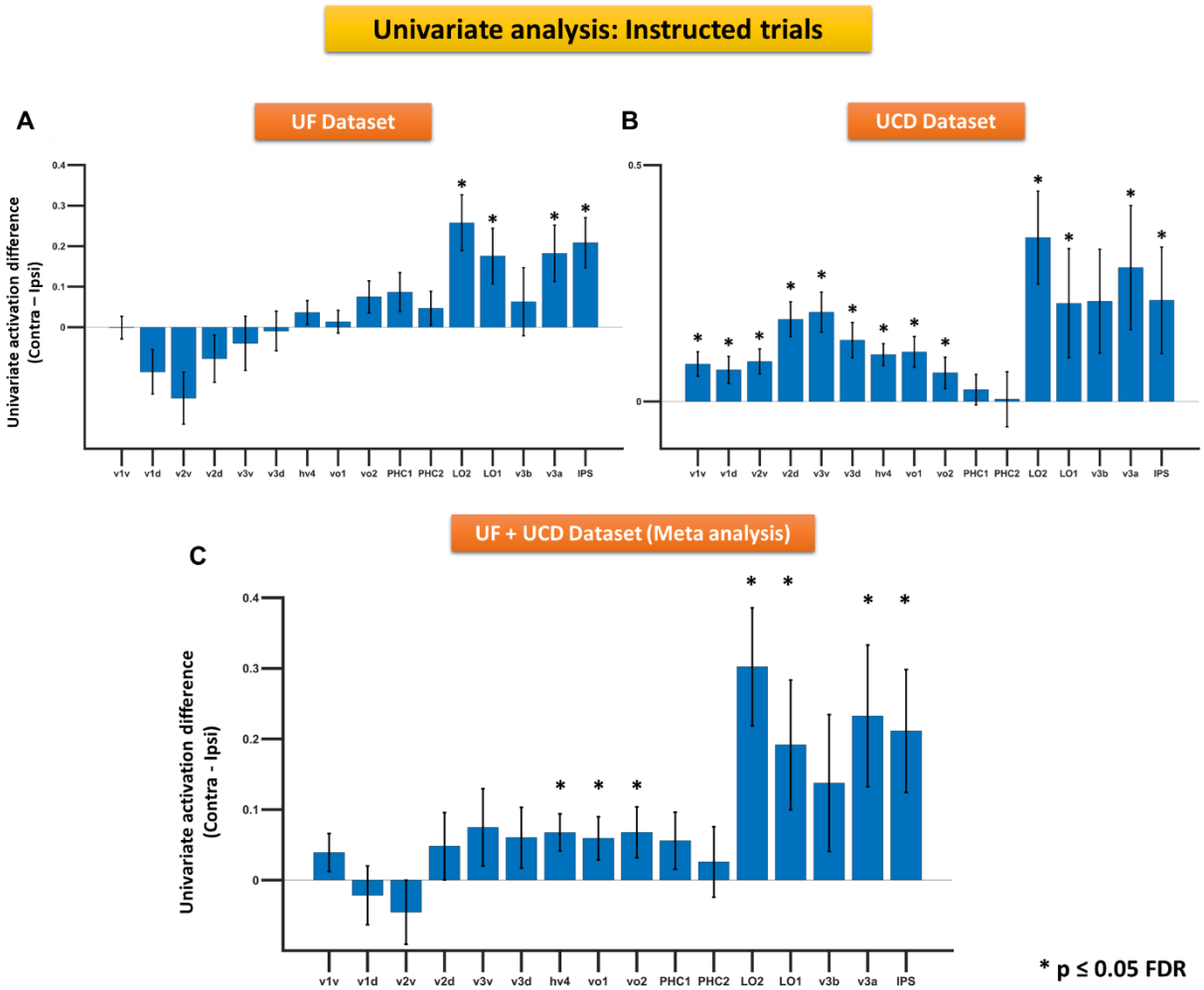


*Figure 4. Univariate analysis of activation evoked by instructional cues. BOLD activity difference between attention to contralateral and ipsilateral visual fields were computed and averaged across the hemispheres for UF (A) and UCD (B) datasets. (C) The activation differences in (A) and (B) were averaged and the p values obtained via meta-analysis. * p ≤ 0.05 FDR.*

IPS, covert attention elicited stronger univariate BOLD activation, and the effects were consistent across the two datasets, in line with previous studies (Giesbrecht *et al.*, 2003;

Heinze *et al.*, 1994; Hopfinger *et al.*, 2000). For early visual areas such as V1 and V2, however, the effects are not consistent across the two datasets. A meta-analysis combining the two datasets confirms these observations (Figure 4C). Similar analysis was carried out for choice trials (Figure 5). Differential activations were mainly found in higher order visual areas with V1v being the notable exception.

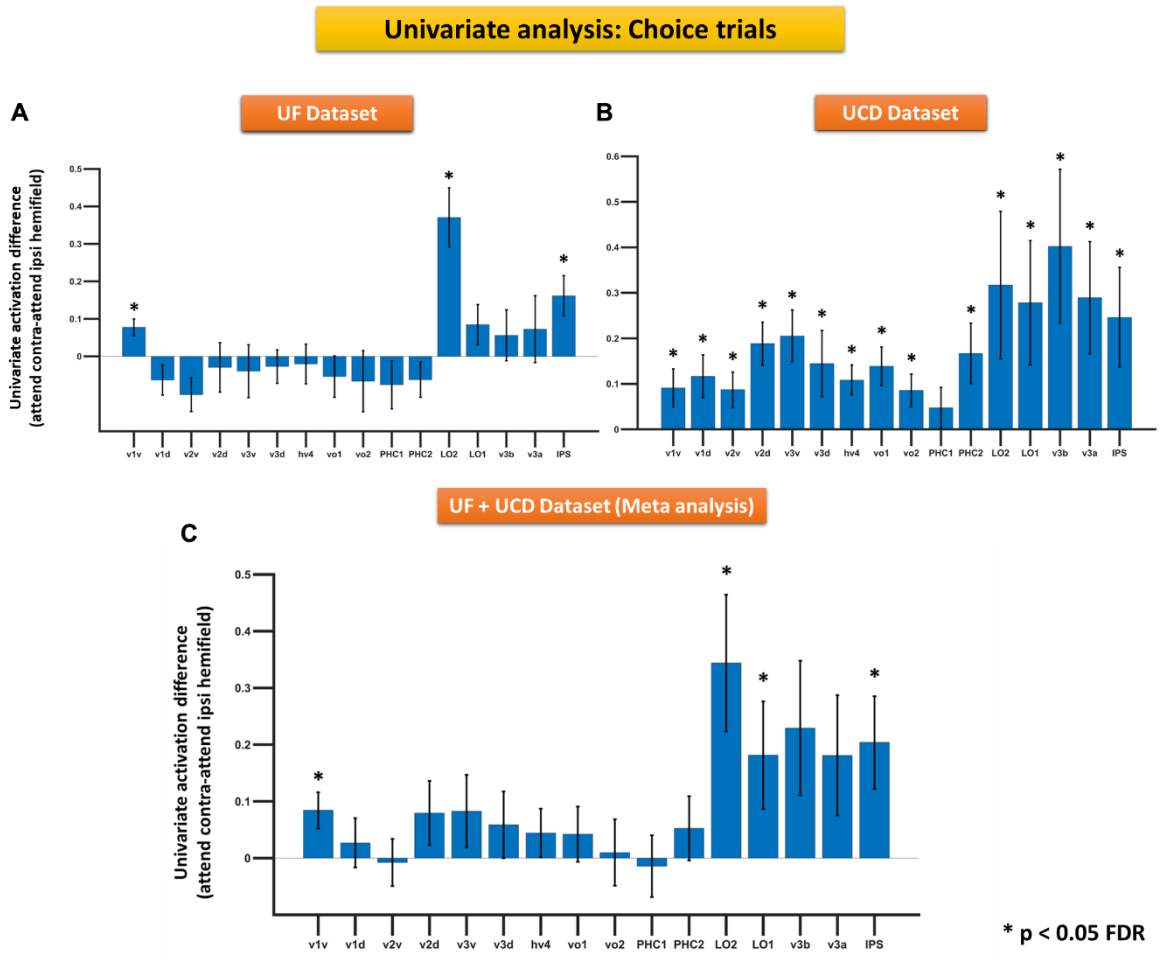


*Figure 5. Univariate analysis of evoked by choice. BOLD activity difference between attention to contralateral and ipsilateral visual fields were computed and averaged across the hemispheres for UF (A) and UCD (B) datasets. (C) The activation differences for instructed trials and choice trials are averaged across the datasets and the p values from both the datasets were combined using meta-analysis. * p < 0.05 FDR.*

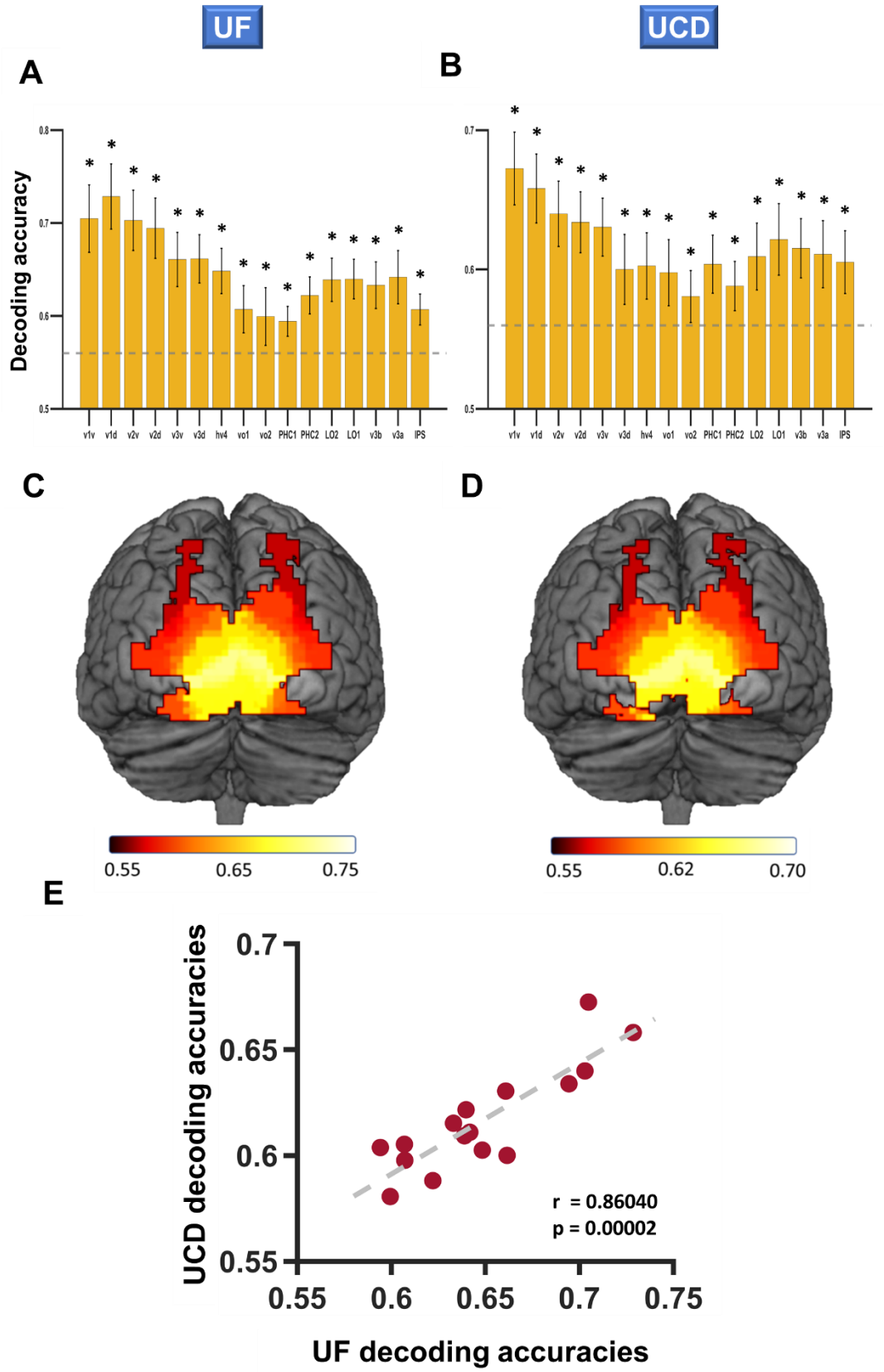


*Figure 6. Decoding accuracy of attend-left vs attend-right using visuo-topic ROIs: Instructed trials. (A & B) Decoding accuracies for different visual ROIs for UF Dataset (A) and UCD Dataset (B). (C & D) Posterior view of color-coded decoding accuracies for UF Dataset (C) and UCD Dataset (D). (E) Scatter plot comparing UCD vs. UF decoding accuracies where each dot represents a visual ROI.*

**Multivariate Analysis of Cue-Evoked BOLD Activation: Instructed Trials**

The decoding accuracy between cue-left and cue-right was above chance level in all visual regions in both UF (Figure 6A) and UCD datasets(Figure 6B). In addition, the decoding accuracy tended to be higher in lower-order visual areas than higher-order areas (Figure 6C & 6D), in sharp contrast to the univariate analysis. To further demonstrate the consistency of the results between the two datasets, for each ROI, we plotted the decoding accuracy averaged over all participants from the UF dataset against that from the UCD dataset in Figure 6E. The correlation across all 15 ROIs was highly significant with $r = 0.86$ ($p = 0.00002$), suggesting a high degree of similarity in the decoding accuracy distribution across visual cortical regions between the two datasets.

The decoding accuracy reflects the degree of distinctness of the neural activity in the two attention conditions, and can be considered a quantitative index of the strength of top-down biasing during attention control. To examine the functional significance of the top-down biasing of sensory cortex, we related the decoding accuracy to behavioral performance. A principal component analysis (PCA) was performed to reduce the dimensionality of 15 ROI-based decoding accuracies. The first PCA component explained 79.75% and 83.49% of the variance for UF and UCD datasets respectively (Figure 7A and 7B). Each subject's score on the first PCA component was used to represent the degree of decoding accuracy for that subject and was then correlated with the z-scored behavioral efficiency (response accuracy/reaction time). A significant positive correlation between decoding accuracy and behavioral performance was found for both datasets; UF Dataset: $r=0.58$, $p=0.04$ (Figure 7C) and UCD Dataset: $r=0.66$, $p=0.003$ (Figure 7D). Combining the two datasets using meta-analysis showed that the

overall correlation effect to be robust and significant (p=0.0007). This finding suggests that the more distinct—as reflected by higher decoding accuracy—were the BOLD patterns evoked by different attention cues in the retinotopic regions, the stronger the top-down biasing signals in these regions, and thence the better the behavioral performance.

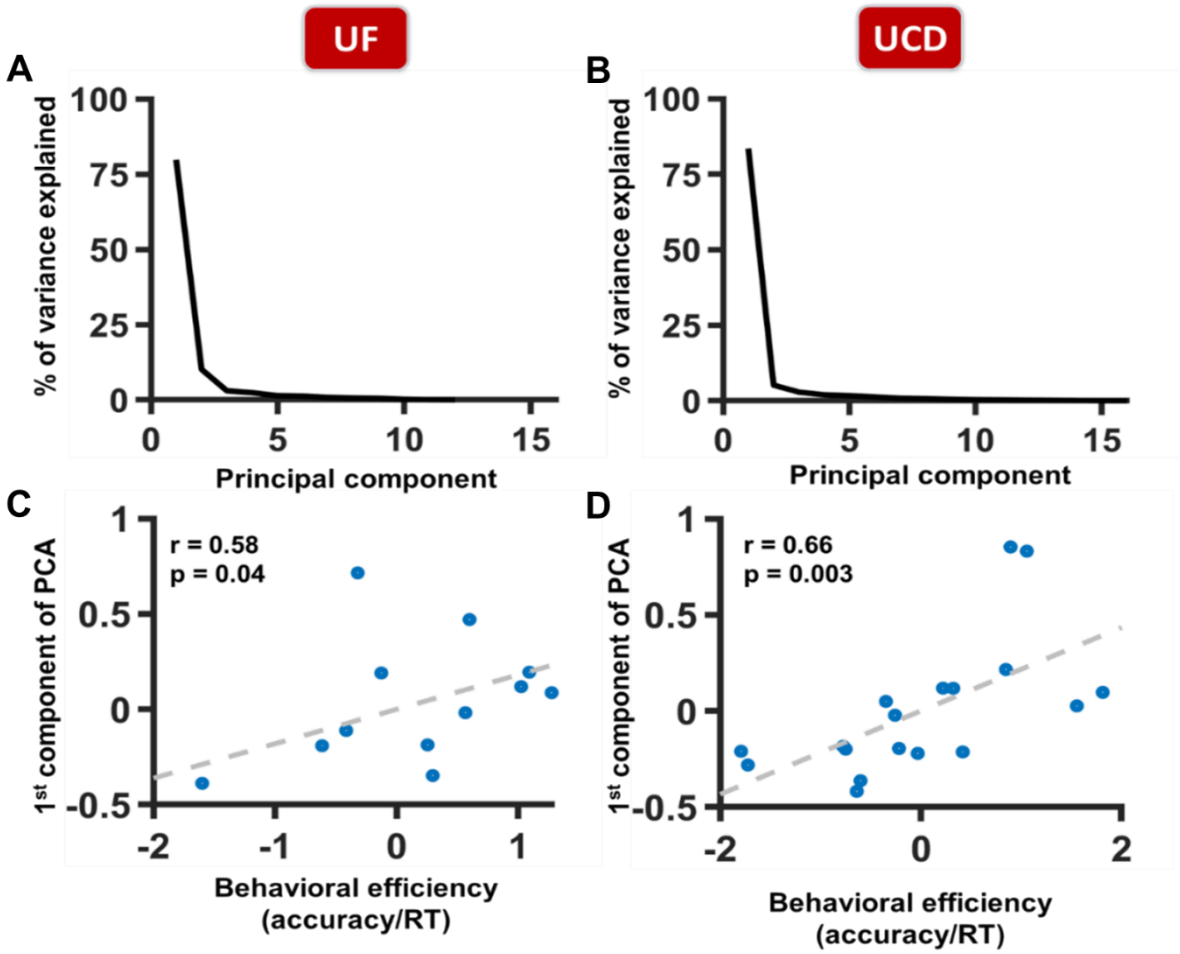


*Figure 7. MVPA decoding accuracy vs behavior: Instructed trials. (A & B) Percentage of variance explained by the principal components for (A) UF and (B) UCD datasets. (C & D) Decoding accuracy vs behavioral efficiency (z-score) for (C) UF and (D) UCD datasets.*

**Multivariate Analysis of Cue-Evoked BOLD Activation: Choice Trials**

Decoding choice-left versus choice-right yielded decoding accuracies that were significantly above chance level in all ROIs except in the ventral-occipital (vo2) and

posterior para-hippocampal cortex regions (PHC1 and PHC2); see Figure 8A for the meta-analysis results combining both datasets. It is worth noting that because we had half as many choice trials as instructed trials (cue-left, cue-right and freely choose cues each accounted for 1/3 of trials), there was less statistical power to detect differences between attention conditions for choose trials.

In Figure 8B, we compared the decoding results from UF and UCD datasets for each ROI, and the correlation between the two datasets was highly significant with $r = 0.65$ ($p = 0.006$), suggesting that for choice trials, the decoding accuracy distribution across visual cortical regions between the two datasets were highly similar. Further, we tested whether the decoding accuracies predict behavioral performance. As described above, we investigated the relationship between decoding accuracy and behavior, by taking each subject's score on the first PCA component of the 15 decoding accuracies (which explained 73% and 65% of the variance for the UF and UCD datasets respectively) and correlating this with the z-scored behavioral efficiency (response accuracy/reaction time). A positive correlation was seen for both datasets: UF dataset: $r=0.17$, $p=0.56$ (Figure 8C) and UCD dataset: $r=0.56$, $p=0.01$ (Figure 8D), with the p-vales from the meta-analysis combining the datasets being $p = 0.05$, suggesting that for choice trials, it remains the case that the more distinct the BOLD patterns evoked by different attention cues in the retinotopic regions, the stronger the top-down biasing signals in these regions, and the better the subsequent behavioral performance.

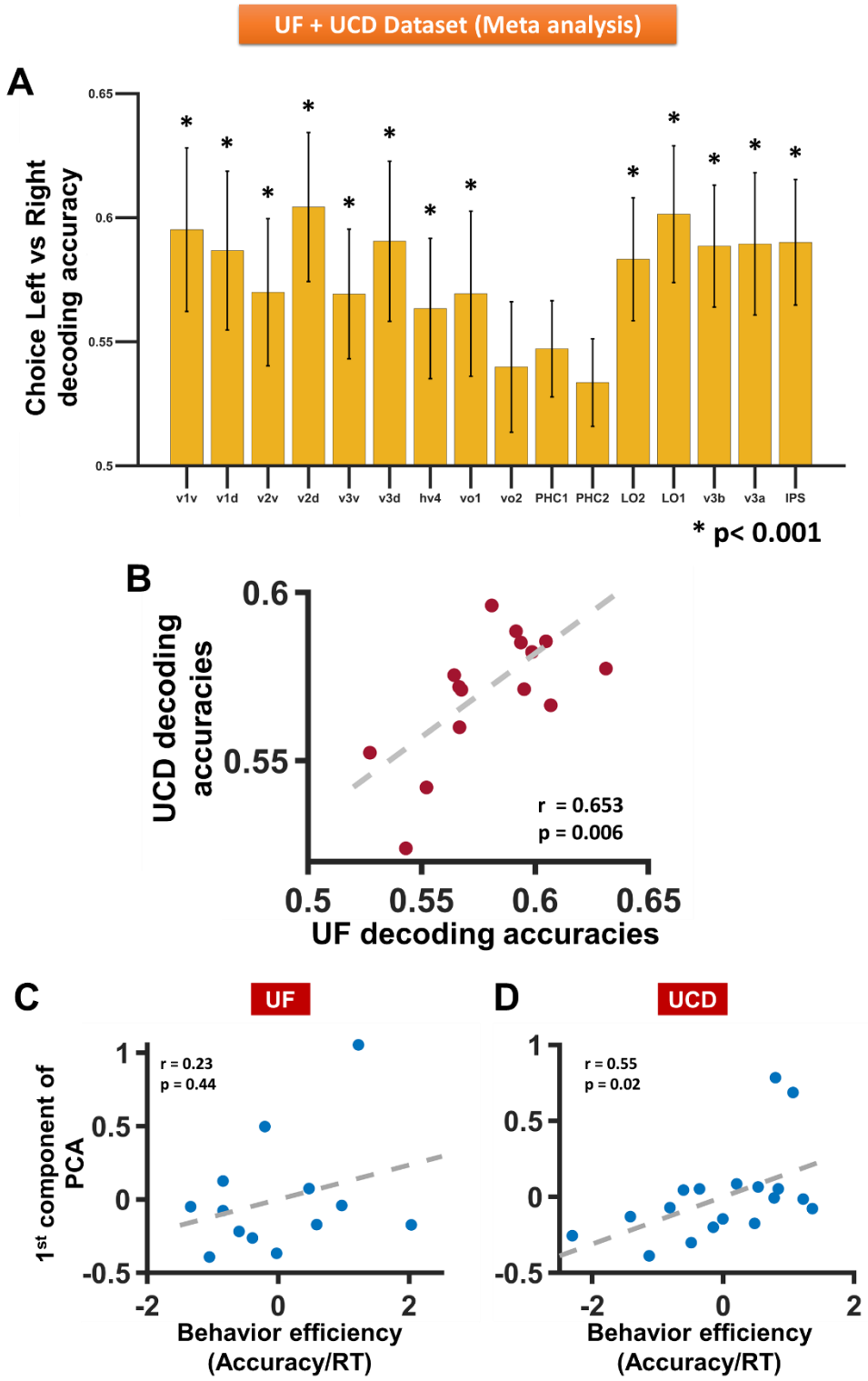


*Figure 8. Decoding accuracy for attend-left vs attend-right for choice trials. (A) Decoding accuracies averaged from UF and UCD datasets for different visual ROIs; p values were determined via meta-analysis. (B) Comparison of UF and UCD decoding accuracies across ROIs; each dot represents a ROI. (C & D) Decoding accuracy vs behavioral efficiency for UF dataset (C) and for UCD dataset (D).*

**Comparing Instructed and Choice Trials**

Three analyses were carried out to compare instructed and choice trials. First, the instructed and choice decoding accuracies (averaged across the two datasets) were compared, and a significant correlation was found ($r = 0.54$ and $p = 0.03$), suggesting that each ROI was similarly modulated by top-down attention whether the attentional state was formed from instructional cues or by pure internal decisions of the subjects; see Figure 9A. Second, for each dataset, we utilized the method of cross-decoding, by taking the SVM classifier trained on **instructed** trials and testing it on **choice** trials. We found the cross-decoding accuracies (Figure 9B) were significantly above chance level in all the ROIs except vo2, PHC1 and PHC2 (these areas were also not significantly decoded when choice-left vs choice-right conditions were compared; see Figure 8A), suggesting that the patterns of neural modulation resulting from instructional cues and from internal choice decisions are similar across visual areas. Third, cross-decoding accuracy (model trained on instructed trials and tested on choice trials) and actual decoding accuracy (model trained and tested on choice trials) were compared, the differences were not statistically significantly ($p>0.05$ FDR; Figure 9C), further confirming that the pattern of decoded neural activity observed in the retinotopic visual cortex reflects top-down attentional biasing signals, and not merely the differences in the stimulus properties of the two cues on instructional trials.

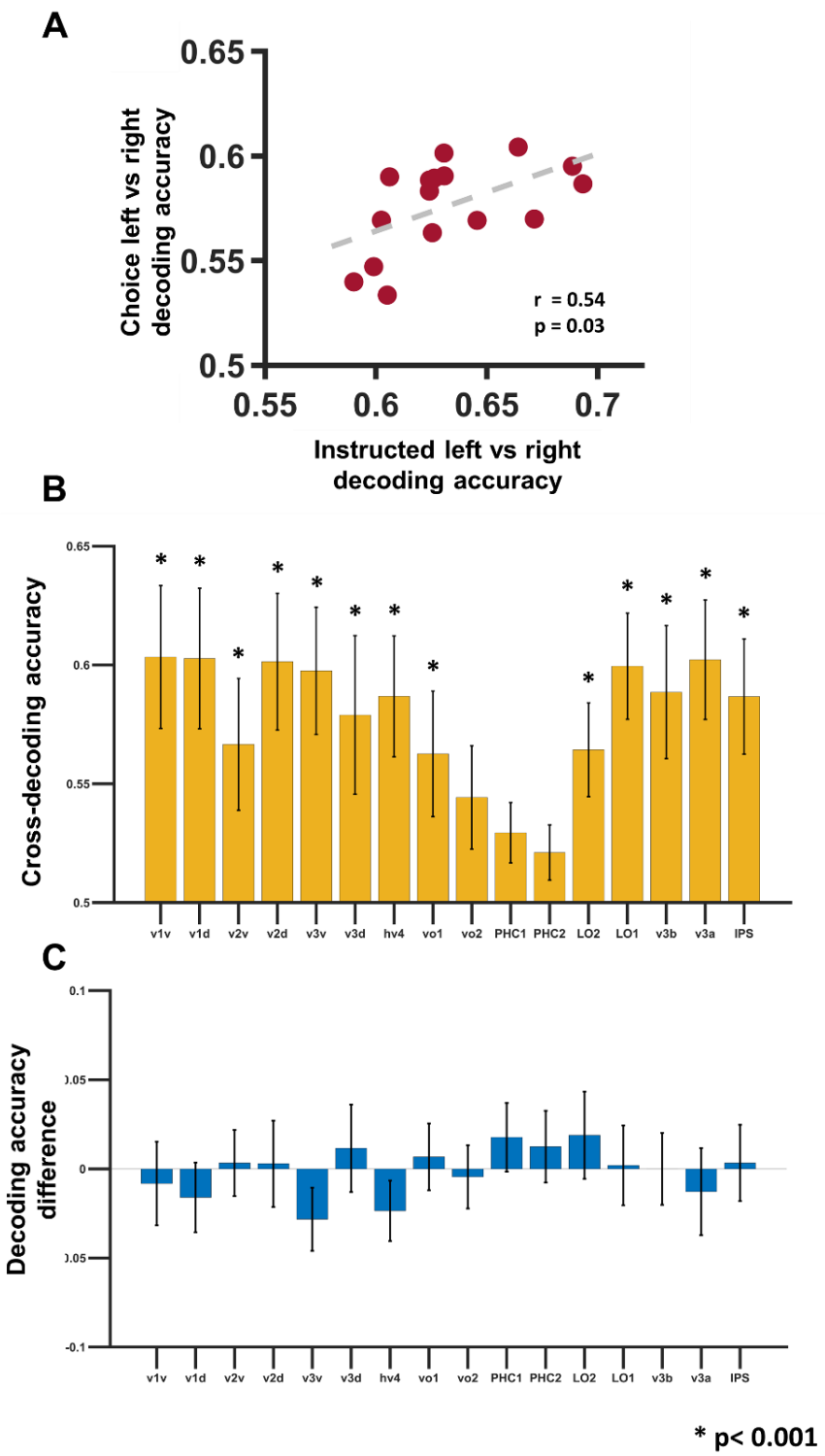


*Figure 9. Comparison of decoding performance between choice and instructed attention conditions averaged from UF and UCD datasets. (A) Choice vs instructed attend-left vs attend-right decoding accuracies; each dot represents a visual ROI. (B) Cross decoding accuracy comparison across ROIs where classifiers were trained on instructed trials and tested on choice trials. (C) Difference between cross-decoding accuracy (classifiers trained on instructed trials and tested on choice trials) and actual decoding accuracy (choice trials) for different visuo-topic ROIs.*

## Discussion

We investigated how top-down voluntary attention biases background neural activity in the visual hierarchy using fMRI and machine learning methods. Two questions were addressed: First, does top-down attentional control bias neural activity across the entire visual hierarchy? Second, how does the strength of top-down biasing relate to subsequent behavioral performance during visual spatial selective attention? To answer these questions, we analyzed fMRI data from two experiments where subjects performed trial-by-trial visual spatial attention tasks. Two different methods of triggering the orienting of spatial attention were included: one involved the use of instructional cues to direct the subject's attention to the left or the right visual field, and the other involved the use of a choice cue that prompted the subject to make voluntary decisions on a trial-by-trial basis about whether to attend the left (choose-left) or the attend (choose-right) visual field. Applying both univariate and multivariate techniques to analyze cue-related neural activity in the retinotopic visual cortex (i.e., baseline shifts), we observed the following results: (1) Among fifteen ROIs, differential attend versus ignore univariate BOLD activations were found in higher-order visual areas but only weakly or not at all in lower-order visual areas (i.e., v1v being the exception for choice trials), (2) multivoxel patterns in all 15 ROIs differentiated the two attention states (attend left vs attend right) with lower-order ROIs having higher decoding accuracy than higher-order visual ROIs, (3) the more distinct the attend-left versus attend-right neural patterns (i.e., the higher the decoding accuracy) in the visual cortex, the better the subject's behavioral performance (i.e., behavioral efficiency), (4) similar results were found for instructed and choice trials, (5) the neural patterns evoked by instructional

cues and choice cues are similar, and (6) the results were replicated across two datasets recorded at two sites utilizing the same experimental paradigm.

**Attentional Modulation of Baseline Activity in Visual Cortex**

Attention cueing improves task performance, but the underlying neural mechanisms have been the subject of intense investigation. Kastner *et al.* (1999) cued subjects on a block-by-block basis to covertly attend the stimuli located in the upper right quadrant of the visual field or to passively view the stimuli. They reported an increase in cue-related BOLD activity (expectation period activity) in areas that included V1, V2, V4, temporal-occipital (TEO) regions (fusiform gyrus), and regions within DAN (FEF and IPS); the BOLD activation was stronger in higher-order visual regions. They found similar results in subsequent work using a modified version of the stimulus and task paradigm (McMains *et al.*, 2007). Despite the seminal nature of this work, because the cued location was not varied in these studies in a fashion that could equate attention demands to and away from the attended region, it is difficult to know whether the patterns of the baseline activity increases encoded spatially-specific attended information or instead reflected nonspecific effects such as arousal or differences in the eccentricity of the focus of attention (i.e., fixation vs. peripheral). However, other studies found similar results in a variety of different experimental, task and stimulus designs (Hopfinger *et al.*, 2000; Ress *et al.*, 2000; Serences *et al.*, 2004; Silver *et al.*, 2007). For example, Hopfinger *et al.* (2000) contrasted the background biasing in visual cortex induced by attend-left versus attend-right cues—thereby equating the contrasting attention demands—and also reported significant attention-related activations in higher-order visual areas in the fusiform and cuneus gyri (corresponding to V2, VP and V4) in the hemisphere contralateral to the attended hemifield, but not in V1. In a series of

studies, (Bressler *et al.*, 2008; Sylvester *et al.*, 2008; Sylvester *et al.*, 2007; Sylvester *et al.*, 2009) reported attention modulation of multiple visual cortical regions during anticipatory attention and found that such neural activity encoded the attended location. Our univariate analysis, combining both UF and UCD datasets through meta-analysis, showed that BOLD activity was enhanced in high-order visual areas such as lateral occipital and parietal regions, but not in early retinotopic visual cortex (i.e., V1 through V4).

Recognizing the univariate methodology might underlie the inconsistent reports in the literature, including our own data presented here between the two sites, we opted to examine the problem by applying the MVPA method to the anticipatory baseline shifts during the cue-target period. The results, replicated across two datasets, show above-chance decoding in all retinotopic visual areas, and the decoding accuracy appears to follow the inverse pattern from the univariate analysis, namely, the decoding accuracy is higher in earlier visual areas and decreases as one ascends the visual hierarchy, suggesting that not only the top-down biasing signals were present in the entire visual system, these signals exhibited patterns that were specific to the attended location and their strengths are ROI dependent. Our findings can also be seen as extending the findings of a recent MVPA study (Park and Serences, 2022) where it is reported that cue-related neural activities can be decoded in the retinotopic visual cortex down to V4-V2 but not in V1.

**Behavioral Significance of Baseline Modulation in Visual Cortex**

Do the biasing signals in the visual cortex impact behavior? This question has been addressed in previous research. Ress *et al.* (2000), using logistic regression modeling to relate relative BOLD activity in visual regions with behavior (the signal

detection measure d'), observed the activity in V1-V3 to be predictive of behavioral performance. Sylvester and colleagues (2007) found the pre-stimulus neural activity in the visual cortex region v3A, indexed by subtracting the BOLD activity between left and right hemispheres (contralateral minus ipsilateral to the attended hemifield) was higher for trials with correct responses than incorrect trials, again suggesting a relation between cue-evoked cortical activity and behavior. However, in prior work from our group (Fannon *et al.*, 2008) using a cued motion-color attention task, found that the increase in cue-related neural activity in the visual cortex (MT and V8) was not predictive of the post-stimulus neural activity or the subsequent behavioral performance. Thus, the issue of whether cue-related neural activity impacts behavior remains unresolved. Univariate methods used in the previous studies may underlie the inconsistent reports.

We examined this issue using the MVPA approach described earlier, and hypothesized that the decoding accuracy, which can be taken as a measure of the strength of anticipatory attentional biasing of visual cortex, should be positively associated with behavioral performance. Indexing the decoding performance across the 15 ROIs in the visual system using the first PCA component and quantifying behavioral performance using efficiency (accuracy/RT), we found that across participants, decoding accuracy was positively associated with behavioral efficiency, thereby establishing a relation between cue-related baseline shift activity in the visual cortex and behavior.

**Study Design Considerations**

Three aspects of our study design that are worth emphasizing. The first is that we included two datasets recorded at two different institutions using two different brands

of scanners but the same experimental paradigm in our analysis. By doing so, we were able to demonstrate the robustness and reproducibility of our findings within a single study, thereby addressing a recent concern that neuroimaging studies often suffer from low reproducibility (Bennett and Miller, 2010; Noble *et al.*, 2017; Poldrack *et al.*, 2017).

The second is in our experimental paradigm, which included choice cues in addition to standard instructional cues. Upon receiving the randomly intermixed choice cue, the subject had to freely decide whether to attend the left or right visual field. While our paradigm was originally designed to investigate willed attention (Bengson *et al.*, 2014; Rajan *et al.*, 2019), the availability of the choice cue allowed us to rule out the possibility that the above-chance decoding of cue-evoked activity in early visual cortex simply reflected the processing of the different physical attributes of the different visual cues (Carlson and Wardle, 2015; Grootswagers *et al.*, 2017), and thus to rule in that it reflected the differences in neural patterns underlying the two different attentional states (attend left vs. attend right). Importantly, the neural patterns between cue left and cue right and between choice left and choice right are highly similar, as indexed by the cross-decoding analysis in which the classifiers were trained on instructed trials and tested on choice trials. This suggests that the visual cortical biasing follows the same principles irrespective of whether the attentional state arose from external instructions or from pure internal decisions.

Finally, one last aspect of the study design bearing considerations is the stimulus array. As shown in Figure 1 and described in the Methods, small, single white dots marked the general location to which targets would be presented. While these were stationary (i.e., not flashing or moving), shifting attention to the dots might result in

attention-related modulations of sensory signals from the contrast border represented by the dots, rather than baseline shifts of background neural activity in the complete absence of sensory signals. Microsaccades could also result in the dot markers serving as bottom-up sensory inputs due to the movement of the dot stimuli on the retina. Because the dots were present in both the attended and unattended visual hemifields, one might be tempted to assume that the physical sensory features of the display are equivalent for cue/choose-left versus cue/choose-right conditions. While this is true for the display independent of attention, it is not necessarily true for the well-known interaction of top-down spatial attention and bottom-up sensory signals. That is, one might predict precisely the pattern of BOLD effects we observed if the activity was the attentional modulation of the dot stimulus itself; we do not believe we can rule this out. Does this, therefore, invalidate the findings and interpretations here? We do not believe so, but it must qualify them. There are reasons to believe the current findings and interpretations of baseline activity are valid. First, the dots marking the possible target locations were very small (fractions of a degree of visual angle) compared to the target stimuli (5 x 5 deg), and it is unclear whether significant BOLD signal increases would be elicited by attention to the stationary (standing) stimulus (to our knowledge, though, this possibility has never been tested). Second, the dots and the flashed gratings are quite different in their physical features, and the task-relevant stimuli (the gratings) are the targets of attention in our design; importantly, the subjects were not instructed to attend to the dots themselves, rather they were reminders of the approximate target locations. Performing the task, one has a clear impression that the dots are irrelevant and provide little assistance. While spatial attention does modulate both attended and ignore stimuli

within its focus, task-irrelevant stimuli are processed less (Hillyard and Munte, 1984), and the spatial locations of the targets was more extensive than of the dots. Third, even if one were to assume that the dots were providing a bottom up signal that was differentially modulated by attention, and therefore could be confounded with pure baseline BOLD shifts in this design, that would not invalidate the basic finding here that the magnitude of top-down attention during the anticipatory period correlates with the later behavioral performance for task-relevant target stimuli. Finally, our univariate BOLD results are generally consistent with findings from prior work that have(Hopfinger *et al.*, 2000; Serences *et al.*, 2004) and have not (Giesbrecht *et al.*, 2006; McMains *et al.*, 2007; Walsh *et al.*, 2011; Weissman *et al.*, 2002) included background markers of spatial locations.

## Conclusion

Our findings in this study from analyzing two datasets with the same experimental paradigm provide evidence to support the notion that top-down attentional control signals result in biasing of neural activity along the entire visual hierarchy including the primary visual cortex, and the strength of these biasing signals modulates subsequent behavioral performance.

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