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Category-selective areas in human visual cortex exhibit preferences for stimulus depth

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Abstract

Multiple regions in the human brain are dedicated to accomplish the feat of object recognition; yet our brains must also compute the 2D and 3D locations of the objects we encounter in order to make sense of our visual environments. A number of studies have explored how various object category-selective regions are sensitive to and have preferences for specific 2D spatial locations in addition to processing their preferred-stimulus categories, but there is no survey of how these regions respond to depth information. In a blocked functional MRI experiment, subjects viewed a series of category-specific (i.e., faces, objects, scenes) and unspecific (e.g., random moving dots) stimuli with red/green anaglyph glasses. Critically, these stimuli were presented at different depth planes such that they appeared in front of, behind, or at the same (i.e., middle) depth plane as the fixation point (Experiment 1) or simultaneously in front of and behind fixation (i.e., mixed depth; Experiment 2). Comparisons of mean response magnitudes between back, middle, and front depth planes reveal that face and object regions OFA and LOC exhibit a preference for front depths, and motion area MT+ exhibits a strong linear preference for front, followed by middle, followed by back depth planes. In contrast, scene-selective regions PPA and OPA prefer front and/or back depth planes (relative to middle). Moreover, the occipital place area demonstrates a strong preference for “mixed” depth above and beyond back alone, raising potential implications about its particular role in scene perception. Crucially, the observed depth preferences in nearly all areas were evoked irrespective of the semantic stimulus category being viewed. These results reveal that the object category-selective regions may play a role in processing or incorporating depth information that is orthogonal to their primary processing of object category information.

Keywords

Category-selective visual regions; Depth perception; fMRI; Occipital place area (OPA); 3D visual perception; Scene perception

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Appendix A. Supplementary data
Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.04.025.

1. Introduction

At any given moment, our visual environment contains a vast array of objects. Recognizing and locating these objects quickly and with ease is a critical aspect of visual processing. The human visual system has a number of dedicated brain regions that allow us to efficiently accomplish the feat of object recognition. However, our visual system must combine information about what objects are with where the objects are. While it was traditionally thought that “what” and “where” information was processed in separate visual pathways (Haxby et al., 1991; Ungerleider, 1982), increasing evidence has suggested that many brain regions contain information about both object identity and location (Arcaro et al., 2009; Carlson et al., 2011; Golomb and Kanwisher, 2011; Kravitz et al., 2010; Sayres and Grill-Spector, 2008; Schwarzlose et al., 2008). However, these studies have primarily focused on two-dimensional location; in the real world, objects appear at multiple positions throughout our visual field *and* span across multiple depth planes. Here we explore whether areas specialized for object recognition are also sensitive to the position-in-depth of stimuli presented in 3D.

Numerous fMRI investigations of functional specialization in the brain have demonstrated that the ventral visual stream contains several major regions that primarily respond to specific object or stimulus categories such as faces, bodies, objects (i.e., shapes), scenes, visual words, and motion (e.g., Kanwisher, 2010; Kanwisher and Dilks, 2013; Katzner and Weigelt, 2013). For example, the fusiform face area (FFA; Kanwisher et al., 1997) and occipital face area (OFA; Pitcher et al., 2007) are highly specialized for processing faces and face-like stimuli. The fusiform body area (FBA; Peelen and Downing, 2005) and extrastriate body area (EBA; Downing et al., 2001) are cortical regions specialized for visual processing of the human body. Areas LO and pFS (together the Lateral Occipital Complex; LOC) are characterized by their selectivity for object shape (Malach et al., 1995). Dedicated regions involved in scene processing include the parahippocampal place area (PPA; Epstein and Kanwisher, 1998), occipital place area (OPA; Dilks et al., 2013), and retrosplenial complex (RSC; Maguire, 2001). The visual word form area (VWFA) is involved in visual word recognition (Cohen et al., 2000). Finally, motion sensitive area MT+ (Tootell et al., 1995) is characterized by its selectivity to moving, rather than stationary, stimuli.

These functionally-specialized, category-selective regions help us effortlessly recognize objects. While these regions are predominately tuned to their respective stimulus categories, they are nevertheless also engaged in processing of other visual features such as geometric regularities (Bona et al., 2014; Caldara and Seghier, 2009; Chen et al., 2006), spatial frequencies (Berman et al., 2017; Henriksson et al., 2008; Rajimehr et al., 2011), retinotopic locations (Golomb and Kanwisher, 2011; Sayres and Grill-Spector, 2008), and 2D spatial locations (Hemond et al., 2007; Kravitz et al., 2010; Levy et al., 2001; Schwarzlose et al., 2008; Silson et al., 2015). Here we investigate whether these regions are also engaged in the processing of depth information, or position-in-depth.

Of particular relevance to the current question is these regions’ sensitivities to 2D spatial location (i.e., location along the x- and y-, or polar angle and eccentricity, axes; Groen et al., 2017). For example, it has been shown that face, object and scene regions all have preferences for stimuli presented in the contralateral visual hemifield (Hemond et al., 2007) indicating sensitivity to x-axis location. It has similarly been demonstrated that face, body, object, and scene regions also have preferences for certain elevations or vertical positions (Schwarzlose et al., 2008; Silson et al., 2016; Silson et al., 2015) demonstrating that these regions are also sensitive to y-axis location. Other studies have found eccentricity biases in face, scene, and word regions such that they prefer either foveal or peripheral stimuli (Gomez et al., 2018; Le et al., 2017; Levy et al., 2001). Taken together, these findings demonstrate that the distinct category-selective regions are not exclusively processing their preferred stimulus category, but rather engage in processing of 2D spatial locations as well. In consideration of the category-selective regions' sensitivity to 2D spatial location, whether and how these regions are also sensitive to position-in-depth (i.e., position along the z-axis), has largely been ignored.

One intriguing finding comes from a multivoxel pattern analysis (MVPA) study showing that the representation of depth information (defined by binocular disparity cues) gradually increases from low- to mid- to higher-level visual brain regions (Finlayson et al., 2017), proposing that spatial representations transition from 2D-dominant to balanced, 3D representations in the brain. This suggests that the category-selective regions that exist farther along this hierarchy should contain information about position-in-depth. However, Finlayson et al. (2017) only tested random dot motion stimuli, occupying small patches of the visual field at only two depth planes: a plane in front of fixation and a plane behind fixation; and they did not localize the major category-selective regions other than LOC and MT+.

Testing a related type of visual information, recent studies have demonstrated that object and scene regions are sensitive to egocentric *distance*– that is, the distance between the observer and observed stimulus (Amit et al., 2012; Persichetti and Dilks, 2016). It has been shown that area LO prefers proximal stimuli while scene areas PPA and OPA prefer distal stimuli (Amit et al., 2012). Amit et al. (2012) presented objects and scenes superimposed onto Ponzo lines to generate the percept of distance with 2D cues, while Persichetti and Dilks (2016) presented 2D photographs of objects and scenes taken from distal and proximal perspectives and tested fMRI adaptation. Others have used voxel-wise modeling to show that most voxels in PPA, OPA, and RSC elicit greater BOLD responses when subjects view 2D scenes containing distant salient objects compared to scenes containing nearby salient objects (Lescroart et al., 2015).

While these aforementioned distance studies used 2D stimuli to probe the percept of distance, the current study looks explicitly at depth information (from binocular disparity) using 3D stimuli. Although depth and distance are related concepts, one major difference is that the previous studies varied the perceived distance of objects *within* a scene, whereas the current study manipulates the depth plane at which the stimulus itself appears. In other words, "distance" in the previous studies was manipulated *within* the 2D images such that the images were always presented at the same physical distance from the observer, and salient objects within the images were perceived to be relatively more distal or proximal to the observer. Our manipulation presents the entire image at specific locations along the depth-axis. Because we are using disparity cues, our stimuli are defined by their position-in-depth (i.e., relative to the “middle” depth plane where the screen – and fixation – are positioned); however, this manipulation could also be thought of as varying distance relative to the observer. The key question is whether category-selective regions exhibit preferences for a specific depth *plane* or *location* (regardless of image content), akin to previous explorations of 2D visual field biases (e.g., Hemond et al., 2007; Levy et al., 2001; Schwarzlose et al., 2008).

In the present study, we used functional MRI (fMRI) to investigate whether the major face, object, scene, and motion regions process 3D depth information—and if so, whether this sensitivity is dependent on each region’s preferred, semantic stimulus category. We stimulated three depth planes (in front of fixation, flush with fixation, and behind fixation, along with a mixed front-and-behind condition in Experiment 2) to examine depth *preferences* of these regions. We measured brain responses across category-selective regions while participants viewed images of faces, objects, scenes, and nonspecific stimuli (i.e., scrambled images and random moving dots) presented at different depth planes. We hypothesized that face and object areas would prefer nearer depth planes while scene areas would prefer a farther depth plane – and that these preferences might interact with stimulus category – consistent with the idea that faces and objects are typically viewed at or appear at near depths, whereas scenes may be more likely to be processed in the background. A fundamental question is whether these depth plane preferences – if present – rely on viewing these face, object, and scene stimuli, or if the category-selective regions maintain preferences for depth information even in the absence of semantically-meaningful stimuli.

2. Experiment 1

2.1. Methods

2.1.1. Participants—Sixteen university students participated in this experiment (ages 18–29; mean age = 22.0; 12 females). One subject was an author (DB). All participants reported having normal or contact-corrected normal vision and were screened for stereovision and stereoscopic acuity. Subjects also completed a depth sensitivity psychophysics experiment wherein they perceptually matched the magnitude of disparity of front and back stimuli (see supplemental methods, Section I). Informed consent was obtained for all participants and The Ohio State Biomedical Sciences Institutional Review Board approved the study protocols.

2.1.2. Stimuli and design—All stimuli were generated using Matlab (Mathworks) and the Psychophysics Toolbox (Brainard, 1997) and were presented on a gray background. Depth from binocular disparity was achieved by using red/green anaglyph glasses with Psychtoolbox’s stereomode. Participants viewed all stimuli through the anaglyph glasses from a distance of 74 cm via a mirror at 45° above their heads.

In one set of runs (category runs), subjects fixated on a central, white fixation dot (0.16° diameter) outlined in black. An array of four grayscale images (3.60° square each) was presented, with one image in each of the four quadrants of the screen (3.04° eccentricity). The array comprised either four unique faces, four real-world objects, four grid-scrambled objects, or an image of a single scene split into four equally-sized quadrants (Fig. 1A). The stimuli were drawn from a database containing 40 unique images of each stimulus category. During any given block, the entire array of four images was presented at one of three depth planes (Fig. 1B): back (behind the fixation plane; −12 arcmin), middle (flush with the fixation plane; 0 arcmin), or front (in front of the fixation plane; +12 arcmin). Additionally, floor and ceiling line-frames (13.4° × 3.2°) flanked the entire display to enhance the perception of a 3D space, each spanning ± 12 arcmin in front of and behind the fixation plane.

Each category run lasted approximately six minutes and twenty-three seconds. Every run consisted of 29 blocks (two blocks per each of the 12 conditions below plus five fixation blocks) that lasted 11.2 seconds each (with 1.3 seconds between each block). The different conditions were: faces (back, middle, front), objects (back, middle, front), scenes (back, middle, front), and scrambled (back, middle, front). For each run, the order of conditions was pseudorandomized for the first 12 blocks and the order of the remaining 12 blocks was the reverse of the first 12. We included five fixation blocks: one at the beginning and one every seven blocks thereafter for a total of 29 blocks. Additional 5 s and 15 s blank fixation periods were presented at the beginning and end of each run respectively.

Within each block, eight image arrays were shown for 1.2 s each, followed by an interstimulus interval (ISI) of 0.2 s. To offer a more compelling depth percept, over the course of the 1.2 s display duration, the entire array slowly moved horizontally across the screen from 0.1° left of center to 0.1° right of center (or from right to left) at a rate of 0.17°/sec. Moving arrays, coupled with binocular disparity, were used instead of static arrays to improve the percept of depth (Ban et al., 2012). Participants performed a one-back task wherein they responded every time the entire image array was presented twice in a row. Depending on time constraints, subjects completed between seven and eight of these category runs.

In another set of runs (RDM runs), subjects fixated on a central, white fixation dot (0.16 diameter) while viewing a full-field of dynamic random dot motion (RDM) stimuli (12.0° square; Fig. 1A) in the periphery. The RDM array was presented at one of three depth planes: back, middle, or front (same depths as in the category runs; Fig. 1B). Additionally, rectangular bars (rectangles colored gray or white at each pixel location; 13.4° × 3.2°) flanked the entire display at the “middle” plane to provide additional depth reference frames in the periphery.

Each RDM run lasted approximately seven minutes and five seconds. Every run consisted of 32 blocks that lasted 12.5 seconds each: Eight blocks per condition plus eight fixation blocks. The conditions were back, middle, and front. For each run, the order of conditions was pseudorandomized. Participants performed a dot-dimming task wherein they responded every time the central, white fixation dot dimmed to gray. Similar to the category runs, there were additional 5 s and 20 s blank fixation periods at the beginning and end of each run respectively. Each subject completed two of these RDM runs.

2.1.3. Data acquisition—All scanning was performed on a 3T Siemens Prisma scanner with a 32-channel head coil at the Center for Cognitive and Behavioral Brain Imaging

(CCBBI) at The Ohio State University. Functional data were acquired with a T2-weighted gradient-echo sequence (TR = 2500 ms, TE 28 ms, 7200B0 flip angle). Slices were oriented to maximize coverage of the occipital lobe and posterior parietal lobes (41 slices, 2 × 2 × 2 mm voxels, 0% gap). A high-resolution MPRAGE anatomical scan was acquired for each participant before collecting any functional data.

Each participant was scanned in a single 2-hour session which included seven to eight category runs, two RDM runs, and one MT + localizer run (described below).

2.1.4. Functional localizers and ROI localization—For each participant, we identified regions of interest (ROIs) using standard functional localization procedures. We focused on well-known category-selective regions FFA, OFA, LOC, PPA, OPA, RSC, and MT+. To localize the face-, object-, and scene-regions, we used the data from the aforementioned category runs but collapsed across depth planes, such that the localizer contrasts were orthogonal to the subsequent main analyses of depth information. For example, FFA and OFA were defined with a [back-faces, middle-faces, and front-faces] > [back-objects, middle-objects, and front-objects] contrast (Kanwisher et al., 1997). Object-selective LOC and scene-selective PPA, OPA, and RSC were similarly defined with objects > scrambled objects (Malach et al., 1995) and scenes > objects (Epstein and Kanwisher, 1998) contrasts, respectively.

An additional localizer task was used to identify motion-sensitive area (MT+). Participants fixated at the center of the screen and passively viewed peripheral random dot stimuli (all middle depth) that were either stationary or moving. The random dot stimuli occupied the full-screen and the moving patterns alternated between concentric motion towards and away from the fixation point at 7.5 Hz. MT+ was functionally defined with a moving > stationary contrast (Tootell et al., 1995).

All ROIs were localized bilaterally in both hemispheres and the voxels were combined to create a single ROI. ROIs were defined using a contrast threshold of $p = 0.001$.

2.1.5. fMRI analysis—fMRI data preprocessing and analysis were conducted using Brain-Voyager QX. The data were corrected for slice acquisition time and head motion, temporally filtered, spatially smoothed with a Gaussian kernel of 4 mm FWHM, and normalized into Talairach space (Talairach and Tournoux, 1988). Univariate analyses of the category and RDM runs were performed on individual subject data using a standard general linear model (GLM). Incorporated into the model for the category runs were regressors for each of the 12 depth-category conditions plus the fixation condition. Incorporated into the model for the RDM runs were regressors for each of the three depth conditions plus the fixation condition. Mean response magnitude was calculated for each ROI and condition of interest, with the fixation condition as a baseline.

2.2. Results

Our primary question was whether the category-selective regions exhibit sensitivity to stimulus depth. We also asked whether this sensitivity is dependent on the stimulus category that is being viewed. That is, do category-selective regions exhibit depth sensitivity only for their preferred category, non-preferred categories, or both? To answer this, we compared ROI activation across different combinations of depth and stimulus categories (Table 1; Fig. 2). We ran a 5 × 3 repeated-measures ANOVA across factors of stimulus category (faces, objects, scenes, scrambled objects, moving dots) and depth plane (back, middle, front) for each ROI. Note that because the ROIs were defined based on a contrast of stimulus category, the main effects of stimulus category are non-independent; for the sake of completeness, these effects are reported in Table 2, but our focus below is on the main effects and interactions of depth plane. To explore the specific patterns of depth preferences in each of these ROIs, we also conducted planned, a priori t tests comparing activation for front, middle, and back depth planes (collapsed across stimulus categories; Table 2; Fig. 3). Even when the main effect of depth was not significant, these pairwise comparisons were still assessed to reveal information about specific preferences for depth.

In both of the face regions (FFA and OFA), activation was numerically greatest for the front (“near”) depth plane; however, only OFA demonstrated a significant main effect of depth. Planned pairwise depth comparisons revealed that activation to the front depth was significantly greater compared to middle depth in both ROIs, and there was a trend for front greater than back depth in OFA. There was no significant difference between the activation for back and middle depth planes in either the FFA or the OFA. The stimulus category × depth interactions were nonsignificant in both regions, due to the fairly similar depth patterns for all stimulus categories.

The object-selective area—LOC—also exhibited a preference for the front depth plane. LOC exhibited a significant main effect of depth, and planned pairwise depth comparisons revealed that front depth was significantly greater compared to both back and middle. As in the face regions, there was no significant difference between the activation for back and middle depth planes in the LOC. Also similar to the face regions, there was no significant interaction between stimulus category and depth.

Of the three scene-selective areas (PPA, OPA, and RSC), OPA exhibited a significant main effect of depth. Planned pairwise depth comparisons revealed that activation in OPA to both the back and front depth planes were significantly greater than to the middle depth plane, with no significant difference in activation for back versus front. The stimulus category × depth interaction was not significant. In PPA, the main effect of depth was not significant (though there was a trend), and the planned pairwise depth comparisons revealed significantly greater activation for back compared to the middle depth. Interestingly, the interaction between stimulus category and depth was significant in PPA. This interaction may have been driven by a different pattern of results for objects and grid-scrambled objects (linear pattern: front > middle > back) relative to the other stimulus types (more parabolic pattern: back & front > middle; Table 1), however, post-hoc analyses revealed that neither the main effects of depth (Fs < 1.33, ps > 0.27, $\eta^2 < 0.09$) nor any of the pairwise depth plane comparisons (ts < 1.60, ps > 0.13, ds < 0.40) for these two categories were significant, making it difficult to interpret this interaction. In RSC, none of our depth contrasts were significant.

Finally, in motion area MT+, both the main effect of depth and the interaction between stimulus category and depth were significant. MT+ exhibited a strong linear preference for front, followed by middle, followed by back depth planes. The planned pairwise depth comparisons revealed that front was significantly greater than both middle and back, and middle was significantly greater than back. The interaction in MT+ seemed to be driven simply by variation in the degree of depth modulation, with the overall front-middle-back depth preference preserved for all stimulus categories (Table 1; Fig. 2D).

2.3. Discussion

In Experiment 1, we found that most of the category-selective ROIs are sensitive to depth, but depth sensitivity does not generally vary as a function of stimulus category. OFA, LOC, and MT exhibited a preference for near depth planes whereas OPA preferred both near and far depth planes relative to middle; these patterns of depth preference were consistent across both preferred and non-preferred stimuli as well as semantically meaningless stimuli. One potential explanation for these results is that the category-selective regions may have developed a depth preference based on the depth plane(s) that their preferred stimulus category is typically viewed at (which we discuss in more detail in the general discussion). We had hypothesized that the scene regions might have a preference for far depth planes, but interestingly, OPA exhibited a preference for more than one depth plane; both front and back relative to middle (this pattern was mimicked in PPA, though was not statistically significant). Perhaps this bimodal preference is because scenes are actually typically viewed as spanning multiple depth planes; i.e., real-world scenes contain both near and far information. This begs the question of how the scene regions (and others) would respond to stimuli presented at mixed depth planes (both back and front in the same image). We address this question in Experiment 2, and predict that stimulating both back and front depth planes together will activate OPA even more than front alone or back alone.

3. Experiment 2

The goals of the second experiment were (1) to replicate the patterns of depth preferences in the category-selective regions found in Experiment 1, and (2) to test an additional “mixed” depth condition, where stimuli were presented both behind and in front of fixation within each image array. In Experiment 2, to increase power we only presented a single stimulus type, opting for the neutral non-semantic stimuli (random moving dots), which well-reflected the overall pattern of depth preferences for each region in Experiment 1. This allowed us to look at depth preferences without semantic stimulus-related confounds (which might have become more problematic with the mixed depth).

3.1. Methods

3.1.1. Participants—Sixteen university students participated in this experiment (ages 18–28; mean age = 23.81; 11 females). One subject was an author (SN). Three subjects from Experiment 1 also completed Experiment 2. All participants reported having normal or contact-corrected normal vision and were screened for stereovision and stereoscopic acuity. Informed consent was obtained for all participants and The Ohio State Biomedical Sciences Institutional Review Board approved the study protocols.

3.1.2. Stimuli and design—The main functional runs (depth runs) used the RDM stimuli and task but were otherwise similar in design to the category runs from Experiment 1, with some minor changes

Subjects fixated on a central, white fixation dot (0.16° diameter) outlined in black. An array of four RDM patches (3.60° square each) were presented at four quadrants of the screen (3.04° eccentricity; Fig. 1A). During any given block, the array of four RDM patches was presented at one of four depth planes: back (behind the fixation plane; −12 arc min), middle (flush with the fixation plane; 0 arc min), in front (in front of the fixation plane; 12 arc min), or mixed (two diagonal quadrants in back and the other two diagonal quadrants in front; Fig. 1B). Additionally, floor and ceiling line-frames (13.4° × 3.2°) flanked the entire display to enhance the perception of a 3D space, each spanning ± 12 arcmin in front of and behind the fixation plane.

Each run lasted approximately six minutes and twenty-three seconds. Every run consisted of 29 blocks that lasted 11.2 seconds (with 1.3 seconds between each block): six per each of the four depth conditions (back, middle, front, mixed) plus five fixation blocks. For each run, the order of conditions was pseudorandomized for the first 12 blocks and the order of the remaining 12 blocks was the reverse of the first 12. We included five fixation blocks: one at the beginning and one every seven blocks thereafter for a total of 29 blocks. Again, there were additional 5 s and 15 s blank fixation periods at the beginning and end of each run respectively.

Participants performed a dot-dimming task wherein they responded every time the central, white fixation dot flickered to gray. Depending on time constraints, subjects completed between five and six of these runs.

3.1.3. Data acquisition—All scanning parameters were the same as Experiment 1.

Each participant was scanned in a single 1.5-hour session which included five to six depth runs, three face-object-scene localizer runs (described below), and one MT+ localizer run (as in Experiment 1).

3.1.4. Functional localizers and ROI localization—In Experiment 2, we localized the same ROIs as Experiment 1. Because the main task contained only RDM stimuli, subjects completed an additional localizer task to identify the face, object, and scene regions. This localizer task included blocks of faces, objects, scenes, and grid-scrambled objects presented at the center of the screen (all middle depth). Participants performed a one-back task wherein they pressed a button every time the same exact stimulus was presented twice in a row. We used the same MT + localizer task as in Experiment 1to localize MT+.

3.1.5. fMRI analysis—Data were processed in the same way as in Experiment 1. Univariate analyses of the main functional runs were performed on individual subject data using a standard general linear model (GLM). Incorporated into the model for the depth runs were regressors for each of the four depth conditions plus the fixation condition.

3.2. Results

We compared ROI activation across the different depth conditions in each ROI (Fig. 4). Raw beta weights for all ROIs and depth conditions as well as statistical tests are reported in Table 3. We were unable to localize FFA in one subject due to inadequate slice coverage, thus subsequent analyses for FFA only include data from 15 subjects.

3.2.1. Replication of original depth preferences—We first performed a 1 × 3 repeated-measures ANOVA testing the original three depth conditions (back, middle, front) for each category region, along with planned pairwise *t* tests comparing activation for front, middle, and back depth planes (Table 3).

As in Experiment 1, FFA did not exhibit a main effect of depth, however OFA did. Planned pairwise depth comparisons revealed a preference for the front (“near”) depth plane in OFA: front depth was significantly greater than middle and back depths. There was no significant difference between the activation for back and middle in OFA. None of these pairwise comparisons for FFA reached significance.

We replicated the significant main effect of depth in the LOC, with the same preference for front depth planes: front was significantly greater compared to both back and middle. There was again no significant difference in activation for back versus middle depth planes in LOC.

We also replicated the main effect of depth in MT+ and again found a strong linear preference for front versus middle, middle versus back, and front versus back depth planes.

Of the scene regions, the main effect of depth was significant in PPA, and planned pairwise depth comparisons revealed that activation to the back depth plane was significantly greater than to the middle and to the front depth planes. Activation to the front depth plane was numerically but not significantly greater than the middle plane. In OPA, the bimodal pattern appeared similar to Experiment 1, but neither the main effect of depth nor the planned pairwise depth comparisons were significant. RSC did not exhibit a significant main effect of depth, but planned pairwise depth comparisons revealed a significant preference for back compared to front.

Finally, we conducted some additional analyses combining the data from both experiments for increased power. In the combined analysis (Table S2) both PPA and OPA exhibited significant main effects of depth, along with significantly greater activity for front versus middle and back versus middle in the planned pairwise depth comparisons. RSC had no significant effects. For the face (OFA), object (LOC), and motion (MT+) regions, the front depth preferences were obvious in both the main effects and pairwise comparisons. Moreover, comparing *across* ROIs (Table S3), there were significant Depth × ROI interactions, supporting the qualitatively different patterns of depth preference across the different regions. Finally, as a supplemental analysis we performed whole-brain analyses on the combined data, yielding depth maps of front-vs-back, front-vs-middle, back-vs-middle, and mixed-vs-avg(back & front) comparisons (Fig. S2).

3.2.2. How do the ROIs respond to the “mixed” depth condition?—The focus of this second experiment was the more intriguing question asking how these ROIs fare when viewing stimuli simultaneously presented at multiple depth planes (back and front). To characterize these responses, we examined each regions’ activation to the “mixed” depth plane compared to each of the following: (1) Activation to the regions’ preferred depth. (2) Activation to the middle depth. (3) The average activation to back and front depths. Statistics for all comparisons are presented in Table 3. If the mixed depth (front plus back) stimulus is processed as a type of average of the two depths, then we would expect activation to the mixed condition to look similar to either the middle depth condition (mean depth of the ensemble) or to the average activation to the front and back conditions (i.e., half front, half back). However, if presenting both front and back depths together increases the overall sense of depth in the stimulus, we may expect a response even greater than to the preferred depth, particularly for the scene regions.

In the face regions (both FFA and OFA), activation to the mixed depth fell somewhere between front and back activations, and mixed was not significantly different from the preferred front depth, the middle depth, or the average of front and back activations.

On the other hand, the LOC exhibited a stronger preference for the mixed depth than the other depth conditions; activation to mixed was significantly greater compared to the preferred front depth plane, compared to middle, and compared to the average of back and front.

Intriguingly, although the scene ROIs PPA and OPA showed relatively similar patterns of depth preference when considering the original three depth conditions (front and back greater than middle, at least numerically), the ROIs diverged strikingly when it came to the mixed depth condition (significant ROI × Depth interaction; Table S3). In PPA, the response to the mixed depth was significantly greater than to the middle depth, but it was not significantly different from back and front depths; if anything, it was numerically lower than both. In contrast, in OPA the mixed condition evoked a boosted response. OPA demonstrated a significantly stronger response to the mixed depth compared to back, middle, and the average of back and front, along with a nonsignificant trend towards a preference compared to front. Finally, in RSC the mixed depth condition did not produce significantly different activation compared to any of the other conditions.

Finally, in the motion regions, the mixed depth produced a similar response to the preferred front depth, with no significant difference between the two. There was a significantly stronger response to mixed depth compared to both middle depth and the average of back and front conditions.

3.3. Discussion

In Experiment 2 we replicated the depth preferences of Experiment 1. Even in the absence of semantically-meaningful stimuli, face (OFA), object (LOC), and motion (MT+) regions showed a preference for front depth. Scene regions PPA and OPA exhibited similar bimodal patterns across Experiments 1 and 2 (both back and front depths preferred to middle), but there was some variability in their statistical reliability; however, the data combined across experiments revealed statistically reliable effects – and large effect sizes – for both regions. The critical contribution of this second experiment was the introduction of the mixed depth condition. While most of the regions did not exhibit a clear difference between their preferred depth and mixed depth, both OPA and LOC demonstrated a strong preference for mixed depth compared to most other depth planes. The OPA pattern was consistent with our predictions, but the LOC preference – and the lack of a preference for mixed in the PPA – were unexpected.

4. General discussion

The current experiments examined whether the major functionally defined category-selective regions are sensitive to stimulus depth. A number of prior studies have investigated the role that these regions play not only in object recognition but also in processing 2D spatial information. Here we used 3D stimuli (via binocular disparity cues viewed through red/green anaglyph glasses) to probe how these regions respond to stimuli presented at different depth planes. Our findings support the idea that many of these category-selective regions are sensitive to depth location information. Across two experiments, we found that the majority of the category-selective regions show depth preferences in the form of significantly greater mean response magnitudes to at least one stimulus depth plane over another. Face (OFA), object (LOC), and motion (MT+) regions exhibited a front preference whereas scene regions (PPA and OPA) generally exhibited a preference for both front and back compared to middle depth. Crucially, the results of Experiment 1 demonstrate that it is likely not the category-selective regions' preferred stimuli alone that give rise to the depth preferences. Rather, we found that for nearly all of the ROIs, the pattern of depth preference did not significantly interact with stimulus type, but was generally present for any stimulus category (preferred or not, semantically meaningful or not) presented with 3D depth information.

4.1. Depth location information in category-selective visual areas

A number of investigations of the category-selective regions' sensitivity for 2D spatial location have found preferences for certain locations in the visual field. For example, Hemond et al. (2007) demonstrated that face and object regions prefer stimuli from the contralateral visual field, and Silson et al. (2015) used pRF modeling to demonstrate that PPA and TOS (i.e., OPA) exhibit clear biases for the contralateral-upper and lower visual fields respectively. Furthermore, Levy et al. (2001) demonstrated that face and scene regions prefer foveal and peripheral stimuli, respectively—another measure of 2D location. Our findings show that, like sensitivities to 2D spatial locations, many of the category-selective regions are also sensitive to position-in-depth, with face (OFA), object (LOC), and motion (MT+) regions showing a preference for front depth, and scene regions PPA and OPA preferring both back and front depths compared to middle. The general lack of interactions between stimulus category and depth information is also consistent with previous reports finding that 2D location information does not vary with stimulus category in category-selective regions (Schwarzlose et al., 2008), nor does sensitivity to egocentric distance (Amit et al., 2012; but see Persichetti and Dilks, 2016).

Our finding of depth sensitivity in LOC and the scene regions complements prior studies showing that object and scene regions process information about perceived egocentric distance (i.e., preferences for apparent proximal or distal elements of stimuli within a 2D image; Amit et al., 2012; Lescroart et al., 2015; Persichetti and Dilks, 2016). However, here we explicitly tested the sensitivity to *depth location* as manipulated by arcmin of binocular disparity. By presenting the entire stimulus image at a specific depth plane (i.e., location along the z-axis), we manipulated depth location in a more analogous way to the 2D location investigations noted above. Because we did not vary the plane of fixation, our conclusions may reflect either depth preferences relative to fixation or distance from the observer, or both.

Our results provide converging evidence that category-selective regions along the "what" pathway (Ungerleider, 1982) – that are defined by their selectivity for specific object categories and thought to allow for the ability to recognize objects – also contain information about object location, including position-in-depth. Why is it that the "what" pathway also contains "where" (e.g., depth) information? One possibility is that the ability to recognize and identify an object is (at least partially) dependent on the ability to locate the object in the 3D environment first. In order to enable object localization, the visual system must undergo computations of an object's exact 2D and 3D coordinates. The sensitivity to depth information in nearly all of our localized ROIs might mean that the presence of depth information facilitates computations of an object's precise position-in-depth which in turn aids the object localization process and therefore the object recognition process.

Another possibility for why the category-selective regions also exhibit depth preferences may be experience-driven, based on how the regions' preferred stimuli are typically encountered. In other words, face and object regions might respond more to stimuli presented at closer depths/distances because processing of faces and objects requires detailed scrutiny and because peripheral faces and objects at nearer depth planes may be more salient than those farther away. Following this logic, faces and objects that appear at nearer depth planes are potentially more likely to be the targets of an upcoming fixation.[1] Scenes, on the other hand, typically span both near- and far-depth planes and may carry relevant information at multiple depth planes. Perhaps an ROI's depth preference is tuned by this experience such that these depth preferences emerge regardless of stimulus category.

Based on this speculation, one might wonder if it is the stimulus categories themselves that are driving these characteristic patterns of depth preference. That is, faces and objects should evoke higher activation at nearer depths and scenes should evoke higher activation at back, front, and mixed depths, regardless of ROI. However, while we found some limited evidence in favor of stimulus-specific patterns, a supplemental analysis (Table S1) revealed that the stimulus-driven patterns were generally weaker than the ROI-driven patterns.

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[1] Note that we are not trying to suggest that faces are typically viewed at a closer depth than fixation; the speculation is more that faces/objects are viewed at relatively more front/near depths than scenes. It is important to keep in mind that all stimuli were presented in the periphery here (3.04° eccentricity), so even in the middle-depth condition, the stimuli were not directly fixated. We did not place any stimuli in the fovea because doing so at different depths would produce changes in eye vergence, which we did not want to confound in the current experiment.

4.2. Depth preferences in scene-selective regions

The patterns of depth preferences in the scene-selective regions were particularly intriguing, as they exhibited a different type of pattern compared to the other ROIs. Rather than exhibiting a preference for either front or back depths, the scene regions exhibited a bimodal preference for both back and front depth planes compared to the middle plane; this effect was significant in OPA in Experiment 1 and PPA in Experiment 2, and in both regions when data were combined across experiments. The RSC did not show much in the way of activation differences in this task, which is not surprising since activation in RSC tends to be rather task specific and only activates under specific viewing conditions (Epstein et al., 2007).

Why would there be a smaller response to the middle depth in OPA and PPA? One potential explanation is that these regions are sensitive to binocular disparity information, regardless of the direction. That is to say, whenever two eyes receive different input – and/or whenever *any* depth information is perceived – these regions respond more compared to stimuli that appear at the fixation plane (zero disparity). This explanation would predict that, in Experiment 2, activation to the "mixed" depth (front plus back) condition would be roughly equal to the activation to front or back depths alone. In other words, since the magnitude of *binocular disparity* in the mixed condition is the same as that of the front and back conditions (in all cases 12 arcmin), we might expect that the magnitudes of *fMRI activation* to the mixed condition would be similar to those of the back and/or front conditions, per the pure disparity account. While the PPA did not exhibit an increased response to the mixed depth condition compared to front or back alone, the OPA exhibited significantly greater activation to mixed compared to back and to the average of front and back. This suggests that at least in OPA the bimodal depth preference found in Experiment 1 cannot be explained by the pure binocular disparity account.

Alternatively, the bimodal depth preference may be better explained by the fact that scenes typically span multiple depths, and scene regions have been shown to represent the spatial features of a scene such as distance, openness, panoramas, layout, and boundaries (Amit et al., 2012; Julian et al., 2016; Kravitz et al., 2011; Lescroart and Gallant, 2019; Park et al., 2011; Robertson et al., 2016). Perhaps the back and front depth planes offered a richer sense of 3D space than the middle depth, given that the central fixation point and stimulus image were presented at different depths. In the mixed condition the range of depth stimulation is even greater (24 arcmin between the front and back stimulus quadrants), and is therefore arguably the most "scene-like".

The fact that the different scene regions exhibited different patterns of results raises interesting implications about the specific properties and functions of each of the scene regions. Our finding that the PPA did not have a preference for the mixed depth condition but OPA did might be reflective of the tasks that they are thought to be implicated in (Persichetti and Dilks, 2018). A number of recent studies have shown that OPA is sensitive to various forms of navigationally-relevant information, proposing that these regions play a role in human navigation (Dilks et al., 2011; Epstein, 2008; Julian et al., 2016; Persichetti and Dilks, 2016, 2018). Furthermore, OPA also automatically encodes pathways for movement and represents first-person perspective motion (Bonner and Epstein, 2017;

Kamps et al., 2016). In the current study, OPA's unique sensitivity to the mixed depth condition might be indicative of its contribution to a navigation system. Recall that the mixed condition was created to evoke a strong sense of scene-like space given that the stimuli spanned multiple depth planes. It is possible then, that OPA treats depth information —particularly the stimulation of multiple depth planes—as navigationally-relevant and therefore exhibited a stronger preference for the mixed depth stimulus condition, relative to its preferred back depth plane.

In contrast, it has been suggested that PPA responds more to information about scene content (MacEvoy and Epstein, 2009) and category (Persichetti and Dilks, 2018; Walther et al., 2009). More specifically, studies have shown that PPA responds more when objects that elicit strong associations to scene context (e.g., an oven) are presented within a scene compared to when the objects elicit weak associations (e.g., a laptop) or are absent (Bar et al., 2007; Bar et al., 2008; Harel et al., 2012). Others have shown that the PPA is particularly sensitive to physical size (i.e., spatial extent of a scene bounded by walls) and clutter of a scene (Park et al., 2014). According to these studies, a fundamental function of the PPA is to encode elements of the scene that aid with categorizing the scene (e.g., beach or mountain). Whereas having a sense of multiple depth planes is relevant for navigation, a glimpse at single depth plane may be enough to conceptually categorize a scene. This notion may explain why we found a boost in activation for mixed depth in OPA but not PPA. It might also explain why there was a different pattern of depth preference in PPA for scenes versus objects in Experiment 1, if PPA is involved in encoding different elements of the scene (e.g. foreground objects and background scene content).

Another reason for why PPA and OPA show different depth preferences may be reflective of the mere fact that PPA is located along the ventral stream while OPA is located along the dorsal visual pathway. Several areas of cortex along the visual hierarchy in both streams have been implicated in depth representation (Backus et al., 2001; Finlayson et al., 2017; Preston et al., 2008), but some key differences have been noted, namely between ventral LO and dorsal V3A/B. For example, a few studies have shown that ventral areas are sensitive to categorical disparity (i.e., disparity sign) whereas dorsal areas are sensitive to metric disparity (i.e., disparity magnitude); or that ventral areas are sensitive to both absolute and relative disparity while dorsal areas reflect absolute disparity (Neri et al., 2004; Preston et al., 2008). Additionally, areas V3A and V3B have been particularly implicated in depth processing in both humans and monkeys (Backus et al., 2001; Ban et al., 2012; Goncalves et al., 2015; Poggio et al., 1988; Preston et al., 2008; Tsao et al., 2003). For example, Backus et al. (2001) found that V3A is sensitive to 3D object structure and Preston et al. (2008) provided evidence that V3B contains highly diagnostic information about disparity-defined depth. The cortical proximity of these dorsal "depth areas" to scene area OPA is worth noting. It is also possible that by sheer virtue of being in the dorsal "where" stream (Ungerleider, 1982), OPA may be more sensitive to and exhibit stronger preferences for location information, including the more nuanced position-in-depth information in the mixed condition.

4.3. Open remarks

These findings raise some additional questions regarding depth preferences in scene and other category-selective areas. For example, the depth planes stimulated in the current experiments (front, middle, back, and mixed) were always relative to a stable fixation plane. Thus, we cannot differentiate whether the depth preferences observed here reflected absolute position-in-depth or were purely in relation to the central (i.e., middle) depth plane—the point of vergence and accommodation. Though, arguably both absolute and relative depth information are important for object localization and navigating around objects we encounter. Additionally, we only stimulated one depth plane in front of and one depth plane behind fixation (±12 arcmin). It is possible that the ROIs would have demonstrated stronger sensitivities to depth information had we presented stimuli farther back or farther front and/or manipulated the plane of fixation.

Additionally, one consistent finding across most of the category-selective regions we localized was a general bias for preferring front depths (at least over the middle depth). This overall asymmetric preference for front raises the question of whether there may have been attentional and/or perceptual differences between the front and back stimuli. For example, while the stimuli were carefully controlled such that the stimulus size and distance from the fixation plane were equal for stimuli presented at +12 arcmin and stimuli presented at −12 arcmin, some behavioral studies have reported faster response times to stimuli presented at near compared to far depths (Finlayson and Grove, 2015; O'Toole and Walker, 1997; Reis et al., 2011). Moreover, it is possible the *perceived* distance between the front and back planes from fixation may have been unequal, such that the stimuli presented behind fixation were not perceived to be as far back as the stimuli presented in front of fixation were perceived to be front. As part of our prescreening, we ran a psychophysics experiment on all subjects in Experiment 1 to test this question (see supplemental analysis Section I). Based on our data collected outside the scanner, we did not find evidence that the "front-ness" of front stimuli was perceptually greater than the "back-ness" of back stimuli (Fig. S1A). However, on a subset of subjects who also completed the perceptual judgments inside the scanner, there may have been a slight asymmetry, though it is a bit difficult to interpret (Fig. S1B). Similarly, an analysis of early visual cortex (EVC) revealed a slight preference for front versus back, but this effect was not significant even when combining across both experiments (supplement Section IV; Table S2). In the future, a more robust test of depth preferences in the category-selective ROIs may be able to take this into account and perceptually match the amount of depth in front and back stimuli on a per subject basis. Regardless, if any perceptual asymmetry did exist in our data, it likely to bias all regions equally, and thus the difference in depth preferences across the different regions is unlikely to be accounted for in this fashion.

Another possible explanation for an overall front bias (i.e., bigger response to front) across all of our regions could be that objects closer to an observer are perceived as moving faster than objects that are farther away (Howard, 2012). Although the stimuli were moving at the same real-world velocity (0.17°/sec) in all depth conditions, it is possible that the motion was *perceived* as faster in the front depth, which in turn made the front stimuli more salient and produced a larger fMRI response.[2] This might be particularly true in area MT+ because of its selectivity for moving stimuli, and could account for the strong linear pattern (front, middle, then back) in this region. A related account takes into consideration the retinal size of the stimuli. While all stimuli were matched for physical size, the retinal size of near stimuli appear to be larger than that of far stimuli (Ittelson, 1951); thus the perceived size may have also made the front stimuli more salient and therefore attended to more than back stimuli. A number of studies have shown that the frontal eye field (FEF) and intraparietal sulcus (IPS) are principally involved in visual attention (Corbetta et al., 1998; Corbetta and Shulman, 2002). Since FEF and IPS were outside the range of our slice coverage, further research is needed to investigate whether the depth preferences (specifically the front bias) found here are related to attentional effects. It is possible that the front preference we find in most of the ROIs may be confounded by some of these factors; but the back preference in scene regions cannot be accounted for by these factors. Thus, much of our discussion focused on what may be the strongest contribution of these findings: the implications the depth preferences have for the scene-selective regions and scene perception.

5. Conclusion

We sought to broadly survey the existence of depth preferences in category-selective visual areas in the visual hierarchy. The current data support the existence of depth information in addition to the well-known category information in these areas. Our findings establish that category-selective regions along the visual hierarchy are sensitive to position-in-depth, such that face (OFA), object (LOC), and motion (MT+) areas prefer stimuli presented at near depth planes while scene areas (PPA and OPA) prefer stimuli presented at both near and far depth planes. These depth preferences are akin to many contemporary reports that have shown preferences for 2D spatial location in these category-selective regions, lending further support to existing literature that suggests “what” and “where” information can coexist in object-selective cortex.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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[2] Note, however, that *retinal* speed was also the same in all depth conditions (given that depth/distance was artificially manipulated via disparity on a computer monitor). Thus, an alternative interpretation of motion parallax based on retinal speed predicts the opposite pattern: objects at far depths inferred to be actually moving faster in the real-world.

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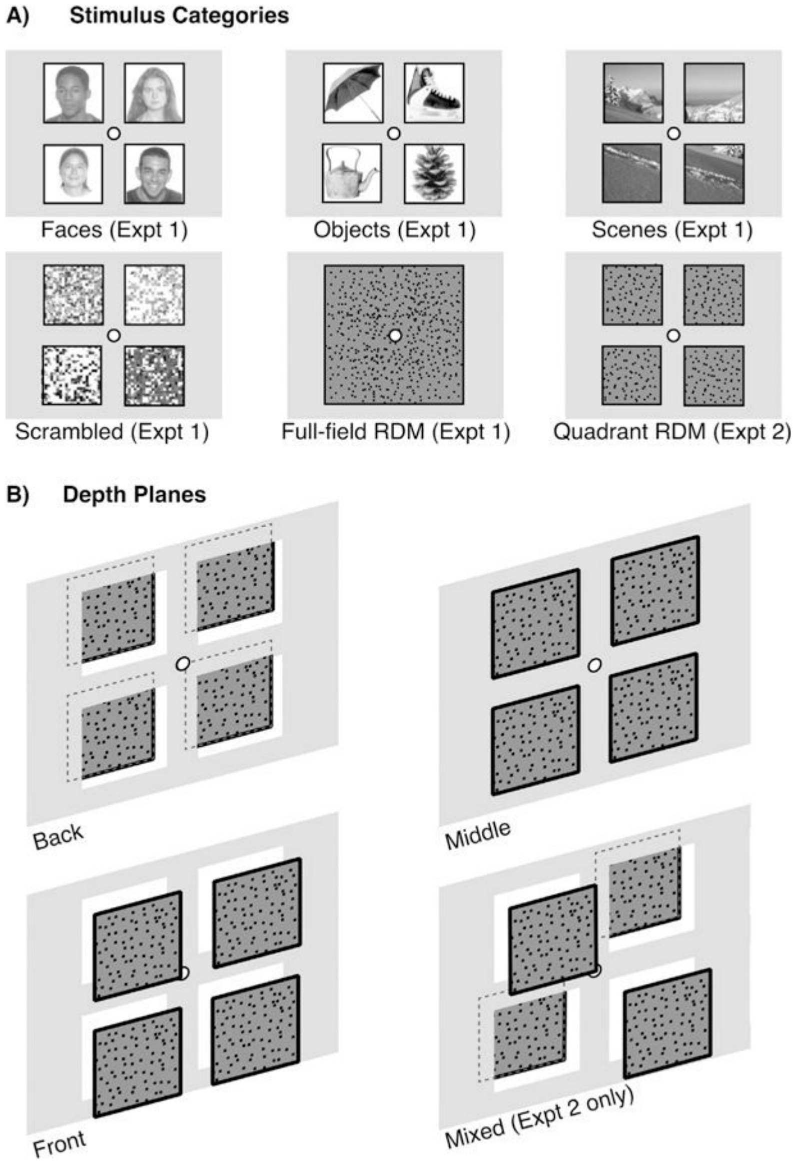

Fig. 1.

(A) Example stimuli. In Experiment 1, stimuli consisted of an array of four unique faces, objects, or grid-scrambled objects, or an image of a single scene split into four quadrants (category runs), or a full visual field random-dot motion stimulus (RDM runs). In Experiment 2, stimuli were RDM presented in the four quadrants. (B) Schematic of the depth plane conditions. Light grey background represents the projection screen and plane of fixation. Experiments 1 and 2 included back, front, and middle depths (where the entire 4-quadrant stimulus array was presented −12 arcmin from fixation, +12 arcmin from fixation, or flush with fixation, respectively). Experiment 2 also included the mixed depth condition (2 quadrants front and 2 quadrants back). The dashed grey lines represent the outline of the "back" RDM patches that are occluded in this 2D depiction but were fully visible to subjects viewing the 3D stimuli.

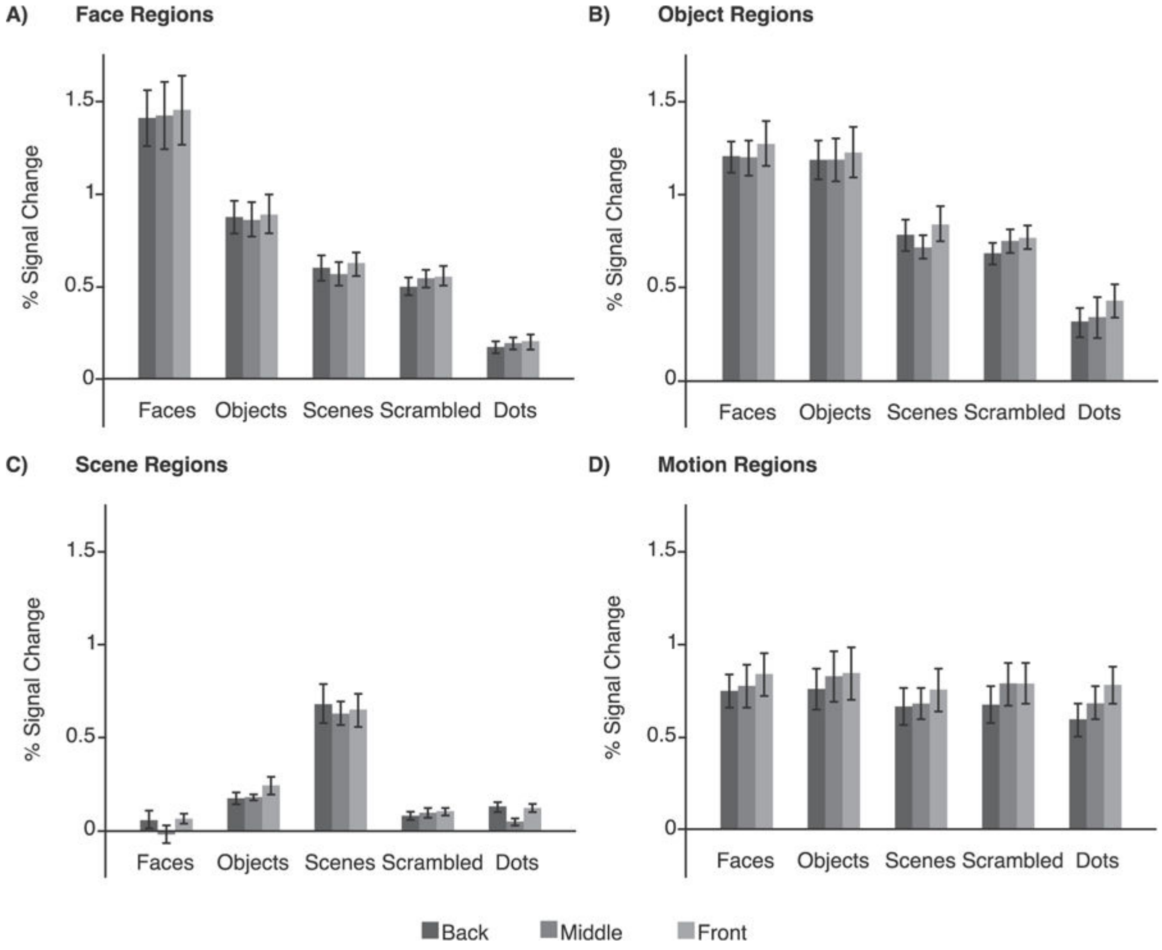

Fig. 2.

Mean response magnitudes of (A) Face Regions, (B) Object Regions, (C) Scene Regions, and (D) Motion Regions to stimuli of faces, objects, scenes, scrambled objects, and random moving dots at front (+12 arcmin), middle (0 arcmin), and back (−12 arcmin) depth planes in Experiment 1. For illustration purposes, ROIs are grouped according to their preferred stimulus type and beta weights are averaged; data for individual ROIs can be found in Table 1. “Face Regions” encompass FFA and OFA; “Object Regions” is LOC; “Scene Regions” encompass PPA, OPA, and RSC; “Motion Regions” is MT+. N = 16, error bars denote standard error.

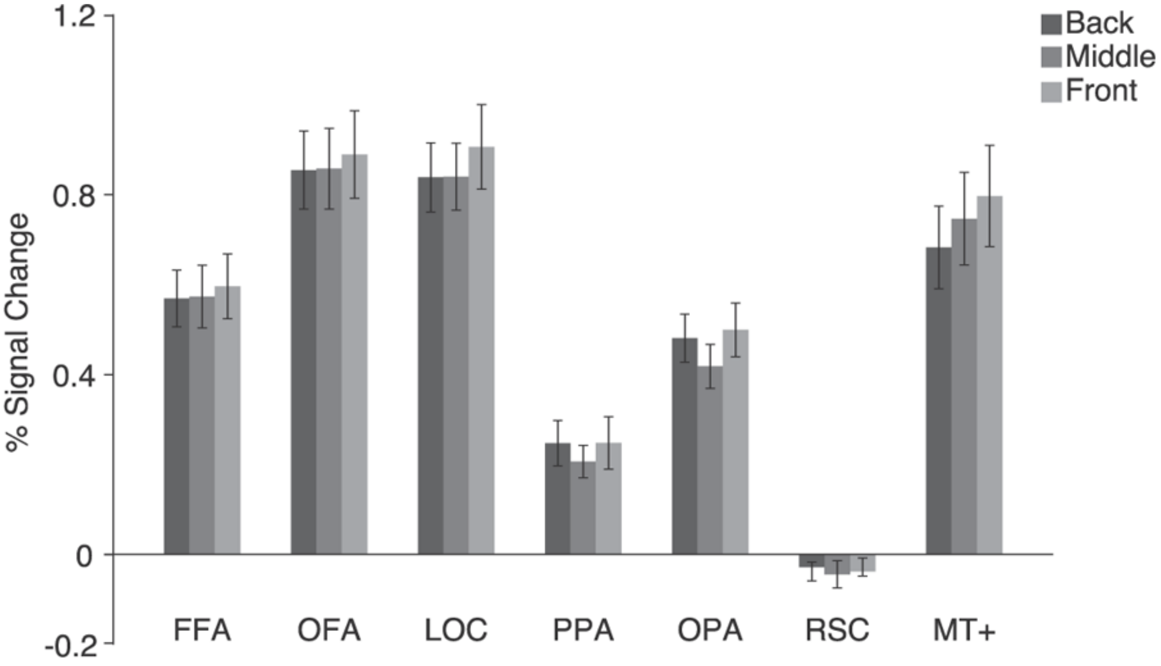

Fig. 3.

Mean response magnitudes of each ROI to front (+12 arcmin), middle (0 arcmin), and back (−12 arcmin) depth planes (collapsed across all stimulus categories) in Experiment 1. N = 16, error bars denote standard error.

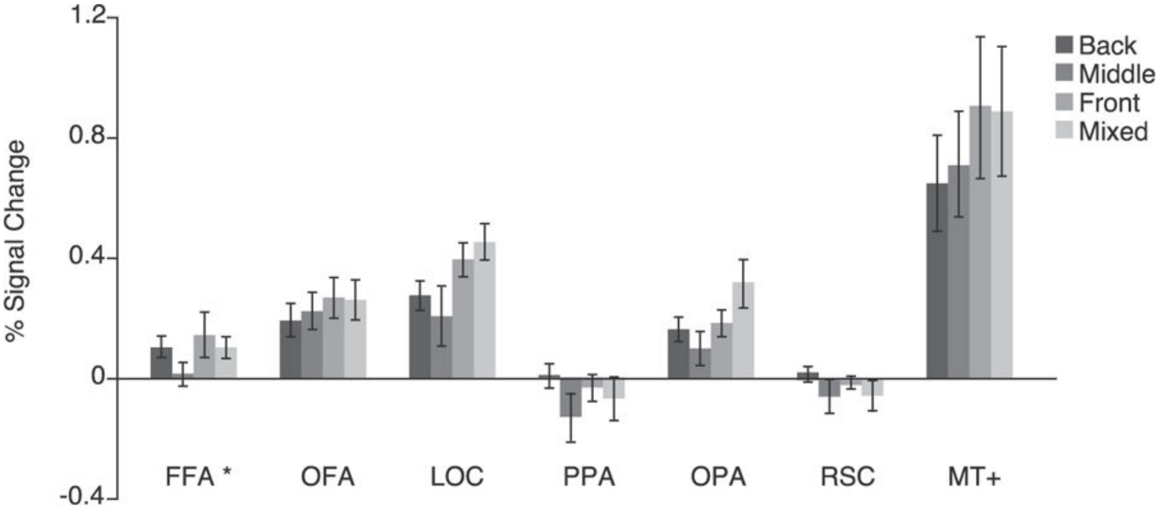

Fig. 4.

Mean response magnitudes of all ROIs to front (+12 arcmin), middle (0 arcmin), back (−12 arcmin), and mixed (±12 arcmin) depth planes in Experiment 2. *N = 15 for FFA, N = 16 for all other ROIs. Error bars denote standard error.

Table 1

Mean and standard deviation of signal change (%) as a function of depth plane and stimulus category in all ROIs for Experiment 1. N = 16.

ROI	Depth Plane	Faces	Objects	Scenes	Scrambled	Dots
FFA	Back	1.21 (0.54)	0.66 (0.32)	0.51 (0.29)	0.36 (0.22)	0.12 (0.11)
	Middle	1.23 (0.70)	0.64 (0.31)	0.47 (0.27)	0.41 (0.22)	0.13 (0.12)
	Front	1.25 (0.63)	0.69 (0.37)	0.51 (0.28)	0.41 (0.24)	0.12 (0.14)
OFA	Back	1.60 (0.71)	1.09 (0.49)	0.69 (0.32)	0.64 (0.22)	0.25 (0.19)
	Middle	1.61 (0.78)	1.07 (0.51)	0.66 (0.29)	0.68 (0.24)	0.27 (0.18)
	Front	1.65 (0.90)	1.08 (0.52)	0.74 (0.31)	0.69 (0.26)	0.29 (0.20)
LOC	Back	1.21 (0.33)	1.19 (0.43)	0.79 (0.34)	0.69 (0.24)	0.31 (0.27)
	Middle	1.21 (0.38)	1.19 (0.46)	0.72 (0.26)	0.75 (0.26)	0.33 (0.24)
	Front	1.28 (0.49)	1.23 (0.55)	0.84 (0.37)	0.77 (0.24)	0.41 (0.28)
PPA	Back	0.03 (0.14)	0.21 (0.17)	0.81 (0.62)	0.05 (0.14)	0.14 (0.22)
	Middle	−0.06 (0.13)	0.22 (0.14)	0.74 (0.44)	0.07 (0.17)	0.06 (0.12)
	Front	0.02 (0.12)	0.28 (0.29)	0.78 (0.56)	0.08 (0.14)	0.09 (0.18)
OPA	Back	0.35 (0.27)	0.49 (0.24)	0.92 (0.44)	0.43 (0.25)	0.22 (0.19)
	Middle	0.25 (0.27)	0.47 (0.24)	0.86 (0.33)	0.42 (0.26)	0.10 (0.20)
	Front	0.37 (0.19)	0.54 (0.30)	0.91 (0.43)	0.45 (0.26)	0.24 (0.22)
RSC	Back	−0.19 (0.27)	−0.16 (0.21)	0.34 (0.28)	−0.22 (0.22)	0.03 (0.22)
	Middle	−0.23 (0.24)	−0.13 (0.17)	0.31 (0.16)	−0.18 (0.18)	0.01 (0.16)
	Front	−0.17 (0.13)	−0.07 (0.13)	0.29 (0.18)	−0.19 (0.28)	0.00 (0.20)
MT+	Back	0.74 (0.37)	0.76 (0.43)	0.66 (0.38)	0.67 (0.39)	0.58 (0.36)
	Middle	0.77 (0.45)	0.82 (0.55)	0.68 (0.34)	0.78 (0.46)	0.67 (0.36)
	Front	0.84 (0.47)	0.84 (0.57)	0.75 (0.45)	0.78 (0.43)	0.77 (0.42)

Table 2

Mean, standard deviation, and statistical tests indicating depth sensitivity and preferences in all ROIs for Experiment 1, collapsed across stimulus category. N = 16. Bold text on the planned pairwise comparisons reflects the depth condition with significantly greater activation.

ROI	Back	Middle	Front	Statistical Tests
FFA	0.57 (0.25)	0.57 (0.28)	0.60 (0.29)	Depth: $F(2, 30) = 2.085$, $p = 0.142$, $\eta^2 = 0.122$
				Stimulus: $F(4, 60) = 41.902$, $p < 0.001$, $\eta^2 = 0.736$ *
				Interaction: $F(8, 120) = 0.994$, $p = 0.444$, $\eta^2 = 0.062$
				Planned Pairwise Depth Comparisons
				Back-Middle: $t(15) = 0.240$, $p = 0.814$, $d = 0.060$
				Back-Front: $t(15) = 1.739$, $p = 0.102$, $d = 0.435$
				Middle-**Front:** $t(15) = 2.338$, $p = 0.034$, $d = 0.585$ *
OFA	0.85 (0.35)	0.86 (0.36)	0.89 (0.39)	Depth: $F(2, 30) = 3.547$, $p = 0.041$, $\eta^2 = 0.191$ *
				Stimulus: $F(4, 60) = 41.464$, $p < 0.001$, $\eta^2 = 0.734$ *
				Interaction: $F(8, 120) = 0.920$, $p = 0.503$, $\eta^2 = 0.058$
				Planned Pairwise Depth Comparisons
				Back-Middle: $t(15) = 0.258$, $p = 0.800$, $d = 0.064$
				Back-Front: $t(15) = 2.119$, $p = 0.051$, $d = 0.530$
				Middle-**Front:** $t(15) = 2.352$, $p = 0.033$, $d = 0.588$ *
LOC	0.84 (0.31)	0.84 (0.30)	0.91 (0.38)	Depth: $F(2, 30) = 5.820$, $p = 0.007$, $\eta^2 = 0.280$ *
				Stimulus: $F(4, 60) = 110.789$, $p < 0.001$, $\eta^2 = 0.88$ *
				Interaction: $F(8, 120) = 1.501$, $p = 0.164$, $\eta^2 = 0.091$
				Planned Pairwise Depth Comparisons
				Back-Middle: $t(15) = 0.121$, $p = 0.905$, $d = 0.030$
				Back-**Front:** $t(15) = 2.923$, $p = 0.011$, $d = 0.731$ **
				Middle-**Front:** $t(15) = 2.328$, $p = 0.034$, $d = 0.582$ *
PPA	0.25 (0.20)	0.21 (0.14)	0.25 (0.23)	Depth: $F(2, 30) = 2.893$, $p = 0.071$, $\eta^2 = 0.162$
				Stimulus: $F(4, 60) = 31.442$, $p < 0.001$, $\eta^2 = 0.677$ *
				Interaction: $F(8, 120) = 2.337$, $p = 0.023$, $\eta^2 = 0.135$ *
				Planned Pairwise Depth Comparisons

ROI	Back	Middle	Front	Statistical Tests
				Back-Middle: $t(15) = 2.490$, $p = 0.025$, $d = 0.623$ *
				Back-Front: $t(15) = 0.028$, $p = 0.978$, $d = 0.007$
				Middle-Front: $t(15) = 1.589$, $p = 0.133$, $d = 0.397$
OPA	0.48 (0.21)	0.42 (0.20)	0.50 (0.24)	Depth: $F(2, 30) = 6.586$, $p = 0.004$, $\eta^2 = 0.305$ *
				Stimulus: $F(4, 60) = 30.789$, $p < 0.001$, $\eta^2 = 0.672$ *
				Interaction: $F(8, 120) = 1.702$, $p = 0.105$, $\eta^2 = 0.102$
				Planned Pairwise Depth Comparisons
				Back-Middle: $t(15) = 3.415$, $p = 0.004$, $d = 0.854$ **
				Back-Front: $t(15) = 0.965$, $p = 0.350$, $d = 0.241$
				Middle-**Front:** $t(15) = 2.642$, $p = 0.018$, $d = 0.661$ *
RSC	−0.04 (0.08)	−0.04 (0.12)	−0.03 (0.08)	Depth: $F(2, 30) = 0.661$, $p = 0.523$, $\eta^2 = 0.042$
				Stimulus: $F(4, 60) = 21.355$, $p < 0.001$, $\eta^2 = 0.587$ *
				Interaction: $F(8, 120) = 1.446$, $p = 0.184$, $\eta^2 = 0.088$
				Planned Pairwise Depth Comparisons
				Back-Middle: $t(15) = 0.460$, $p = 0.652$, $d = 0.115$
				Back-Front: $t(15) = 0.947$, $p = 0.358$, $d = 0.237$
				Middle-Front: $t(15) = 0.924$, $p = 0.370$, $d = 0.231$
MT+	0.68 (0.37)	0.75 (0.41)	0.80 (0.45)	Depth: $F(2, 30) = 18.530$, $p < 0.001$, $\eta^2 = 0.553$ *
				Stimulus: $F(4, 60) = 2.083$, $p = 0.094$, $\eta^2 = 0.122$
				Interaction: $F(8, 120) = 2.726$, $p = 0.009$, $\eta^2 = 0.154$ *
				Planned Pairwise Depth Comparisons
				Back-Middle: $t(15) = 4.025$, $p = 0.001$, $d = 1.006$ **
				Back-**Front:** $t(15) = 4.621$, $p < 0.001$, $d = 1.155$ **
				Middle-**Front:** $t(15) = 3.579$, $p = 0.003$, $d = 0.895$ **

[*] denotes statistical significance at $p < 0.05$.

[**] denotes statistical significance at $p < 0.05$ (Bonferroni-corrected for multiple post-hoc comparisons).

Table 3

Mean, standard deviation, and statistical tests indicating depth sensitivity and preferences in all ROIs for Experiment 2. N = 16, except for FFA (N = 15). Bold text on the planned pairwise comparisons reflects the depth condition with significantly greater activation. “Pref” denotes preferred depth plane, “(F)” denotes front, “(B)” denotes back, and “Avg(B + F)” denotes the average of back and front. Since none of the pairwise comparisons reached significance in FFA, the preferred depth for the mixed comparison was determined by the greatest numeric activation. Since the scene regions generally demonstrated a bimodal depth preference, we compare the mixed depth activation to both back and front in PPA, OPA, and RSC.

ROI	Back	Middle	Front	Mixed	Statistical Tests
FFA	0.07 (0.14)	0.01 (0.16)	0.12 (0.21)	0.07 (0.10)	$F(2, 28) = 1.669$, $p = 0.207$, $\eta^2 = 0.107$
					Planned Pairwise Depth Comparisons (same as Expt 1)
					Back-Middle: $t(14) = 1.020$, $p = 0.325$, $d = 0.263$
					Back-Front: $t(14) = 1.925$, $p = 0.075$, $d = 0.497$
					Middle-Front: $t(14) = 1.344$, $p = 0.200$, $d = 0.347$
					Planned Pairwise Comparisons for Mixed-depth
					Mixed-Pref(F): $t(14) = 1.124$, $p = 0.280$, $d = 0.290$
					Mixed-Middle: $t(14) = 1.501$, $p = 0.156$, $d = 0.387$
					Mixed-Avg(B + F): $t(14) = 0.792$, $p = 0.442$, $d = 0.204$
OFA	0.17 (0.21)	0.20 (0.23)	0.24 (0.25)	0.24 (0.24)	$F(2, 30) = 8.444$, $p = 0.001$, $\eta^2 = 0.360^{*}$
					Planned Pairwise Depth Comparisons (same as Expt 1)
					Back-Middle: $t(15) = 1.776$, $p = 0.096$, $d = 0.444$
					Back-**Front:** $t(15) = 3.755$, $p = 0.002$, $d = 0.939^{**}$
					Middle-**Front:** $t(15) = 2.519$, $p = 0.024$, $d = 0.630^{*}$
					Planned Pairwise Comparisons for Mixed-depth
					Mixed-Pref(F): $t(15) = 0.296$, $p = 0.771$, $d = 0.074$
					Mixed-Middle: $t(15) = 1.788$, $p = 0.094$, $d = 0.447$
					Mixed-Avg(B + F): $t(15) = 1.205$, $p = 0.247$, $d = 0.301$
LOC	0.28 (0.18)	0.21 (0.35)	0.40 (0.20)	0.45 (0.20)	$F(2, 30) = 9.424$, $p < 0.001$, $\eta^2 = 0.386^{*}$
					Planned Pairwise Depth Comparisons (same as Expt 1)
					Back-Middle: $t(15) = 1.353$, $p = 0.196$, $d = 0.338$
					Back-**Front:** $t(15) = 5.651$, $p < 0.001$, $d = 1.413^{**}$
					Middle-**Front:** $t(15) = 3.615$, $p = 0.003$, $d = 0.904^{**}$

ROI	Back	Middle	Front	Mixed	Statistical Tests
					Planned Pairwise Comparisons for Mixed-depth
					Mixed-Pref(F): $t(15) = 2.764$, $p = 0.014$, $d = 0.691$ **
					Mixed-Middle: $t(15) = 4.060$, $p = 0.001$, $d = 1.015$ **
					Mixed-Avg(B + F): $t(15) = 5.442$, $p < 0.001$, $d = 1.360$ **
PPA	0.01 (0.14)	−0.13 (0.33)	−0.03 (0.16)	−0.07 (0.28)	$F(2, 30) = 4.762$, $p = 0.016$, $\eta^2 = 0.241$ *
					Planned Pairwise Depth Comparisons (same as Expt 1)
					Back-Middle: $t(15) = 2.346$, $p = 0.033$, $d = 0.586$ *
					Back-Front: $t(15) = 3.210$, $p = 0.\ 006$, $d = 0.803$ **
					Middle-Front: $t(15) = 1.863$, $p = 0.082$, $d = 0.466$
					Planned Pairwise Comparisons for Mixed-depth
					Mixed-Pref(B): $t(15) = 1.672$, $p = 0.115$, $d = 0.418$
					Mixed-Pref(F): $t(15) = 0.913$, $p = 0.376$, $d = 0.228$
					Mixed-Middle: $t(15) = 2.722$, $p = 0.016$, $d = 0.680$ **
					Mixed-Avg(B + F): $t(15) = 1.331$, $p = 0.203$, $d = 0.333$
OPA	0.16 (0.23)	0.10 (0.26)	0.19 (0.28)	0.32 (0.35)	$F(2, 30) = 3.199$ $p = 0.055$, $\eta^2 = 0.176$
					Planned Pairwise Depth Comparisons (same as Expt 1)
					Back-Middle: $t(15) = 2.087$, $p = 0.054$, $d = 0.854$
					Back-Front: $t(15) = 0.853$, $p = 0.407$, $d = 0.213$
					Middle-Front: $t(15) = 1.841$, $p = 0.085$, $d = 0.460$
					Planned Pairwise Comparisons for Mixed-depth
					Mixed-Pref(B): $t(15) = 2.647$, $p = 0.018$, $d = 0.662$ *
					Mixed-Pref(F): $t(15) = 1.910$, $p = 0.075$, $d = 0.477$
					Mixed-Middle: $t(15) = 5.830$, $p < 0.001$, $d = 1.458$ **
					Mixed-Avg(B + F): $t(15) = 2.277$, $p = 0.038$, $d = 0.569$ *
RSC	0.01 (0.10)	−0.06 (0.21)	−0.01 (0.09)	−0.05 (0.21)	$F(2, 30) = 1.531$, $p = 0.233$, $\eta^2 = 0.093$
					Planned Pairwise Depth Comparisons (same as Expt 1)
					Back-Middle: $t(15) = 1.368$, $p = 0.191$, $d = 0.342$
					Back-Front: $t(15) = 2.146$, $p = 0.049$, $d = 0.536$ *
					Middle-Front: $t(15) = 0.921$, $p = 0.372$, $d = 0.230$

ROI	**Back**	**Middle**	**Front**	**Mixed**	**Statistical Tests**
MT+	0.65 (0.42)	0.71 (0.44)	0.91 (0.71)	0.89 (0.58)	*Planned Pairwise Comparisons for Mixed-depth*
					Mixed-Pref(B): $t(15) = 1.391$, $p = 0.185$, $d = 0.348$
					Mixed-Pref(F): $t(15) = 0.917$, $p = 0.374$, $d = 0.229$
					Mixed-Middle: $t(15) = 0.174$, $p = 0.864$, $d = 0.044$
					Mixed-Avg(B + F): $t(15) = 1.178$, $p = 0.257$, $d = 0.295$
					$F(2, 30) = 8.587$, $p = 0.001$, $\eta^2 = 0.364$ *
					Planned Pairwise Depth Comparisons (same as Expt 1)
					Back-**Middle:** $t(15) = 3.085$, $p = 0.008$, $d = 1.771$ **
					Back-**Front:** $t(15) = 3.360462$ $p = 0.004$, $d = 0.840$ **
					Middle-**Front:** $t(15) = 2.579$, $p = 0.021$, $d = 0.615$ *
					Planned Pairwise Comparisons for Mixed-depth
					Mixed-Pref(F): $t(15) = 0.507$, $p = 0.619$, $d = 0.127$
					Mixed-Middle: $t(15) = 3.642$, $p = 0.002$, $d = 0.910$ **
					Mixed-Avg(B + F): $t(15) = 5.623$, $p < 0.001$, $d = 1.406$ **

[*] denotes statistical significance at $p < 0.05$.

[**] denotes statistical significance at p < 0.05 (Bonferroni-corrected for multiple post-hoc comparisons).