Large-scale dissociations between views of objects, scenes, and reachable-scale environments in visual cortex

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Space-related processing recruits a network of brain regions separate from those recruited in object-related processing. This dissociation has largely been explored by contrasting views of navigable-scale spaces compared to close-up views of isolated objects. However, in naturalistic visual experience, we encounter spaces intermediate to these extremes, like the tops of desks and kitchen counters, which are not navigable but typically contain multiple objects. How are such reachable-scale views represented in the brain? In two functional neuroimaging experiments with human observers, we find evidence for a large-scale dissociation of reachable-scale views from both navigable scene views and close-up object views. Three brain regions were identified which showed a systematic response preference to reachable views, located in the posterior collateral sulcus, the inferior parietal sulcus, and superior parietal lobule. Subsequent analyses suggest that these three regions may be especially sensitive to the presence of multiple objects. Further, in all classic scene and object regions, reachable-scale views dissociated from both objects and scenes with an intermediate response magnitude. Taken together, these results establish that reachable-scale environments have a distinct representational signature from both scene and object views.

Scene-based and object-based representations form a major joint in the organization of the visual system. Scene-selective brain regions are broadly concerned with performing global perceptual analysis of a space (Epstein & Kanwisher, 1998; Kravitz, Peng & Baker, 2011; Lescroart & Gallant, 2019; Park, Brady, Greene, & Oliva, 2011), computing its navigational affordances (Bonner & Epstein, 2017; Kamps, Julian, Kubilius, Kanwisher & Dilks, 2016), and linking the present view to stored memory about the overall location (Vass & Epstein, 2017; Marchette, Vass, Ryan, & Epstein, 2015). In contrast, object-selective regions are engaged in representing bounded entities, and do so in a manner that is robust to confounding low-level contours, minor changes in size or position, or the specific visual cues that delineate the objects (Grill-Spector, Kourtzi, & Kanwisher, 2001; Grill-Spector, Kushnir, Edelman, Itzchak & Malach, 1998). Are these two systems, one for processing spatial-layout and another for bounded-objects, together sufficient to represent any view that our visual system regularly encounters?

Consider views of reachable-scale environments - the countertops where we combine ingredients for a cake, or the worktables where we assemble the components of a circuit board. These views are intermediate in scale to scenes and objects, typically consisting of an extended surface supporting collections of related manipulable objects, and are the locus of many everyday actions (Figure 1a). How are such intermediate-scale views represented in the visual system?

One possibility is that reachable-scale environments are represented similarly to navigable-scale scenes, driving similar activations across the ventral and dorsal streams, with little detectable difference at the resolution of functional magnetic resonance imaging. This outcome might be expected given that views of reachable environments are spatially extended, have 3D layout features, and need to be situated within larger environments, all of which are hypothesized functions of scene-selective regions. Indeed, this possibility is often assumed: in some cases, reachable views have been used interchangeably with scene views in both neuroimaging and behavioral studies on scene processing (e.g. Epstein, Graham & Downing, 2003; Võ & Wolfe, 2013). However, everyday views of reachable-scale environments also prominently

feature collections of multiple objects, and differ meaningfully from scenes by affording object-centered actions rather than navigation. Thus, a second possibility is that reachable-scale views will partially dissociate from full-scale scenes, driving object-preferring cortex in addition to scene-preferring regions.

A final, and not mutually-exclusive possibility, is that visual responses to reachable-scale environments might recruit distinct brain regions, separate from both object- and scene- preferring cortex. There are both action-related and perception-related arguments for this hypothesis. First, considering action-related processing, it is clear that near-scale spaces have different behavioral demands than far-scale spaces (Previc, 1998; Grüsser, 1983, Rizzolatti & Camarda, 1987). Indeed, there are well-known motor dissociations between reach-related fronto-parietal circuits versus navigation-related medial networks (di Pellegrino & Làdavas, 2015; Graziano & Gross, 1995; Maguire, 2001). Next, considering perceptual processing, the statistics of visual images also differ as a function of environment scale (Torralba & Oliva, 2002). We recently showed that the human perceptual system is sensitive to these differences: observers performing a visual search task were faster to find an image of a reachable environment among distractor scenes or objects, and vice versa (Josephs & Konkle, 2019). In fact, the perceptual search advantage found between reachable-scale images and scene images was nearly twice as strong as the perceptual search advantage found when spanning semantic categories (e.g. kitchens among dining room images). These visual search results show that the scale of the depicted environment is a major factor in perceptual similarity computations, even more so than semantic category information.

These prior studies suggest that reachable-scale views dissociate from singleton objects views and navigable-scale scene views in both their input-related image statistics and output-related action requirements. Importantly, such visual input and behavioral output pressures have been proposed to be jointly essential for the large-scale functional clustering observed in visual cortex for different kinds of visual domains (e.g. faces, scenes; c.f. Op de Beeck, et al., 2019; Mahon & Caramazza, 2011; Konkle & Oliva, 2012; Arcaro & Livinsgtone, 2017). Thus, it is possible that views of reachable environments are distinct enough in form and purpose so as to draw on distinct visual processing regions.

In the present work, we examined how views of reachable-scale environments are represented in the human brain using functional magnetic resonance imaging. To anticipate, we find clear evidence that reachspace brain representations dissociate from those of scenes and objects. Specifically, views of reachable environments elicited greater activity than both scenes and objects in regions of ventral and dorsal occipitoparietal cortex, in a manner that was robust to variations in low-level visual features (e.g. luminance and global spatial frequency), and to variations in the semantic category depicted (e.g. kitchen reachspaces vs office reachspaces). Reachable-scale environments also elicited differential responses in classic object- and scene-preferring regions, generally leading to intermediate levels of activation distinct from both full-scale scenes and close-up object views. Regions preferring reachable-scale environments showed a peripheral eccentricity bias but also responded particularly strongly to images of multiple objects, a functional signature that is distinct from both scene and object regions. Taken together, these results strongly suggest that the visual processing of near-scale environments is functionally dissociable from that of objects and scenes.

Results

Preferential responses to reachable-scale spaces in visual cortex

To examine the neural representation of reachable-scale environments compared to navigable-scale scenes and singleton objects, we created a stimulus set with images from each of the three environment scales (see Figure 1a; Supplementary Figure 1). Object images depicted close-scale views of single objects (within 8-12 inches from the object) on their natural background. Reachable-scale images, which we will refer to with the term "reachspaces", depicted near-scale environments that were approximately as deep as

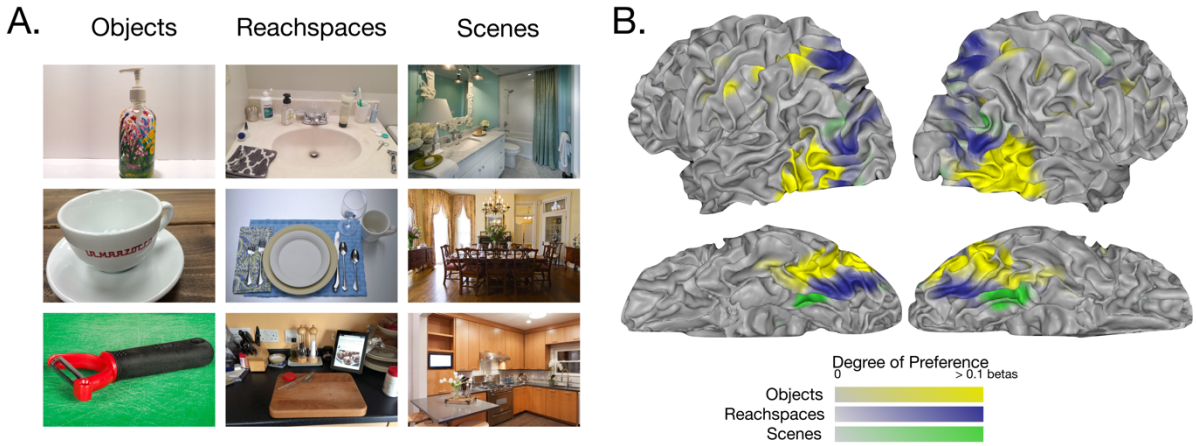

Figure 1. Experiment 1 stimuli and results. A) Examples of object, reachspace and scene views. B) Preference mapping results. Colored regions have preference for either objects (yellow), reachspaces (blue) and scenes (green). Color saturation indicates the magnitude of the preference relative to the next most preferred category, operationalized as the difference between betas for that voxel.

arm's reach (3-4ft), and consisted of multiple small objects arrayed on a horizontal surface. Scene images depicted views of the interior of rooms. Images were drawn from 6 different semantic categories (bar, bathroom, dining room, kitchen, office, art studio). Note that we use the term "environment scale" to refer to the distinction between the object, reachspace, and scene conditions, but caution the reader against interpreting our results in terms of subjective distance only. Rather, differences observed here likely reflect differences across a constellation of dimensions that co-occur with scale (e.g. number of objects, number of surfaces, action affordances, and perceived reachability). Two stimulus sets were collected, with 90 images each (ImageSetA, ImageSetB; 30 images per environmental scale per set; see In-text Methods).

In Experiment 1, twelve participants viewed images of objects, reachspaces, and scenes, in a standard blocked fMRI design. We first visualized the spatial distribution of object, reachspace and scene preferences within visually-responsive cortex. We excluded early visual regions using a separate retinotopy localizer, to isolate occipitotemporal cortex (see Supplementary Methods). Voxels were colored according to the condition that most strongly activated them and were projected to the cortical surface. If reachable environments are processed like navigable ones, then voxels should not reliably differentiate between scenes and reachspaces in their univariate responses. Instead, we observed a clear organization by environment scale, with distinct zones of preference for each stimulus type, both at the group level (Figure 1b) and at the single-subject level (Supplementary Figure 2). Reachspace preferences (blue) were evident in three distinct zones: posterior ventral cortex, occipital cortex, and superior parietal cortex. These zones of preference lay adjacent to known object-preference zones (yellow), and scene-preference zones (green).

To estimate the magnitude of reachspace preferences, we defined reachspace-preferring regions of interest (ROIs) around the peaks in reachspace-preference appearing in anatomically consistent locations across subjects. Half of the data (activations from Image Set A) were submitted to a conjunction analysis to find voxels with a preference for reachspaces over both objects and scenes individually. This procedure yielded three reachspace-preferring ROIs: a ventral region (vROI), primarily located in the posterior collateral sulcus, an occipito-parietal region (opROI), variably located in the middle or superior occipital gyri, and a superior parietal region (spROI), in the anterior portion of the superior parietal lobe. Talairach (TAL) coordinates for these ROIs are given in Supplementary Table 1.

Next, we examined activation magnitude in the remaining half of the data (activations from Image Set B), and found that reachspace views elicited significantly higher activations than both scene and object

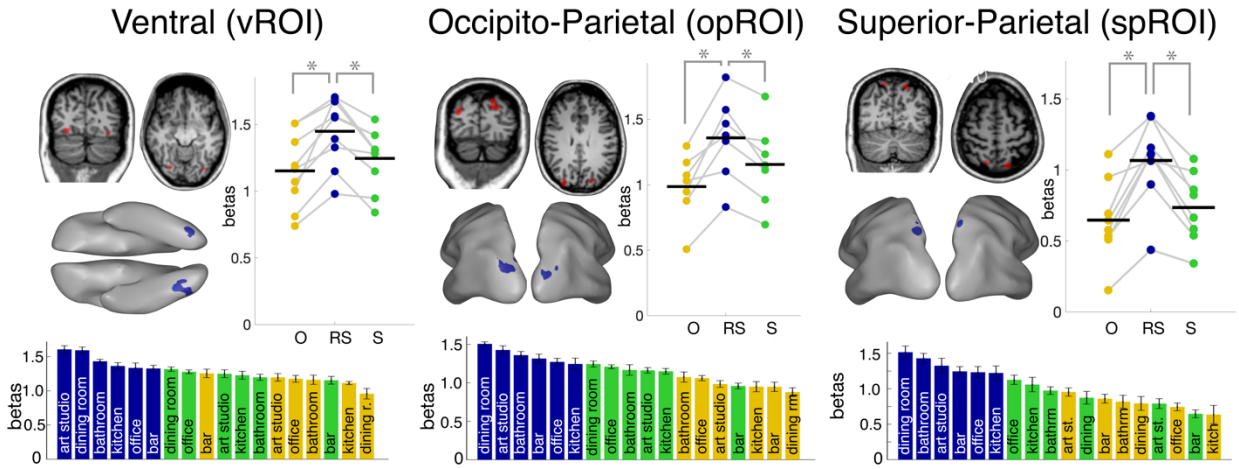

Figure 2: Locations and activations of reachspace-preferring ROIs. ROI locations are shown in the volume and on the inflated surface of an example participant. Top plots show each region's overall activation (y-axis) to images of objects (O), reachspaces (Rs), and scenes (S). Each dot is a participant. The group mean is indicated by the black horizontal bar. Statistical significance is indicated for paired 1-sided t-tests. Lower plots show each region's overall activation (y-axis) plotted for each scale-by- semantic category cross (18-bar plot). Error bars represent the within-subject standard error of the mean.

views in all three ROIs (Figure 2, vROI: RS>O: $t(8)=5.33$, $p<0.001$, RS>S: $t(8)=4.66$, $p=0.001$; opROI: RS>O: $t(6)=5.20$, $p=0.001$, RS>S: $t(6)=4.55$, $p=0.002$; spROI: RS>O: $t(7)=6.16$, $p<0.001$, RS>S: $t(7)=5.22$, $p=0.001$). These results were also obtained when swapping the image set used to define the ROIs and test for activation differences: reachspaces elicited significantly greater activity than objects and scenes in all three ROIs (see Supplementary Table 2 for all statistics). Finally, when the same data were broken out by semantic category, the reachspace categories elicited the highest overall responses (Figure 2).

Taken together, these analyses show that there are portions of cortex with systematically stronger responses to images of reachable-scale environments than to images of navigable-scale scenes and single objects. Peaks in the size of this preference occurred in consistent locations across subjects, allowing us to identify reachspace-preferring ROIs, which will provide targets for future study. Broadly, the existence of such regions suggests that the visual processing of reachable environments relies at least partly on cortical resources that lie outside the classic object- and scene-processing networks.

Low-level Control and Replication

In Experiment 2, we aimed to replicate the finding that reachspaces elicit greater activity than scenes and objects in some regions of cortex, and to test whether the response preferences for reachspaces are attributable to factors beyond very simple feature differences. Twelve participants (2 of whom had completed Experiment 1) viewed Image Set A ("original" images), and a version of Image Set B with low-level image feature controlled ("controlled" images, matched in mean luminance, contrast, and spatial frequency content; see Figure 3a and Supplementary Figure 3 for examples).

Preference maps elicited by original and controlled images had highly similar spatial organization (Figure 3b, see Supplementary Figure 4 for single-subject maps). A percent-match analysis on group-level maps showed that 69.9% of voxels had the same preference between image conditions (chance= 33.3% , see Supplementary Methods). We also computed this index at the single-subject level: the average percent match across individuals was 50.3% (SEM=1.5%; chance=33.3%). There were no consistent qualitative

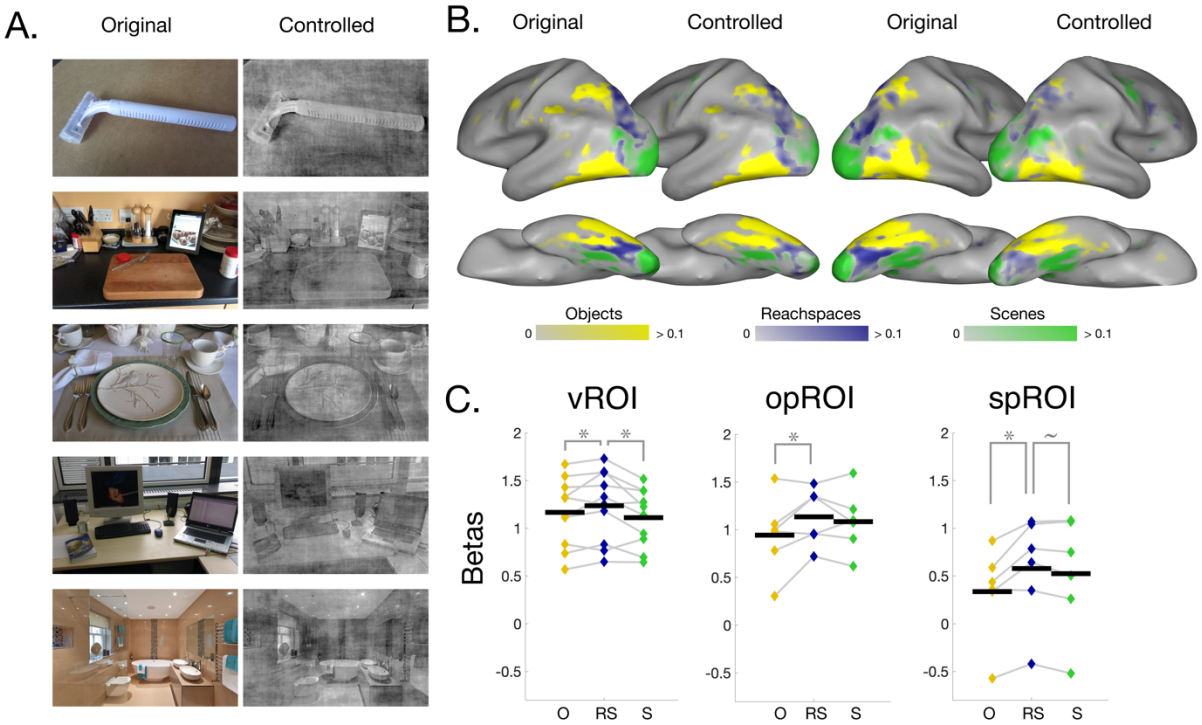

Figure 3: Stimuli and results for Experiment 2. A) Example images with original and controlled variants. B) Group-level preference mapping results, for both original and controlled image sets. Colored regions have preference for either objects (yellow), reachspaces (blue) and scenes (green). Color saturation indicates the magnitude of the preference relative to the next most preferred category, operationalized as the difference between betas for that voxel. C) Reachspace-preferring ROIs were defined in original images, and the overall activation in response to controlled images is shown on the y-axis. Single subject data are shown in dots, with the group average indicated with the thick horizontal black line. Stars indicate statistical significance.

differences in the location of preferences from original and controlled images across subjects. Thus, the reachspace-preference in these cortical regions, and their relative locations across the cortex, is not solely a product of overall differences in color, luminance, contrast or spatial frequency content.

The topography of responses in Experiment 2 also closely matched Experiment 1. The correspondence between E1 and E2 group-level maps for original images was high (67.4%, chance=33.3%), indicating that this topography generalizes to different samples of the population.

Additionally, the ROI results also replicated with controlled images. ROIs were defined in Experiment 2 subjects using original images (and a semi-automated procedure using anatomical location priors from Experiment 1, see In-Text Methods), and activations were extracted for controlled images (Figure 3c). Overall, controlled images elicited much weaker activity than original images. However, importantly, the preferential responses to reachspaces were generally maintained (vROI: RS>O: $t(9)=2.08$, $p=0.034$, RS>S: $t(9)=2.72$, $p=0.012$; opROI: RS>O: $t(5)=2.38$, $p=0.032$; spROI: RS>O: $t(5)=3.61$, $p=0.008$, RS>S: $t(5)=2.02$, $p=0.05$; RS>S in opROI was not significant: $t(5)=0.79$, $p=0.234$).

Taken together, Experiment 2 provides a replication and extension of Experiment 1. The large-scale distribution of preferences for reachable-scale views was reproducible across a new sample of subjects, and was still evident when differences in overall low-level image information was controlled.

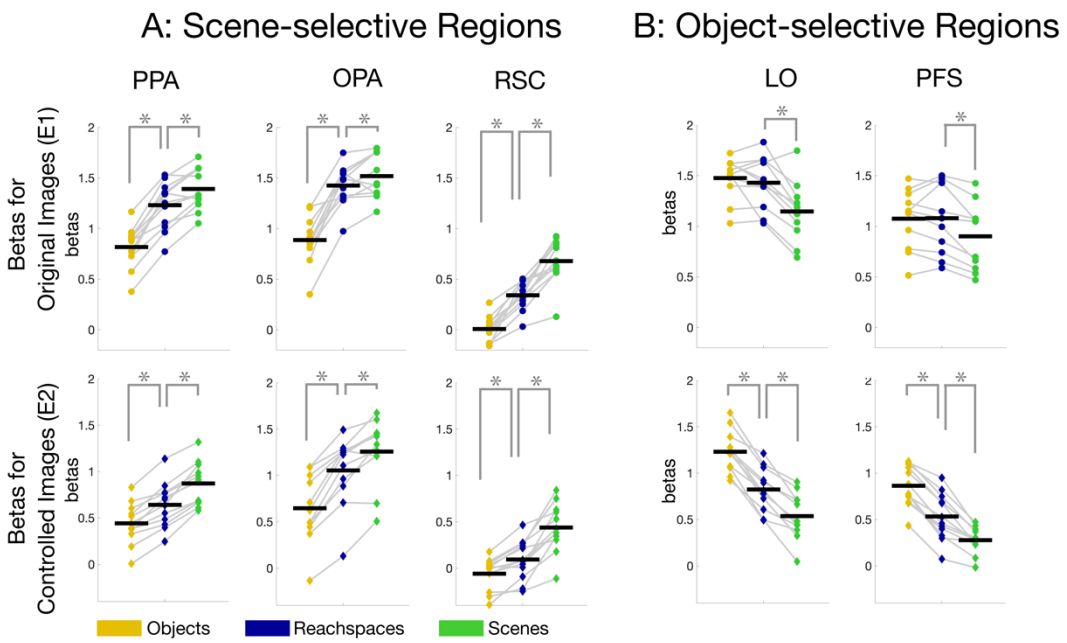

Figure 4: Result for classic category-selective ROIs. Univariate response to objects, scenes, and reachspaces in both scene-selective regions (A), and object-selective regions (B), for both original images (top row), and controlled images (bottom row). Connected dots reflect data from single participants. Group average values are indicated with the black horizontal bar. Stars indicate statistical significance in paired one-sided t-tests.

Responses to reachable-scale environments in scene- and object-preferring regions

We next evaluated reachspace-evoked activity in scene- and object-selective regions using data from both Experiment 1 (original images) and Experiment 2 (controlled images). All category-selective ROIs were defined using independent localizer runs (see Supplementary Methods).

In scene-preferring regions (parahippocampal place area, PPA; occipital place area, OPA; retrosplenial cortex, RSC), reachspaces elicited an intermediate level of activation for both original and controlled images (Figure 4a). That is, reachspace images evoked stronger activation than object images (original images: PPA: $t(11)=11.29$, $p<0.001$; OPA: $t(10)=9.16$, $p>0.001$, RSC: $t(11)=9.15$, $p=0.000$; controlled images: PPA: $t(11)=8.43$, $p<0.001$; OPA: $t(10)=9.32$, $p<0.001$; RSC: $t(11)=5.24$, $p<0.001$). Additionally, reachspace images evoked weaker activation than scene images, although this difference was marginal in OPA for original images (original image set: PPA: $t(11)=4.50$, $p<0.001$, OPA: $t(10)=1.63$, $p=0.067$; RSC: $t(11)=6.80$, $p<0.001$; controlled images: PPA: $t(11)=9.69$, $p<0.001$; OPA: $t(10)=4.25$, $p=0.001$, RSC: $t(11)=6.48$, $p<0.001$; see Supplementary Table 1 for results in original images where the ROI-defining and activation-extracting runs were swapped).

In object-preferring regions (lateral occipital, LO; and posterior fusiform sulcus, pFs), reachspaces also showed intermediate activation levels of activation in most of the comparisons (Figure 4b). Specifically, reachspace images elicited significantly more activity than scene images (original images: LO: $t(10)=5.55$, $p<0.001$; pFs: $t(10)=4.86$, $p<0.001$; controlled images: LO: $t(11)=8.10$, $p<0.001$; pFs: $t(11)=6.04$, $p<0.001$). Additionally, reachspace images elicited significantly weaker activation than objects for controlled images (LO: $t(11)=11.20$, $p<0.001$; pFs: $t(11)=12.19$, $p<0.001$), but showed a similar overall activation with object images in their original format (LO: $t(10)=0.86$, $p=0.204$; pFs: $t(10)=-0.12$, $p=0.547$)

These results generally point to a dissociation between objects and reachspaces in object-preferring regions as well.

Taken together, these analyses demonstrate that reachspaces elicit an intermediate degree of activity in both scene- and object-preferring ROIs. This provides complementary evidence that, in visual system responses, views of near-scale environments are dissociable from both single objects and full-scale scenes.

New territory vs. new subdivisions of scene-preferring regions

One question that arises from these data is whether the regions that exhibit reachspace-preferences reflect a subset of the voxels in scene- or object-selective regions, or whether they reflect regions of cortex not typically defined in standard object and scene localizers.

Given the position of the ventral ROI, it is possible that it overlaps a posterior subdivision of PPA (Bar & Aminoff , 2003; Baldassano et al., 2013). However, we found that neither anterior or posterior PPA showed a reachspace-preference, for either original or controlled images (original images: anterior PPA: RS>O: $t(11)=11.51$, $p<0.001$; S>RS: $t(11)=6.22$, $p<0.001$; posterior PPA: RS>O: $t(11)=9.71$, $p<0.001$; S>RS: $t(11)=2.49$, $p=0.015$; controlled images: anterior PPA: RS>O: $t(11)=6.48$, $p<0.001$; S>RS: $t(11)=10.15$, $p<0.001$; posterior PPA: RS>O: $t(11)=7.62$, $p<0.001$; S>RS: $t(1\ 1)=7.18$, $p<0.001$; see Supplemental Methods). Thus, the ventral reachspace-preferring ROI does not correspond to the known subdivision within PPA.

Additionally, ROIs with reachspace preference did not substantially overlap classic category-selective ROIs (see Supplementary Methods). For the ventral ROI, the percent voxels that overlapped with other ROIs was: 4.4% with PPA (±1.8% standard error of the mean), 4.6% with pFs (±2.1%), and 0.1% with FFA (±0.1%). For the occipital parietal ROI, the percent voxels overlapped was: 3.5% ± 2.3% with LO, 0.1% ± 0.06% with hand-selective regions, and 14.9% ± 3.9% with OPA. The superior parietal ROI had 0% overlap with all tested ROIs. The relationship among these ROIs is visualized for three individual participants in Figure 5, and for all participants in Supplementary Figure 5. Overall, reachspace-preferring ROIs largely occupy different regions of cortex than object-, scene-, face- or hand-selective cortex.

Functional signatures of reachspace-preferring cortex

Next, we examined how object-, scene-, and reachspace-preferring ROIs differ in their broader functional signatures. We first report opportunistic analyses from Experiment 1, which leverage stimulus conditions present in our localizer runs. Then, we report data from a new Experiment 3, with planned functional signature analyses.

In our first opportunistic analysis, we examined the responses of regions with object, reachspace, and scene preferences to the eccentricity conditions present in our retinotopy protocol in Experiment 1 (Figure 6a). Reachspace-preferring regions showed a peripheral bias, which was significant at a conservative post-hoc statistical level for the ventral and occipital reachspace regions, but not in the superior parietal region (Figure 6a; vROI: $t(8)=3.90$, $p=0.005$; opROI: $t(6)=4.82$, $p=0.003$; spROI: $t(7)=3.29$, $p=0.013$; two tailed post-hoc paired ttest with Bonferri-corrected alpha=0.006). Similarly,

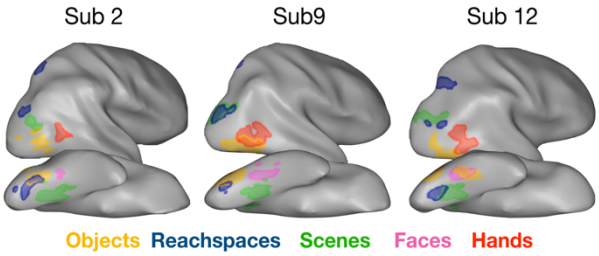

Figure 5: Depiction of the location of the ROIs with reachspace preferences, in relation to scene-, object-, and face-preferring ROIs, shown in the right hemispheres of three example subjects.

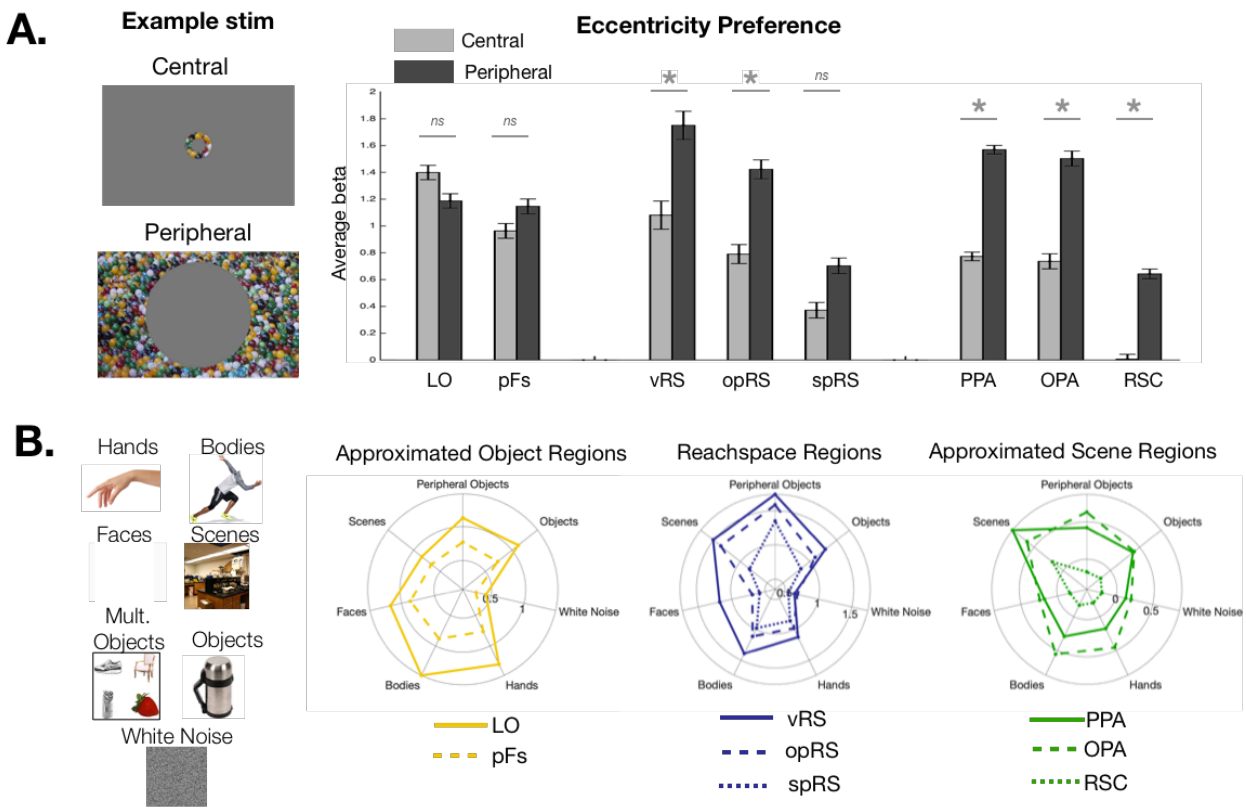

Figure 6: Broader response properties of reachspace regions, compared with scene and object regions. A) Stimuli and results for an analysis measuring the eccentricity bias of object, reachspace, and scene-preferring areas. Error bars show the within-subjects standard error of the mean, and stars indicate statistical significance. B) Stimuli and results for an analysis measuring the profile of responses across a range of categories for reachspaces regions, and regions corresponding to the anatomical locations of object- and scene-selective areas (see Methods). Negative values were thresholded to 0 for visibility. *Note that the example stimulus for "Faces" was removed in this version of the manuscript to comply with preprint standards.*

scene regions were strongly peripherally-biased (PPA: $t(11)=17.59$, $p<0.001$; OPA: $t(10)=9.27$, $p<0.001$; RSC: $t(11)=12.49$, $p<0.001$). In contrast, object regions showed mixed biases, which did not reach significance after Bonferroni correction (LO: foveal bias, $t(10)=2.68$, $p=0.023$; pFs: peripheral bias, $t(10)=2.26$, $p=0.047$). These results show that regions which responded preferentially to reachspaces, like scene-selective regions, are most sensitive to peripherally presented stimuli.

In our second opportunistic analysis, we investigated whether these ROIs differed in their response profile to a broad selection of categories present in our Experiment 1 localizer: faces, bodies, hands, objects, multiple objects, white noise, and scenes. Activations were extracted from reachspace-preferring ROIs. Since localizer runs were no longer available to define scene and object ROIs, they were approximated using a 9-mm radius sphere around the average TAL location for that ROI as determined from a meta-analysis (see Supplementary Methods). Activations for all regions are plotted as fingerprint profiles in Figure 6b.

In all three reachspace-preferring ROIs, images of multiple objects elicited the highest activation (significant in ventral and superior parietal ROIs: vROI: Multiple Objects>Scenes, $t(8)=3.49$, $p<0.01$; spROI: Multiple Objects>Bodies, $t(7)=5.54$, $p<0.01$; marginal in opROI: Multiple Objects>Scenes $t(6)=2.32$, $p=0.03$). In contrast, scene and object preferring ROIs showed different functional signatures. The approximated PPA and RSC regions preferred for scenes over all other conditions, including Multiple

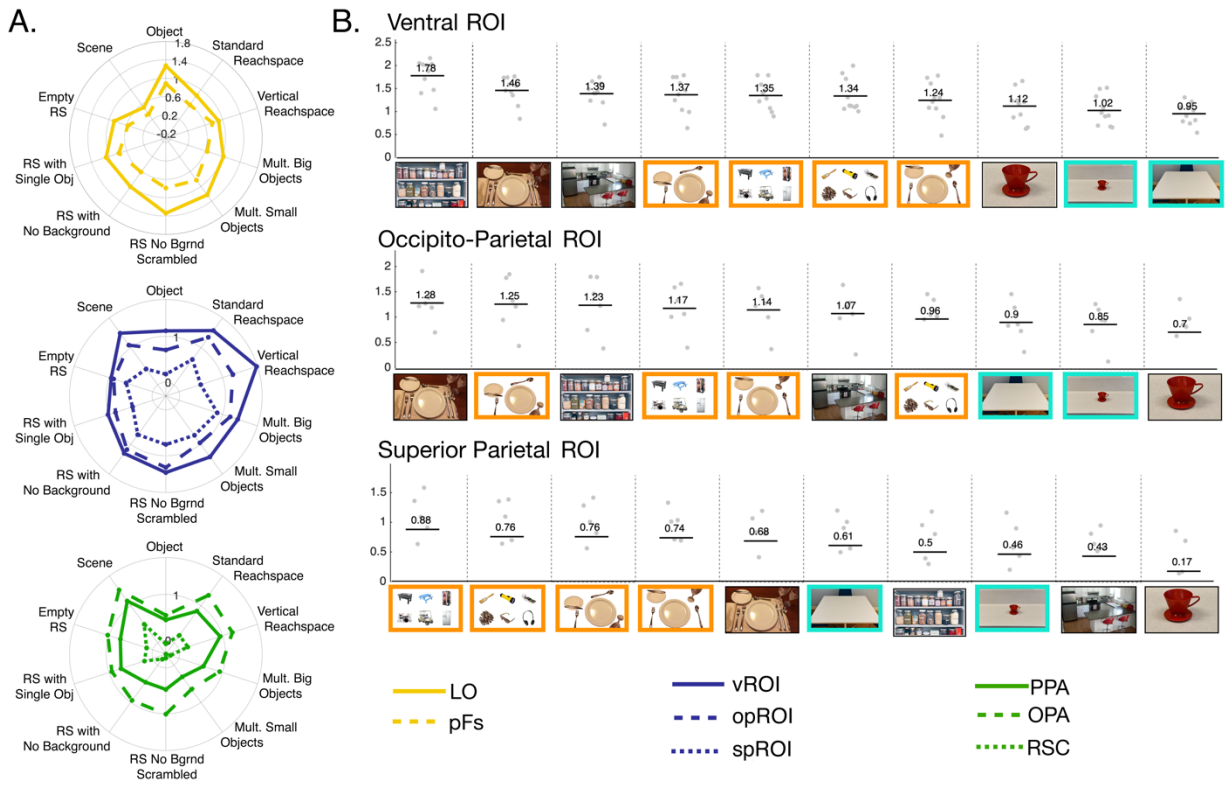

Figure 7: Experiment 3 results. A) Fingerprint profile of responses over all conditions in object, reachspace, and scene ROIs. B) Overall activation (betas, y-axis), in regions with reachspace-preferences, plotted in order from highest to lowest activations over the 10 stimulus conditions in Experiment 3. For visualization purposes, images with orange borders indicate conditions depicting multiple individuated objects, and images with cyan borders indicate conditions depicting reachable space with minimal to no object content.

Objects (Scenes>Multiple objects in PPA: $t(11)=12.02$, $p> 0.001$; in RS: $t(11)=7.87$, $p> 0.001$; one-tailed paired t-test, post hoc alpha level=0.02). This difference was not significant for approximated OPA ($t(11)=-0.18$, $p=0.57$). Finally, approximated LO and pFs regions showed a maximal response to bodies, with broad tuning to hands, faces, object and multiple objects, and no differences between single objects and multiple objects in either ROI (LO: $t(11)=-0.15$, $p=0.56$; pFs: $t(11)=-0.85$, $p=0.79$). Overall, these exploratory analyses suggest that regions with a reachspace preference have a distinct profile from scene and object preferring regions. Additionally, these ROIs seem to be particularly sensitive to the presence of multiple objects, which may be a distinguishing factor from known scene and object regions.

To test this formally, Experiment 3 probed responses in all ROIs to a broad range of conditions (Figure 7, Supplementary Figure 6). These conditions included views of standard reachspaces, objects and scenes, as well as four different *multi-object conditions* (all depicting multiple objects with no background), and two different *minimal object conditions* (depicting near-scale spatial layouts with one or no objects). A final condition depicted *vertical* reachspaces, where the disposition of objects was vertical rather than horizontal (e.g. shelves, peg-boards). Experiment 3 was conducted in the same session as Experiment 2, so involved the same participants, and the same ROIs. Note that this means that object-, reachspace- and scene-preferring ROIs were functionally defined, not approximated. Activations from all conditions were extracted from each ROI and the fingerprints were compared.

Across these 10 probe conditions, reachspace-preferring regions had a different fingerprint of activation than scene and object regions (Figure 7a). To test the significance of the difference in fingerprint

profiles, responses across all conditions were averaged over the reachspace ROIs to create a RS-ROI fingerprint, then compared to the scene-ROI fingerprint (averaged over scene regions) and object-ROI fingerprint (averaged over object regions) using a 2-way ANOVA. An omnibus test of ROI-type (object, reachspace or scene) by condition revealed an ROI type-by-condition interaction ($F(9, 329)=65.55$, $p<0.001$), showing that the patterns of activations across the 10 conditions varied as a function of ROI-preference type. This difference held when RS-type ROIs were compared to scene- and object-type ROIs separately (interaction effect for RS versus S ROIs: $F(9, 219)=32.20$, $p<0.001$; for RS versus O ROIs: $F(9, 219)=47.89$, $p<0.001$). These results replicate the main claim of the first exploratory fingerprint analyses: reachspace-preferring cortex has a distinct signature of activation.

Additionally, in all three of these ROIs, responses were higher to all multi-object conditions (Figure 7b, orange outline) than to empty reachspaces and to single-object reachspaces (blue outline). To quantify this, responses were averaged over the two condition-types respectively, and compared with a post hoc t-test (vROI: $t(9)=7.75$, $p <0.01$; opROI: $t(5)=4.57$, $p <0.01$; spROI: $t(5)=4.50$, $p < 0.01$). This pattern of data suggests that the presence of multiple easily-individuated objects may be particularly critical for driving the strong response to typical reachspace images relative to full-scale scenes, where object content may be less prominent than layout information. In contrast, in scene-preferring regions, the empty reachspace images generated higher responses than multiple object arrays, although this difference was marginal in OPA (Supplementary Figure 7; PPA: $t(11)=-8.16$, $p < 0.01$; OPA: $t(10)=-1.49$, $p=0.08$; RSC: $t(11)=-7.28$, $p < 0.01$). This result is consistent with prior work showing scene-regions strongly prefer empty full-scale rooms over multiple objects, and generally reflect spatial layout properties (Epstein & Kanwisher, 1998).

These activation profiles also illustrate how the stimulus conditions used to a define a region do not allow us to directly infer what specific information is encoded there. For example, scene images depict both spatial layout and multiple objects, but scene-selective regions are relatively more sensitive to the spatial layout content of the images. Analogously, reachspace images depict both spatial layout and multiple objects, but the regions which respond more strongly to reachspaces are relatively more sensitive to the multi-object content of the images. Future work will be required to further articulate the distinctive roles of these regions, perhaps using more parametric and controlled stimuli. Critically, the current results provide clear support that these regions have different functional signatures, and provide initial insight into the separable functional roles of these regions.

Discussion

The aim of this study was to characterize how the visual system responds to views of reachable environments relative to views of full-scale scenes and close-up singleton objects. We found that (1), reachable environments activate distinct response topographies from both scenes and objects, with reachspace preferences in posterior ventral cortex and throughout the dorsal visual stream, (2) peaks in this preference are present in consistent locations across participants, allowing us to define ROIs in the posterior collateral sulcus, dorsally in occipto-parietal cortex, and the superior parietal lobule; (3) the response topographies of reachspace preferences are maintained when low-level features are controlled; (4) reachspaces elicit dissociable activity in scene and object ROIs, driving these regions to an intermediate degree; (5) reachspace-preferring regions have peripheral biases and (6) have distinctly higher response to the presence of multiple isolated objects over near-scale spatial layout with minimal object content, a combination that is unique among the ROIs explored here.

Taken together, these results demonstrate that the representation of reachable-scale environments in visual cortex is dissociable from that of navigable-scale scenes and singleton objects. The presence of regions that respond preferentially to naturalistic reachable-scale views suggests that visually parsing such environments may require processing mechanisms that supplement scene- and object-based mechanisms.

However, our evidence also suggests that scene and object mechanisms play some role in the visual representation of reachspaces, since both scene and object networks were activated to an intermediate degree during reachspace viewing. Broadly, these data suggest that the scale of depicted views is a major factor in the organization and structure of responses across the visual system (see also Peer et al., 2019 for related ideas beyond the visual system). Below, we discuss how the current results fit into the literature, and offer some speculation about the role of these regions in representing the reachable world.

Situating reachspace-preferring cortex

The topography of reachspace preference described here resembles activations described in other tasks, which may provide initial clues into their functional contributions in processing reachable-scale environments. Activations across a similar constellation of regions were found when participants attended to the reachability of objects versus their color or location (Bartolo, Coello, Edwards, Delepoulle, Endo & Wing, 2014), and when participants attended to a ball approaching their hand versus a more distant target (Makin, Holmes, & Zohary, 2007). In addition, the three ROIs corresponding to peaks in reachspace preference appear to overlap a subset of the parcels from Fischer, Mikhael, Tenenbaum & Kanwisher (2016), which are involved in making predictions about the physical behavior of objects. Taken together, the correspondence between these results suggest that the ROIs which preferred reachable-scale views may be generally important for reachability judgments, and suggest a potentially broader role in behaviors that rely on accurate predictions regarding objects in the physical world.

Taken individually, the three reachspace-preferring ROIs seem to fall near parts of the cortex that have been implicated with different kinds of processing. The ventral reachspace ROI lies near a swath of cortex sensitive to features of object ensembles (Cant & Xu, 2012), and to the texture and surface properties of single objects (Cant, Arnott & Goodale, 2009). The occipital reachspace ROI lies in the vicinity of inferior parietal regions associated with the maintenance of multiple objects in working memory (Todd & Marois, 2004; Xu & Chun, 2006). Finally, the superior parietal reachspace ROI falls in the territory thought to contain information about the reachability of an object (Gallivan, Cavina-Pratesi & Culham, 2009; Gallivan, McLean & Culham, 2011), and the type of object-directed hand movement that is planned (Gallivan, McLean, Valyear, Pettypiece & Culham, 2011). Interestingly, this ROI also appears to overlap the posterior locus of the Multiple-Demand Network, a network of fronto-parietal regions associated with the control of visual attention and the sequencing of cognitive operations (Duncan, 2010; Fedorenko, Duncan & Kanwisher, 2013). Future studies with targeted comparisons will be required to map these functions together and assess the degree to which they draw on common representations.

Importantly, the reachspace-preferring regions did not appear to be a subset of the classic category-selective areas. Visualization of the ROIs, and analysis of the overlap among them, showed that these largely occupy different regions of visual cortex. Put another way, it is not the case that the inclusion of reachspaces in the stimulus set revealed new divisions in regions that have long been discussed in the literature, but rather that they revealed an unexpected pattern of preference in regions adjacent to them.

Implications for the visual representation of reachable space

What can we infer about the representation of reachable-scale environments from the current results? The existence of reachspace-preferring cortex suggests that everyday near-space environments requires some particularly distinctive processing relative to navigable-scale scenes and individual objects. While perceived depth has been shown to affect activation strength in scene regions (Persichetti & Dilks, 2016; Lescroart, Stansbury, & Gallant, 2015; Henderson, Larson, & Zhu, 2008), the current evidence suggests that ROIs that prefer reachspaces to scenes and objects do not do so on the basis of scale alone: environments which were near-scale, but contained only one or no objects elicited low responses in these regions. Instead, these regions responded more to images that contained multiple objects even in the absence

of spatial layout. Based on these data, we have suggested that reachable-scale environments may be represented partially on the basis of their multi-object content. However, there are other factors that co-vary with scale and number of objects that might contribute to the distinction between objects, reachspaces, and scene views.

First, objects, reachspaces and scenes differ in the kinds of high-level goals and behaviors they afford. Objects afford grasping, reachspaces afford the coordinated use of multiple objects, and scenes afford locomotion and navigation. Second, they differ in the geometric and structural components that dominate at each scale, which would likely be reflected in systematic mid-level feature differences (c.f. Greene, & Oliva, 2009). Object views are dominated by the surface planes of the objects themselves, reachspaces have a layout structure created by the placement of objects on a supporting surface, and scenes are dominated by the layout of walls, floors and ceilings. Third, these views have been found to differ in hierarchical image statistics extracted from convolutional neural nets (Josephs & Konkle, 2019). Indeed, variations in the number of perceptually distinct objects could contribute to mid-level feature differences (akin to clutter). Finally, these views might differ in terms of the basic visual mechanics they rely on (e.g.: binocular disparity, motion parallax vary by depth). While these binocular factors cannot explain the brain responses in the present experiment, as all images were presented at the same stereoscopic depth, these factors may be critical in how the visual system derives these distinctions as we learn to see and interact in the world. Thus, it is clear that there are many new questions raised about how these different high-level properties, mid-level features, and low-level input factors all relate to each other, and how they contribute to the cortical responses to reachable-scale environments.

Methods

In-text methods provide details about subjects, stimuli and ROI definitions. All other method details are available in the Supplement (see below).

Subjects. Twelve participants were recruited for Experiment 1 and Experiment 2. Two participants overlapped. Experiment 3 was conducted in the same session as Experiment 2. All participants gave informed consent and were compensated for their participation. All procedures were approved by the Harvard University Human Subjects Institutional Review Board.

Stimuli. All stimuli are available on the Open Science Framework (https://osf.io/g9aj5/). For Experiment 1, we collected views of objects, scenes, and reachable environments, each with 10 images from 6 semantic categories (bar, bathroom, dining room, kitchen, office, art studio), yielding 60 images per scale. These images were divided into 2 equal sets—Image Set A and Image Set B. Object images depicted close-scale views (within 8-12 inches from the object) on their natural background, e.g.: a view of a sponge with a small amount of granite countertop visible beyond it. Reachspace images depicted near-scale environments that were approximately as deep as arm's reach (3-4ft), and consisted of multiple small objects arrayed on a horizontal surface, e.g.: a knife, cutting board and an onion arrayed on kitchen counter. Scene images depicted views of the interior of rooms, e.g.: a view of a home office.

For Experiment 2, we created a controlled version of Image Set B where all images were grayscaled, matched in average luminance, contrast, and global spatial frequency content using the SHINE toolbox (Willenbockel, et al, 2010).

Experiment 3 included 10 stimulus conditions: (1) reachspaces images with the background removed in photoshop, yielding images of multiple objects in realistic spatial arrangements; (2) reachspaces images with background removed and the remaining objects scrambled, where the objects from the previous condition were moved around the image to disrupt the realistic spatial arrangement; (3) 6 objects with large real-world size, e.g. trampoline, dresser, arranged in a 3x2 grid on a white background; (4) 6 objects with small real world size, e.g. mug, watch, arranged in a 3x2 grid on a white background, and presented at the same visual size as the previous image condition; (5) reachable environments with all objects removed except the support surface; (6) reachspaces containing only a single object on the support surface; (7) vertical reachspaces, where the disposition of objects was vertical rather than horizontal, e.g. shelves, peg-boards; (8) regular reachspaces, i.e. horizontal, as in earlier experiments (9) objects, i.e. close-up views of single objects on their natural background; and (10) scenes, i.e. navigable scale environments. Further details on stimulus selection and controls are available in the supplement.

Defining ROIs with reachspace preferences. For Experiment 1, Reachspace-preferring ROIs were defined manually in Brain Voyager by applying the conjunction contrast RS>O & RS>S, using four experimental runs with the same image set. We decided a priori to define all reachspace ROIs using Image Set A runs, and extract all activations for further analysis from Image Set B runs. These results are reported in the paper, but we also validated all analyses by reversing which image set was used to localize vs extract activations, and these results are reported in the supplement.

For the ROIs used in Experiments 2 and 3 (run in the same session), we designed an automatic ROI-selection algorithm, guided by the anatomical locations of these regions in Experiment 1. This method allowed for the precise location of ROIs to vary over individuals, while still requiring them to fall within anatomically-constrained zones. The algorithm located the largest patch in the vicinity of the average location of the ROIs from E1 where the univariate preference for reachspaces over the next-most-preferred category exceeded 0.2 beta (more details in supplement). This automated procedure was developed using a separate pilot data set and all parameters were decided a priori (but see Supplementary Figure 8 for a visualization of the consequences of this parameter choice).

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Author Contributions

E.J. and T.K. designed the research, E.J. performed the research, E.J. and T.K. wrote the paper

Competing Interests statement

The authors have no competing interests to report.

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Supplementary Methods

Subjects. Twelve participants were recruited each for Experiment 1 and Experiment 2. Experiment 3 was conducted in the same session as Experiment 2, and thus represents the same participants. Two people participated in both E1 and E2, and author EJ participated in E1. Participants were between the ages of 20 and 31, and 13 out of 22 participants were female. One additional person participated in E1, but was excluded prior to analysis for falling asleep in the scanner. All participants gave informed consent and were compensated for their participation. All procedures were approved by the Harvard University Human Subjects Institutional Review Board.

Acquisition and Pre-processing. All neuroimaging data were collected at the Harvard Center for Brain Sciences using a 32-channel phased-array head coil with a 3T Siemens Magnetom Prisma fMRI Scanner (Siemens Healthcare, Erlangen, Germany). The Siemens Auto-Align tool was used to ensure reproducible placement of image fields of view. High-resolution anatomical images were collected with a T1-weighted magnetization-prepared rapid gradient multi-echo sequence (multi-echo MPRAGE [1], 176 sagittal slices, TR=2530 ms, TEs=1.69, 3.55, 5.41, and 7.27 ms, TI=1100 ms, flip angle=7°, 1 mm3 voxels, FOV=256 mm, GRAPPA acceleration=2). For functional runs, blood oxygenation level-dependent (BOLD) data were collected via a T2*-weighted echo-planar imaging (EPI) pulse sequence that employed multiband RF pulses and Simultaneous Multi-Slice (SMS) acquisition [2-5]. For the task runs, the EPI parameters were: 69 interleaved axial-oblique slices (25 degrees toward coronal from ACPC alignment), TR=1500 ms, TE=30 ms, flip angle=75°, 2.0 mm isotropic voxels, FOV=208 mm, in-plane acceleration factor (GRAPPA)=2, SMS factor=3). The SMS-EPI acquisition used the CMRR-MB pulse sequence from the University of Minnesota.

Functional data were preprocessed using Brain Voyager QX software with MATLAB scripting. Preprocessing included slice-time correction (ascending trilinear interpolation), 3D motion correction (sinc interpolation), linear trend removal, temporal high-pass filtering (0.0078 Hz cutoff), spatial smoothing (4 mm FWHM kernel), AC-PC alignment and transformation into Talairach (TAL) coordinates. Three dimensional models of each subject's cortical surface were generated from the high-resolution T1-weighted anatomical scan using the default segmentation procedures in FreeSurfer. For visualizing activations on inflated brains, surfaces were imported into Brain Voyager and inflated using the BV surface module. Gray matter masks were defined in the volume based on the Freesurfer cortex segmentations.

E1 and E2 Stimuli. All stimuli are available for download on the Open Science Framework (https://osf.io/g9aj5/). We collected views of objects, scenes, and reachable environments, each with 10 images from 6 semantic categories (bar, bathroom, dining room, kitchen, office, art studio), yielding 60 images per scale. These images were divided into equal 2 sets—Image Set A and Image Set B. Object images depicted close-scale views (within 8-12 inches from the object) on their natural background, e.g.: a view of a sponge with a small amount of granite countertop visible beyond it. Reachspace images depicted near-scale environments that were approximately as deep as arm's reach (3-4ft), and consisted of multiple small objects arrayed on a horizontal surface, e.g.: a knife, cutting board and onion arrayed on kitchen counter. Scene images depicted views of the interior of rooms, e.g.: a view of a home office.

Additionally, using Image Set B we created a controlled image set, where all images were grayscaled, matched in average luminance, contrast, and global spatial frequency content using the SHINE toolbox (Willenbockel, et al, 2010). Images were spatial frequency-matched using the specMatch function, then luminance-matched using the histMatch function, both with default parameters.

Experiment 1 reachspace preference analyses. The main experimental protocol for Experiment 1 consisted of a blocked design with 18 image conditions, depicting three scales of space (object, reachspace, scene views), drawn from six different semantic categories (bar, bathroom, dining room, kitchen, office,

studio). Each run contained two blocks per condition, with blocks lasting 6s and consisting of 5 unique images and 1 repeated image. Within a block, each image was presented in isolation on a uniform gray background for 800ms followed by a 200ms blank. There were twelve 10s fixation blocks interleaved throughout the experiment, and each run started and ended with a 10s fixation block. A single run lasted 5.93 min (178 volumes). Participants viewed eight runs of the experimental protocol. Four runs were completed with Image Set A and four with Image Set B (see Stimuli), presented in alternating order over the course of the scan session. Participants' task was to detect a image repeated back-to-back, which happened once per block.

General linear models (GLMs) were computed using Brain Voyager software. In Experiment 1, for each participant, separate GLMs were fit for runs containing Image Set A and Image Set B, and a third GLM was fit to all experimental runs together (this combined GLM was only used for Experiment 1 preference map analysis). Data were modeled first with 3 condition regressors (object, reachspace, scene), and then again with 18 condition regressors (3 scales of space x 6 semantic category) for the finer-grained analyses by category and the searchlight analysis. The regressors were constructed based on boxcar functions for each condition, convolved with a canonical hemodynamic response function, and were used to fit voxel-wise time course data with percent signal change normalization and correction for serial correlations. The beta parameter estimates from the GLM were used as measures of activation to each condition for all subsequent analyses.

Preference Mapping. Group-level preference maps were computed by extracting responses to objects, reachspaces and scenes in each voxel from single-subject GLMs, then averaging over subjects. The preferred condition for each voxel was identified in the group-average, and the degree of preference was computed as the activation differences (in betas) between the most preferred condition and the next-most-preferred condition. Responses were visualized for visually-responsive voxels only, which were defined as those that were active in an All vs Rest contrast at a threshold of $t>2.0$ in at least 30% of the participants. Early visual regions (V1-V3) were defined by hand on inflated brain, guided by the contrast of horizontal vs. vertical meridians from a retinotopy run (see below for run details). Group average V1-V3 was obtained by generating single subject early visual cortex maps, and selecting voxels that fell within V1-V3 in at least 30% of the participants. These voxels were removed from the visualization. Preference maps were visualized by projecting these voxels' preferred condition (indicated by color hue) and the degree of preference (indicated by color intensity) onto the cortical surface of a sample participant. For Experiment 1, preference maps were computed from a GLM modeled with data from all 8 experimental runs.

RS ROI definition: For Experiment 1, three reachspace-preferring ROIs were defined manually in Brain Voyager by applying the conjunction contrast RS>O & RS>S, using four experimental runs with the same image set. Conjunction contrasts reveal voxels that show both a preference for reachspaces over scenes and reachspace over objects (assigning them the statistical value corresponding to the less robust of those contrasts). We had decided a priori to define all reachspace ROIs using Image Set A runs, and extract all activations for further analysis from Image Set B runs. These results are reported in the paper, but we also validated all analyses by reversing which image set was used to localize vs extract activations, and these results are reported in the supplement.

Region-of-Interest Analysis. For ROI-based analyses, univariate activations were obtained by taking the average beta for each condition in each ROI, then averaging over subjects to obtain the group-level activations. Reachspace-preferring ROIs were defined from 4 runs of the experimental protocol, and activation were extracted from the remaining 4 runs. Experiment 1 activations were examined at two levels, with separate GLMs generated for each. At the environment-scale level we examined the activations to 3 conditions: objects, reachspaces and scenes. In each ROI, we tested whether the preferred condition activated the ROI significantly more than the other conditions, using a priori paired one-sided t-tests. We also extracted responses to objects, scenes and reachspaces at the more granular scale-by-category level (18

conditions: 6 semantic categories represented at each of 3 scales). These data were visualized in a bar graph, where the bars are ordered by the strength of the activation.

Experiment 2 reachspace preference analyses. The main experimental protocol for Experiment 2 was the same as Experiment 1. Four runs used original images, specifically Image Set A from Experiment 1, and four runs used controlled images, specifically Image Set B with the low level controls described above. Experiment 2 GLMs were computed as above, and the data were modeled with 3 condition regressors (object, reachspace, scene).

Preference mapping. Experiment 2 preference mapping used the same procedure as Experiment 1, with the difference that V1-V3 were not removed from the visualization and subsequent quantification, since these regions were not localized in E2. For Experiment 2, separate preference maps were computed from original- and controlled-image runs, each estimate from a GLM with 4 runs.

To quantitively compare the similarity of preference maps elicited by original and controlled images, we assessed the proportion of voxels that showed the same preference across image sets. For the group-level preference map, we first extracted the preferred category and the strength of that preference for each voxel within the group-level mask, for original and controlled images separately (as described above). Next, we extracted the number of voxels that showed the same preference in the two maps (original vs controlled), then divided this by the total number of voxels in the visually-evoked mask, to obtain the proportion of voxels with consistent preference over the image sets. For group-level comparisons, we performed the analyses above on single-subject data, then averaged these values over all subjects.

This method was additionally used to compute the replicability of the original image activations between Experiment 1 and Experiment 2. To do so, the preference map for Experiment 1 was generated from Image Set B only, so that the preference maps being compared were generated from GLM parameter estimates made using the same amount of data (4 runs). Additionally, a common activity mask for the two preference maps was defined by taking the voxels that showed an All-vs-Rest preference of t>2.0 betas in 60% of all of the subject included (i.e. E1 and E2 subjects). Since this analysis was between subjects and no within-subject comparisons were available, the match in preference maps across experiments was only computed at the group-level.

RS ROI definition: For Experiment 2, we designed an automatic ROI-selection algorithm, guided by the locations of these regions in Experiment 1. ROIs were defined separately for each participant using the following procedure. First, a spherical proto-ROI was defined around the average central locations of each ROI from E1. The size of the proto-ROI was set to a radius of 6 voxels (18 mm) for the ventral and superior parietal patches, and 9 voxels (27mm) for the occipital patch, to account for different amounts of variation in the expected ROI locations. Then, the reachspace conjunction map with RS>O & RS>S was computed and spatially smoothed (5-mm gaussian kernel, sigma=1). Next, the single voxel with the highest reachspace-preference falling in each proto-ROI was selected and used as the center of 6mm spherical ROI. Finally, the voxels within this sphere with the most statistically robust preference for reachspaces were retained for the final ROI, using the following procedure. Low-preference voxels were iteratively dropped from the ROI until the region's univariate preference for reachspaces over the next-most-preferred category exceeded 0.2 beta. This method allowed us to define the largest ROI that still showed a relatively high reachspace bias. This automatic ROI-selection regime was developed in a separate pilot data set before being applied here, and all parameters were decided a priori, but see Supplemental Fig for visualization of how parameter variation affected significance of the final analysis. Activations within these ROIs were always assessed from independent data sets.

Region-of-Interest Analysis: ROI analysis of reachspace regions used the same procedure as Experiment 1, with the exception that this analysis was only performed at the environment scale level (i.e.

betas were extracted for objects, reachspaces, and scenes separately, pooling over semantic category). ROIs were defined with the 4 runs depicting original images, and activations were extracted from the 4 controlled-image runs, and compared using a priori paired one-sided t-test.

Experiment 1 classic category-selective ROI analysis. Classic category-selective ROIs were defined in Experiment 1 using a standard localizer protocol. Stimuli included images of bodies, faces, hands, objects, multiple objects, scenes, and white noise. Body images showed clothed bodies with the head erased in photoshop, in a variety of poses. Face images were cropped from the chin to the top of the head, and depicted a variety of facial expressions from humans of different ages, races, and genders. Object images showed single objects on a white background. Multi-object images showed four randomly-selected unique objects occupying four quadrants around the center fixation location, presented over a white background. Scene images showed indoor and outdoor images of navigable-scale spaces.

The localizer protocol contained 8 blocks per image condition, with blocks lasting 6s and consisting of 5 unique images and 1 repeated image. All images were presented in isolation on a uniform gray background for 800ms followed by a 200ms blank. There were eight 8s fixation blocks interleaved throughout the experiment, and each run started and ended with an additional 8s fixation block. A single run lasted 6.9 min (208 volumes), and participants viewed four runs of the localizer protocol. Participants' task was to detect an image repeated back-to-back, which happened once per block.

ROIs were defined using standard contrasts, and ROI activations were extracted from 4 runs of the main experimental protocol using the same univariate approach described above. Activations were extracted separately for Image Set A runs and Image Set B runs. The latter are reported in the paper, as explained above, and the former appear in the supplement. All stats were a priori paired one-sided t-test.

Reachspace ROI overlap analysis. In order to quantify whether the reachspace ROIs consistently overlapped any of the classic ROIs, we first divided them into ventral (PPA, pFs, vRS), and lateral-dorsal ROIs (OPA, LO, hand-preferring, opRS, spRS). Next, we assessed the overlap between the RS ROIs in a given division with each of the other ROIs in that division. For each subject, whole-brain masks were created for each ROI in the pair under comparison, and the number of voxels appearing in both masks was extracted. Then, the number of overlapping voxels was divided by the total number of voxels in the reachspace region, to obtain the percentage of the reachspace ROI voxels that overlapped the comparison ROI. With this definition, overlap estimates of 100% indicate that the reachspace-preferring regions fall fully into existing known regions; estimates of 0% indicate complete separation. This was computed separately for each hemisphere, and for RS ROIs created from each image set (Image Set A vs Image Set B).

Experiment 2 classic ROI analysis. Scene- and object-selective regions were defined in Experiment 2 from the main experimental protocol runs with the original images: LO and pFs were defined as objects>scenes; PPA, OPA and RSC were defined as scenes>objects. Activations from all regions were extracted from the 4 experimental runs depicting controlled images, and the analysis was otherwise carried out as described in Experiment 1.

Experiment 1 and Experiment 2 PPA subdivision. For Experiment 1 and 2, we additionally subdivided PPA. For each subject, we separately split the PPA from the left and right hemisphere at the midpoint along the anterior to posterior axis. Anterior and posterior PPA were then submitted to the same ROI analysis described above. Statistical tests were completed using Bonferroni-corrected paired one-sided t-test with alpha 0.0125 (i.e. 0.05/4, reflecting the four comparisons being performed in each image set).

Eccentricity profile analysis. Data for the eccentricity analysis were collected in the same run as Experiment 1, and thus represent the same subjects and reachspace ROIs. The retinotopy protocol consisted

of 4 stimulus conditions: horizontal bands, vertical bands, central stimulation, and peripheral stimulation. Vertical and horizontal bands (subtending ~1.7° × 22° and ~22° × 1.7° respectively) showed checkerboards which cycled between states of black-and white, white-and-black, and randomly colored at 6hz. Central and peripheral rings (radius ~1.2° to 2.4° and radius ~9.3° to the edges of the screen, respectively) showed photograph fragments which cycled between patterns of object ensembles (e.g. beads, berries, buttons) and scene fragments (c.f. Cant & Xu, 2012; Zeidman, Silson, Schwarzkopf, Baker & Penny, 2018). Each run contained 5 blocks per condition, with blocks lasting 12 seconds. There were four 12s fixation blocks interleaved throughout the experiment, and each run started and ended with an additional 12s fixation block. Each run lasted 4.4 min (162 volumes), and participants viewed two runs of the retinotopy protocol. Participants' task was to maintain fixation and press a button when the fixation dot turned red, which happened at a random time once per block.

ROI analysis. We explored the eccentricity preference of object, reachspace, and scene ROIs (defined as described for Experiment 1 above), and for ROIs corresponding to scenes- and object ROIs. Average betas were extracted for two eccentricity conditions: central stimulation, and peripheral stimulation. Activations in the two conditions were compared using a paired one sided t-test with a Bonferroni corrected alpha value of 0.0125 (i.e. 0.05/8, reflecting the 8 ROIs where we tested for a difference between these conditions).

Post-hoc fingerprint profile analysis. To examine the broader tuning of object, scene and reachspace ROIs, we performed a post-hoc analysis, using activations extracted from the Experiment 1 localizer. The localizer runs included bodies, faces, hands, objects, multiple objects, scenes, and white noise). We extracted responses in Experiment 1 reachspace-preferring ROIs to these 8 conditions for each subject, and averaged the activations over subjects. First, we visualized these responses in a polar plot. Next, we noted what the most preferred condition was, and tested whether this was significantly different than the next-most preferred condition using one-tailed pair t-tests with Bonferroni-corrected alpha 0.0167 (0.05/3, reflecting the 3 reachspace-preferring ROIs where we tested for this difference).

We also examined activations to these conditions in object- and scene-processing cortex. Since the localizer runs were used to extract activations, we couldn't use them to define ROIs. Instead, ROIs were defined as a spherical ROI with a 9-mm radius centered on the typical anatomical location of each region based on an internal meta-analysis (for left/right hemisphere, ROI centers were as follows: PPA: -25 -41 -6/ 25 -42 -7; OPA: -25 -76 25/ 28 -81 26; RSC: -16 -51 9/ 18 -49 8; LO: -39 -71 -4/ 41 -68 -4; pFs: -38 -53 -13/ 38 -50 -14).The difference between the preferred and next-most-preferred condition was assess using one-tailed pair t-tests with Bonferroni-corrected alpha 0.025, and 0.0167 respectively for areas corresponding to the anatomical location of object and scenes ROIs.

Experiment 3 fingerprint profile analysis. Experiment 3 stimuli contained 10 conditions intended to further probe the response profile of the reachspace regions. The conditions were the following: 1) reachspaces images with the background removed in photoshop, yielding images of multiple objects in realistic spatial arrangements; 2) reachspaces images with background removed and the remaining objects scrambled, where the objects from the previous condition were moved around the image to disrupt the realistic spatial arrangement; 3) 6 objects with large real-world size (e.g. trampoline, dresser) arranged in a 3x2 grid one a white background; 4) 6 objects with small real world size (e.g. mug, watch) arranged in a 3x2 grid a white background (presented at the same visual size as the previous image condition); 5) reachable environments with all objects removed except the support surface; 6) reachspaces containing only a single object on the support surface; 7) vertical reachspaces, where the disposition of objects was vertical rather than horizontal (e.g. shelves, peg-boards); 8) regular (i.e. horizontal) reachspaces; 9) objects (i.e. close-up views of single objects on their natural background); and 10) scenes (i.e. navigable scale environments).

Images from conditions 1 and 2 above (reachspace with background removed, and reachspace with background removed and remaining objects scrambled) were generated from the same original images. First, condition 1 images were generated by selecting high-quality reachspace images, and erasing all image content except the 6 salient objects which conveyed the identity and layout of the space. Then, condition 2 images were generated by scrambling the arrangement of the 6 remining objects in the image, and occasionally rotating objects, to break the sense of spatial congruity among them. We ensured that the average placement of objects across all the images (i.e. the heatmap of object locations) was equivalent between condition 1 and condition 2. Images in conditions 5, 6 and 9 (empty reachspaces, reachspaces with single objects, and close up view of single objects) were taken by the experimenter, and represented the same environments. Specifically, a suitable reachspace was selected by the experimenter and cleared of all objects for condition 5, and an images was taken with a camera on a tripod. Then a single salient object was placed in the center of the reachspace for condition 6, at which point a second picture was taken without moving the tripod. Finally, condition 9, the singleton object view, was generated by closely cropping the condition 6 image in Photoshop. Images in conditions 3 and 4 (large and small objects respectively) were programmatically generated by randomly 6 objects drawing from a database of large and small objects, and placing them in 3-across by 2-down grid. Images for condition 7 (vertical reachspaces) were selecting by finding reachable environments where the spatial layout of the objects was primarily on a vertical, rather than horizontal plane. This ranged from spaces with no horizontal extent (e.g. pegboard organization) to spaces with minimal horizontal extent (e.g. shelves). Finally, condition 8 and 10 images (regular reachspaces and scenes) were selected according to the same criteria as E1.

The main experimental protocol for Experiment 3 consisted of a blocked design with the 10 image conditions described above. Each run contained 4 blocks per condition, with blocks lasting 8s and consisting of 7 unique images and 1 repeated image. Within a block, each image was presented in isolation on a uniform gray background for 800ms followed by a 200ms blank. There were eight 10s fixation blocks interleaved throughout the experiment, and each run started and ended with a 10s fixation block. A single run lasted 7 min (210 volumes). Participants viewed four runs of the experimental protocol. Participants' task was to detect a image repeated back-to-back, which happened once per block.

ROI definition. Experiment 3 used the same subjects and ROIs as Experiment 2.

Analysis. Responses across the 10 conditions were extracted from all object, scene, and reachspace ROIs. These responses were first visualized in a fingerprint profile. Next, to assess whether object, scene and reachspace ROIs had significantly different response profiles, we performed an analysis of variance to compare ROI types. Responses across the 10 conditions were averaged for all reachspace ROIs, scene ROIs and objects ROIs. These three response profiles were then submitted to a 2-way, condition-by-ROI type ANOVA.

References for fMRI sequence design

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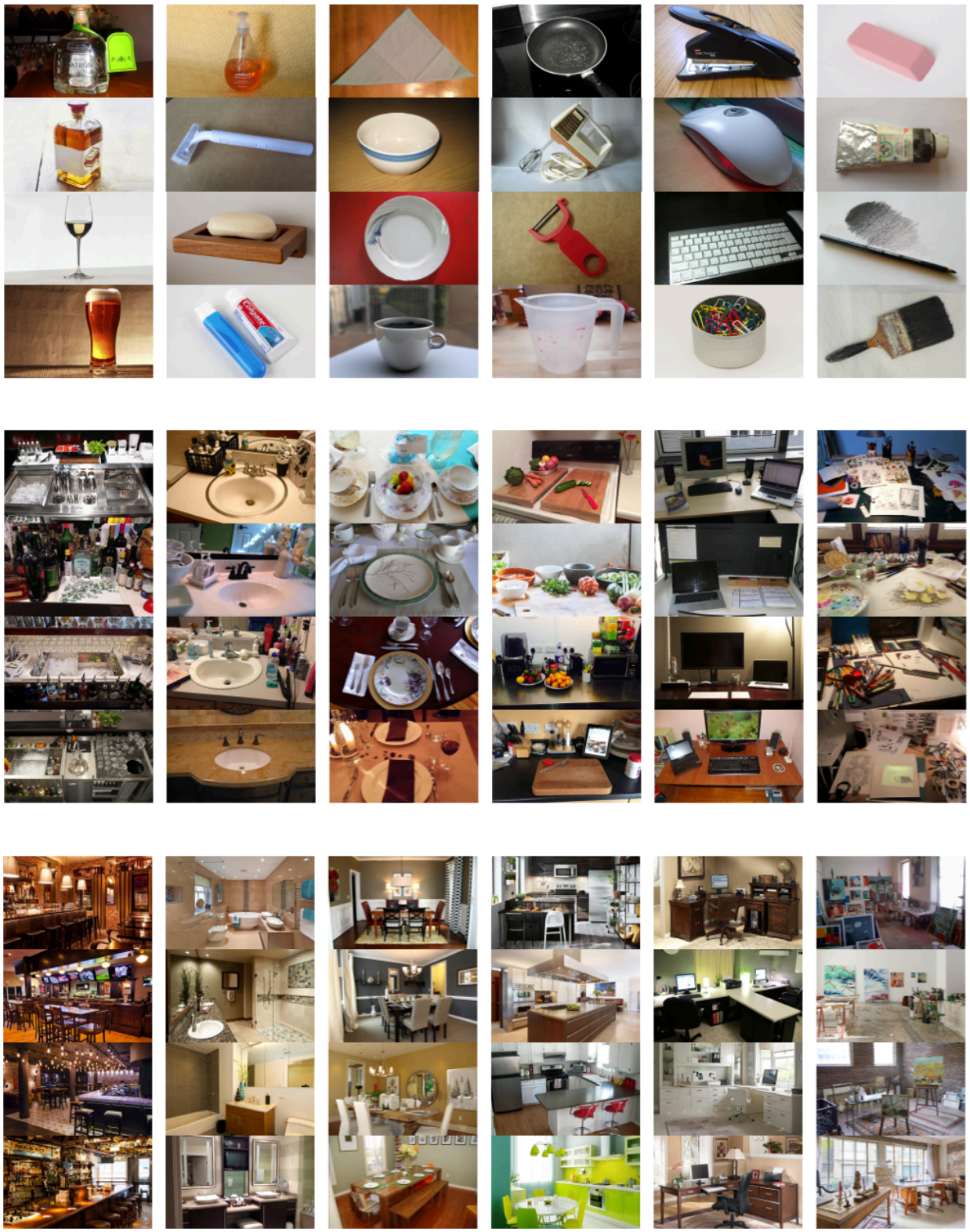
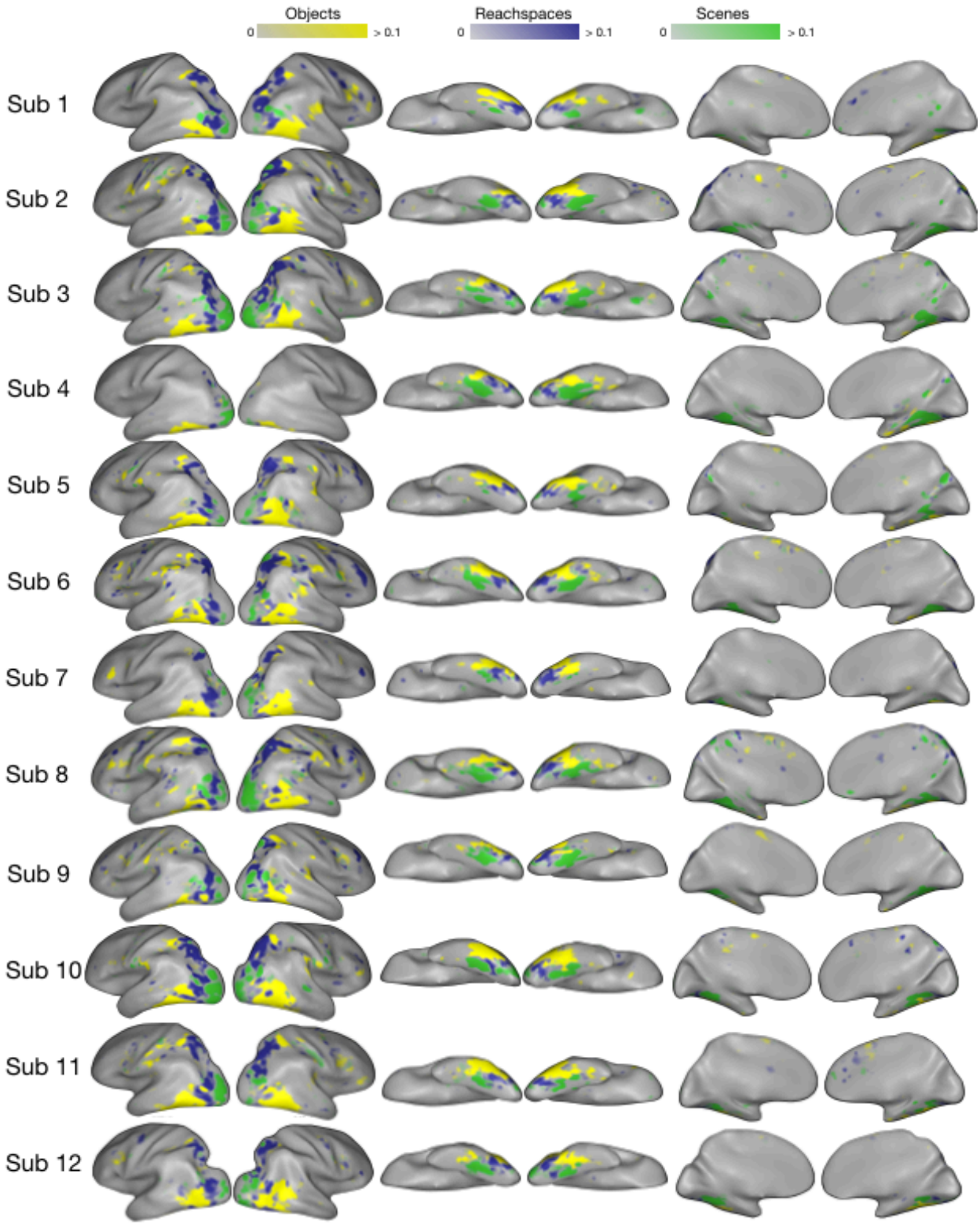


Supplementary Figure 1: Additional examples of the object (top), reachspace (middle), and scenes (bottom) stimuli used in Experiment 1



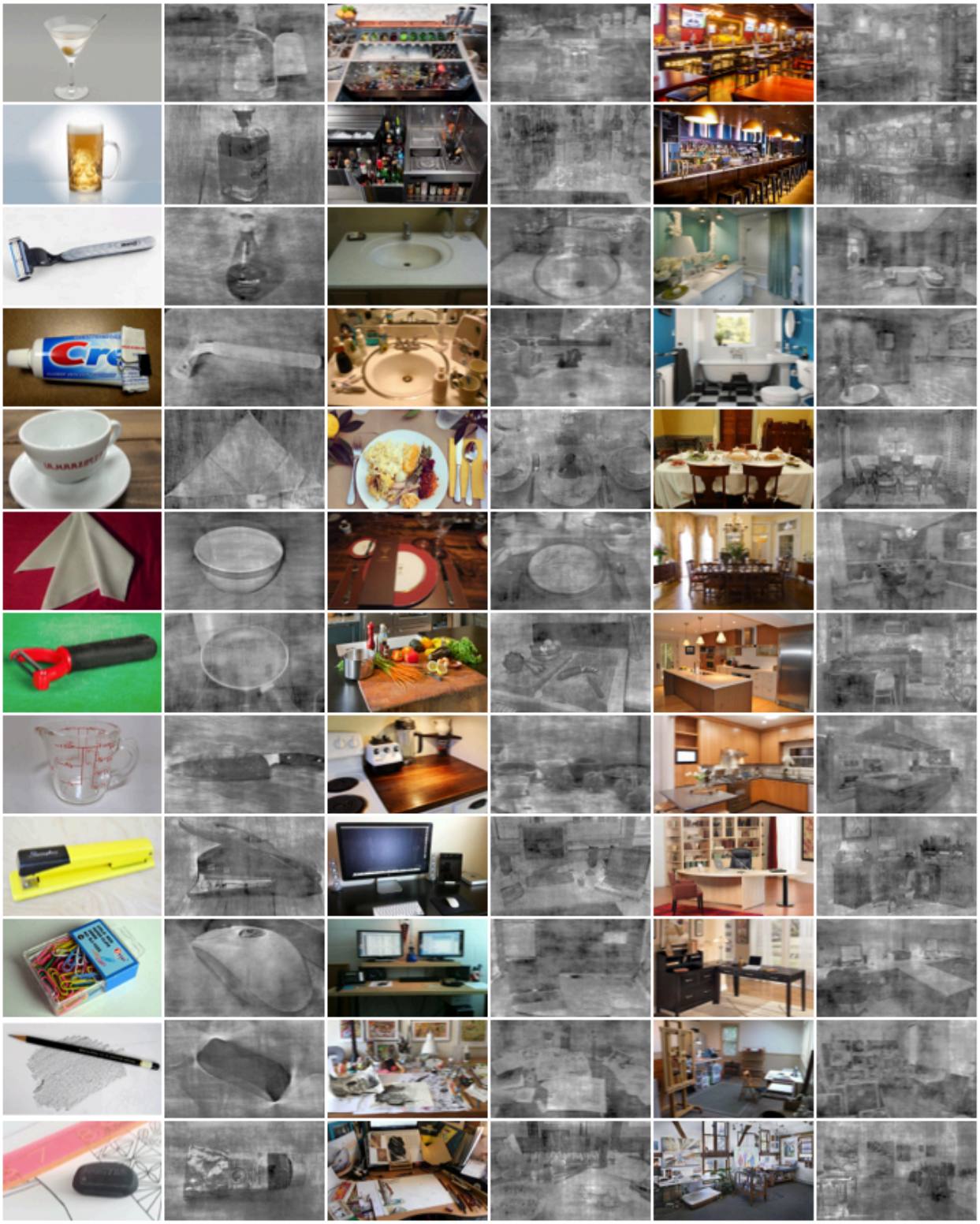
Supplemental Figure 2: Single-subject preference maps from Experiment 1.

ROI	Hemi	Exp 1 Set A			Exp 1 Set B			Exp2 Auto ROIs		
		x	*y*	*z*	*x*	*y*	*z*	*x*	*z*	*z*
VRSP	LH	-28	-69	-9	-24	-70	-11	-28	-67	-12
	RH	26	-71	-10	20	-71	-11	24	-71	-14
ORSP	LH	-24	-82	17	-29	-82	16	-28	-81	17
	RH	27	-82	18	25	-80	20	27	-79	17
SPRSP	LH	-23	-65	48	-21	-65	51	-21	-66	48
	RH	17	-69	52	15	-66	57	14	-67	53

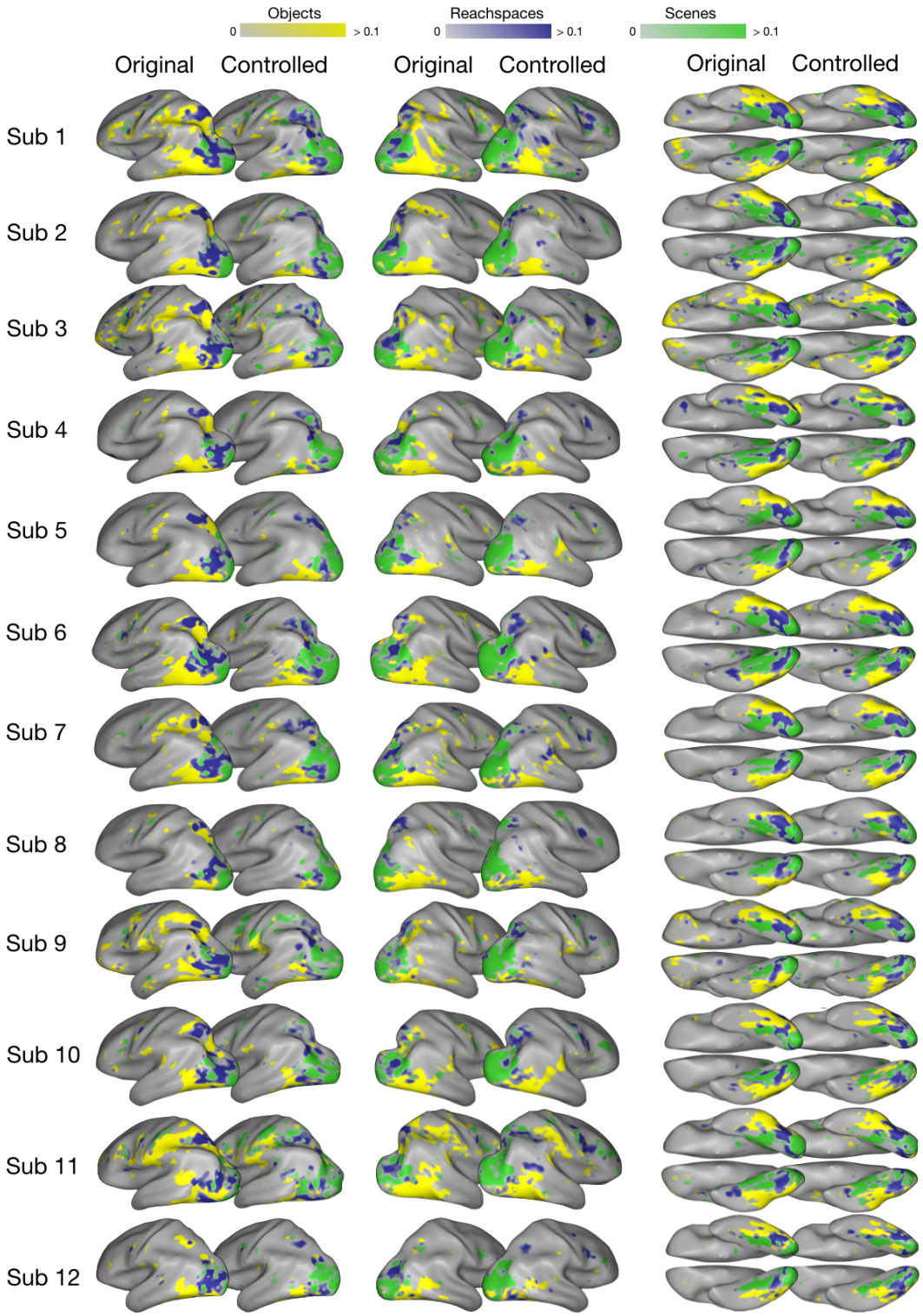
Supplemental Table 1: Average TAL coordinates for reachspace-preferring ROIs in all experiments.

		Experiment 1		Experiment 2
ROI	**Comparison**	**ROIs defined in Set A**	**ROIs defined in Set B**	**Controlled images**
VRSP	RS > S	*t(8) = 4.655, p = 0.001	*t(10) = 4.940, p < 0.001	*t(9) = 2.719, p = 0.012
	RS > O	*t(8) = 5.326, p < 0.001	*t(10) = 4.118, p < 0.001	*t(9) = 2.082, p = 0.034
ORSP	RS > S	*t(6) = 4.546, p = 0.002	*t(10) = 4.802, p < 0.001	t(5) = 0.785, p = 0.234
	RS > O	*t(6) = 5.199, p = 0.001	*t(10) = 5.239, p < 0.001	*t(5) = 2.382, p = 0.032
SPRSP	RS > S	*t(7) = 5.221, p = 0.001	*t(7) = 5.984, p < 0.001	t(5) = 2.021, p = 0.050
	RS > O	*t(7) = 6.155, p < 0.001	*t(7) = 5.587, p < 0.001	*t(5) = 3.608, p = 0.008
PPA	S > RS	*t(11) = 4.765, p < 0.001	*t(11) = 2.572, p = 0.013	*t(11) = 9.685, p < 0.001
	RS > O	*t(11) = 11.288, p < 0.001	*t(11) = 10.240, < 0.001	*t(11) = 8.427, p < 0.001
OPA	S > RS	*t(10) = 2.145, p = 0.029	t(10) = 1.277, p = 0.115	*t(10) = 4.254, p = 0.001
	RS > O	*t(10) = 9.157, p < 0.001	*t(10) = 10.236, < 0.001	*t(10) = 9.316, p < 0.001
RSC	S > RS	*t(11) = 6.958, p < 0.001	*t(11) = 8.098, < 0.001	*t(11) = 6.482, p < 0.001
	RS > O	*t(11) = 9.154, p < 0.001	*t(11) = 9.240, < 0.001	*t(11) = 5.241, p < 0.001
LO	O > RS	t(10) = 0.863, p = 0.204	*t(10) = 6.570, < 0.001	*t(11) = 11.197, p < 0.001
	RS > S	*t(10) = 5.546, p < 0.001	*t(10) = 3.934, p = 0.001	*t(11) = 8.098, p < 0.001
PFS	O > RS	t(10) = -0.122, p = 0.547	t(10) = 0.643, p = 0.267	*t(11) = 12.186, p < 0.001
	RS > S	*t(10) = 4.855, p < 0.001	*t(10) = 4.293, p = 0.001	*t(11) = 6.037, p < 0.001

Supplemental Table 2: Statistical test for all ROIs in Experiments 1 and 2. In Experiment 1, we defined ROIs in Set A and extracted activations from them using Set B. Those statistical test are reported in the main text. Additionally, to confirm that the results were stable, we defined ROIs in Set B and extracted activations from Set B. These statistical results are reported here.



Supplemental Figure 3: Additional examples of stimuli for Experiment 2.



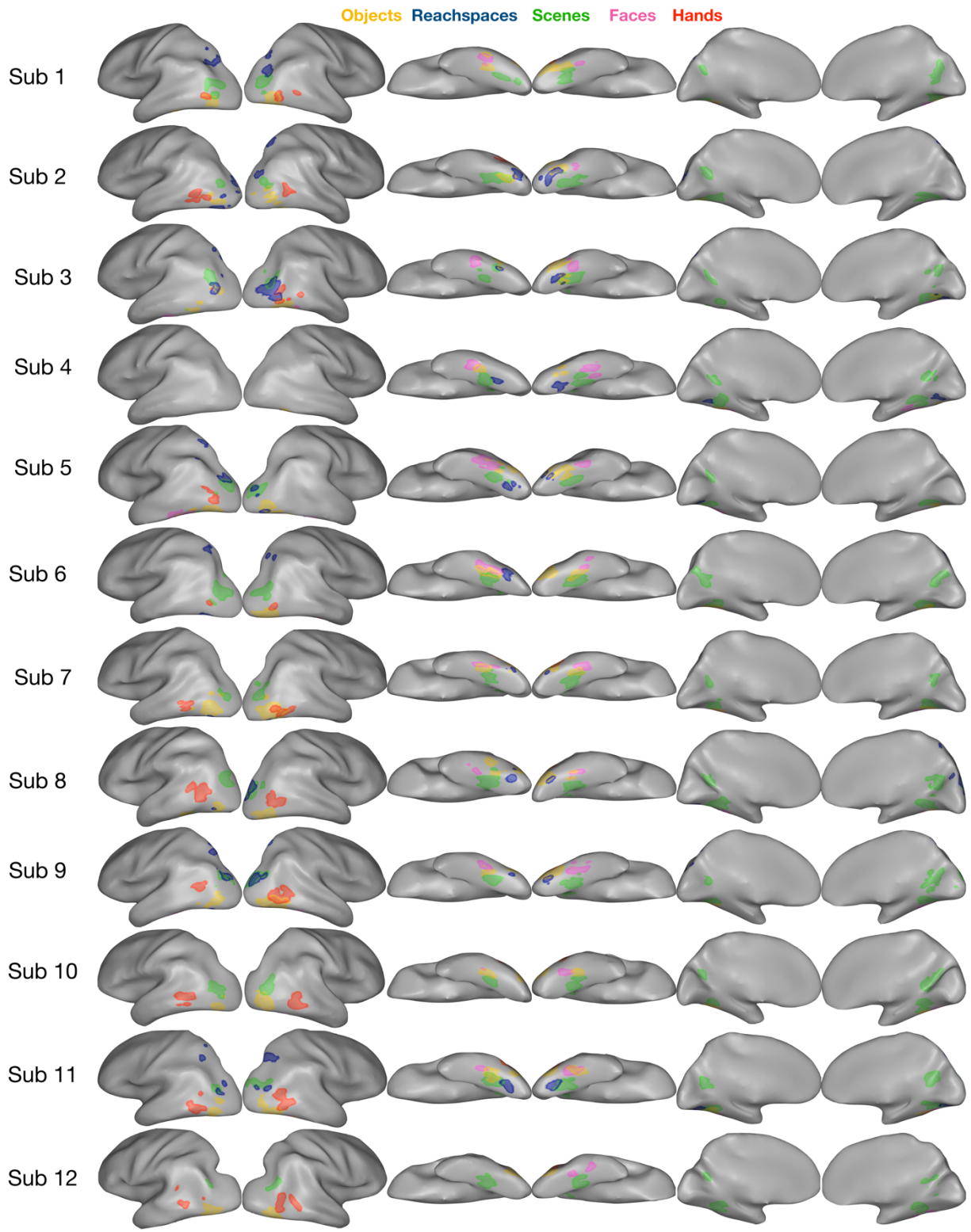
Supplemental Figure 4: Single-subject preference maps from Experiment 2, obtained from original and controlled images (same color scale used for both original and controlled)

ROIs to compare (ROI1, ROI2)		Left Hemisphere					Right Hemisphere				
		ROI1 size	ROI2 size	overlap	overlap percent		ROI1 size	ROI2 size	overlap	overlap percent
PPA, VRS (SetA)	Sub1	70	-	-	-	Sub1	68	-	0	-
	Sub2	114	57	0	0	Sub2	111	69	0	0
	Sub3	93	14	7	50	Sub3	64	28	3	10.7
	Sub4	56	16	0	0	Sub4	76	33	0	0
	Sub5	76	36	0	0	Sub5	50	41	0	0
	Sub6	97	32	0	0	Sub6	78	-	-	-
	Sub7	66	19	0	0	Sub7	89	24	0	0
	Sub8	115	32	0	0	Sub8	94	20	0	0
	Sub9	51	10	0	0	Sub9	93	24	0	0
	Sub10	46	-	-	-	Sub10	82	-	-	-
	Sub11	93	34	1	2.9	Sub11	80	34	5	14.7
	Sub12	88	-	-	-	Sub12	86	-	-	-
			average % overlap:		5.88			average % overlap:		3.18
				sem	5.52				sem	2.11
PPA, VRS (SetB)	Sub1	70	53	0	0	Sub1	68	41	0	0
	Sub2	114	17	0	0	Sub2	111	43	0	0
	Sub3	93	-	-	-	Sub3	64	35	10	28.6
	Sub4	56	-	-	-	Sub4	76	-	-	-
	Sub5	76	35	0	0	Sub5	50	-	-	-
	Sub6	97	34	0	0	Sub6	78	43	0	0
	Sub7	66	43	0	0	Sub7	89	37	0	0
	Sub8	115	22	0	0	Sub8	94	27	0	0
	Sub9	51	102	1	1.0	Sub9	93	32	5	15.6
	Sub10	46	37	0	0	Sub10	82	-	-	-
	Sub11	93	30	8	26.7	Sub11	80	37	3	8.1
	Sub12	88	98	0	0	Sub12	86	20	0	0
			average % overlap:		2.77			average % overlap:		5.81
				sem	2.66				sem	3.38
FFA, VRS (SetA)	Sub1	45	-	-	-	Sub1	43	-	-	-
	Sub2	-	57	-	-	Sub2	14	69	0	0
	Sub3	38	14	0	0	Sub3	42	28	0	0
	Sub4	38	16	0	0	Sub4	60	33	0	0
	Sub5	104	36	0	0	Sub5	84	41	0	0
	Sub6	94	32	0	0	Sub6	46	-	-	-
	Sub7	92	19	0	0	Sub7	58	24	0	0
	Sub8	59	32	0	0	Sub8	48	20	0	0
	Sub9	35	10	0	0	Sub9	95	24	0	0
	Sub10	22	-	-	-	Sub10	37	-	-	-
	Sub11	38	34	0	0	Sub11	102	34	0	0
	Sub12	-	-	-	-	Sub12	50	-	-	-
			average % overlap:		0.00			average % overlap:		0.00
				sem	0.00				+/-	0.00
FFA, VRS (SetB)	Sub1	45	53	0	0	Sub1	43	41	0	0
	Sub2	-	17	-	-	Sub2	14	43	0	0
	Sub3	38	-	-	-	Sub3	42	35	0	0
	Sub4	38	-	-	-	Sub4	60	-	-	-
	Sub5	104	35	0	0	Sub5	84	-	-	-
	Sub6	94	34	1	2.9	Sub6	46	43	0	0
	Sub7	92	43	0	0	Sub7	58	37	0	0
	Sub8	59	22	0	0	Sub8	48	27	0	0
	Sub9	35	102	0	0	Sub9	95	32	0	0
	Sub10	22	37	0	0	Sub10	37	-	-	-
	Sub11	38	30	0	0	Sub11	102	37	0	0
	Sub12	-	98	-	-	Sub12	50	20	0	0
			average % overlap:		0.36			average % overlap:		0.00
				sem	0.36				+/-	0.00
pFs, VRS (SetA)	Sub1	91	-	-	-	Sub1	69	-	-	-
	Sub2	55	57	1	1.8	Sub2	65	69	18	26.1
	Sub3	49	14	6	42.9	Sub3	27	28	8	28.6
	Sub4	36	16	0	0	Sub4	44	33	0	0
	Sub5	68	36	0	0	Sub5	88	41	0	0
	Sub6	78	32	0	0	Sub6	71	-	-	-
	Sub7	75	19	0	0	Sub7	102	24	0	0
	Sub8	78	32	0	0	Sub8	62	20	0	0
	Sub9	51	10	0	0	Sub9	-	24	-	-
	Sub10	49	-	-	-	Sub10	59	-	-	-
	Sub11	75	34	0	0	Sub11	69	34	0	0
	Sub12	-	-	-	-	Sub12	-	-	-	-
			average % overlap:		4.97			average % overlap:		7.81
				sem	4.75				sem	5.05
pFs, VRS (SetB)	Sub1	91	53	0	0	Sub1	69	41	0	0
	Sub2	55	17	0	0	Sub2	65	43	0	0
	Sub3	49	-	-	-	Sub3	27	35	15	42.9
	Sub4	36	-	-	-	Sub4	44	-	-	-
	Sub5	68	35	0	0	Sub5	88	-	-	-
	Sub6	78	34	0	0	Sub6	71	43	0	0
	Sub7	75	43	0	0	Sub7	102	37	0	0
	Sub8	78	22	0	0	Sub8	62	27	0	0
	Sub9	51	102	0	0	Sub9	-	32	-	-
	Sub10	49	37	0	0	Sub10	59	-	-	-
	Sub11	75	30	1	3.3	Sub11	69	37	0	0
	Sub12	-	98	-	-	Sub12	-	20	-	-
			average % overlap:		0.37			average % overlap:		6.13
				sem	0.37				sem	6.13

Supplemental Table 3: Analysis of voxel overlap between the ventral reachspace-preferring region and other classic ventral ROIs.

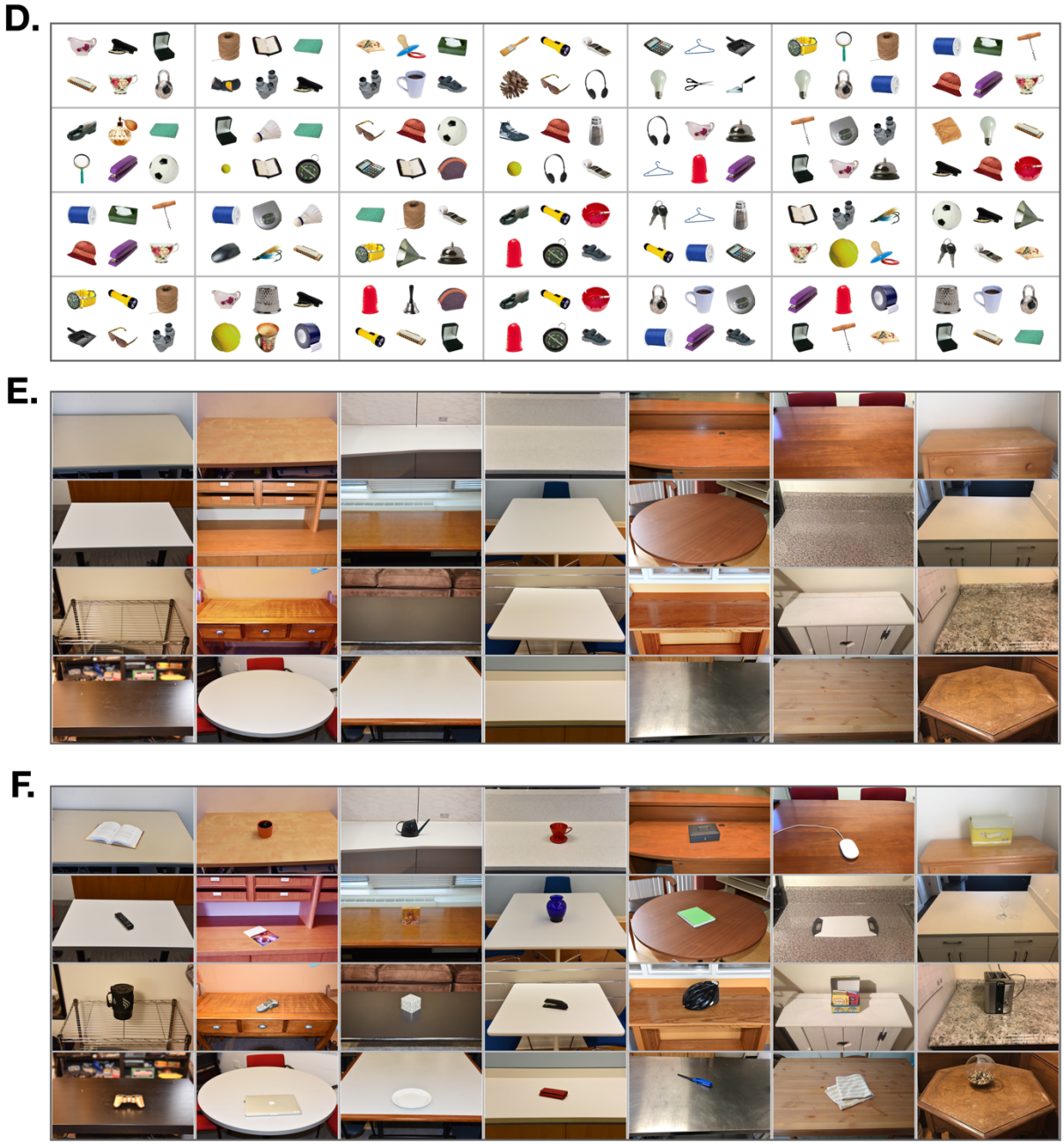
ROIs to compare (ROI1, RIO2)		Left Hemisphere					Right Hemisphere			
		ROI1 size	**ROI2 size**	**overlap**	**overlap percent**		**ROI1 size**	**ROI2 size**	**overlap**	**overlap percent**
OPA, ORS (SetA)	**Sub1**	94	-	-	-	**Sub1**	57	33	0	0
	Sub2	38	28	0	0	**Sub2**	31	20	0	0
	Sub3	80	60	3	5.0	**Sub3**	100	127	27	21.3
	Sub4	-	-	-	-	**Sub4**	-	-	-	-
	Sub5	184	32	2	6.3	**Sub5**	157	27	18	66.7
	Sub6	144	-	-	-	**Sub6**	106	-	-	-
	Sub7	37	-	-	-	**Sub7**	78	-	-	-
	Sub8	80	-	-	-	**Sub8**	89	75	9	12.0
	Sub9	87	40	6	15.0	**Sub9**	102	66	38	57.6
	Sub10	107	-	-	-	**Sub10**	94	-	-	-
	Sub11	89	17	7	41.2	**Sub11**	90	36	3	8.3
	Sub12	67	-	-	-	**Sub12**	72	-	-	-
			average % overlap:		**13.50**			**average % overlap:**		**23.70**
				sem	**7.33**				**sem**	**10.35**
OPA, ORS (SetB)	**Sub1**	94	28	2	7.1	**Sub1**	57	29	0	0
	Sub2	38	11	0	0	**Sub2**	31	22	0	0
	Sub3	80	10	0	0	**Sub3**	100	36	0	0
	Sub4	-	-	-	-	**Sub4**	-	-	-	-
	Sub5	184	66	29	43.9	**Sub5**	157	13	9	69.2
	Sub6	144	-	-	-	**Sub6**	106	11	0	0
	Sub7	37	31	0	0	**Sub7**	78	-	-	-
	Sub8	80	59	10	16.9	**Sub8**	89	26	0	0
	Sub9	87	47	9	19.1	**Sub9**	102	30	14	46.7
	Sub10	107	24	1	4.2	**Sub10**	94	-	-	-
	Sub11	89	14	1	7.1	**Sub11**	90	20	0	0
	Sub12	67	46	0	0	**Sub12**	72	42	0	0
			average % overlap:		**9.83**			**average % overlap:**		**12.88**
				sem	**4.38**				**sem**	**8.72**
LO, ORS (SetA)	**Sub1**	76	0	0	0	**Sub1**	97	33	0	0
	Sub2	78	28	0	0	**Sub2**	130	20	0	0
	Sub3	138	60	16	26.7	**Sub3**	121	127	0	0
	Sub4	-	-	-	-	**Sub4**	-	-	-	-
	Sub5	83	32	0	0	**Sub5**	54	27	0	0
	Sub6	128	-	-	-	**Sub6**	-	-	-	-
	Sub7	214	-	-	-	**Sub7**	187	-	-	-
	Sub8	96	-	-	-	**Sub8**	128	75	0	0
	Sub9	159	40	0	0	**Sub9**	177	66	0	0
	Sub10	84	-	-	-	**Sub10**	104	-	-	-
	Sub11	114	17	0	0	**Sub11**	79	36	0	0
	Sub12	177	-	-	-	**Sub12**	197	-	-	-
			average % overlap:		**4.45**			**average % overlap:**		**0.00**
				sem	**4.45**				**+/-**	**0.00**
LO, ORS (SetB)	**Sub1**	76	28	0	0	**Sub1**	97	29	0	0
	Sub2	78	11	0	0	**Sub2**	130	22	0	0
	Sub3	138	10	1	10.0	**Sub3**	121	36	0	0
	Sub4	-	-	-	-	**Sub4**	-	-	-	-
	Sub5	83	66	0	0	**Sub5**	54	13	0	0
	Sub6	128	-	-	-	**Sub6**	-	11	-	-
	Sub7	214	31	21	67.7	**Sub7**	187	-	-	-
	Sub8	96	59	0	0	**Sub8**	128	26	0	0
	Sub9	159	47	0	0	**Sub9**	177	30	0	0
	Sub10	84	24	0	0	**Sub10**	104	-	-	-
	Sub11	114	14	0	0	**Sub11**	79	20	0	0
	Sub12	177	46	0	0	**Sub12**	197	42	0	0
			average % overlap:		**7.77**			**average % overlap:**		**0.00**
				sem	**6.73**				**sem**	**0.00**
Hand, ORS (SetA)	**Sub1**	38	-	-	-	**Sub1**	67	33	0	0
	Sub2	122	28	0	0	**Sub2**	48	20	0	0
	Sub3	73	60	0	0	**Sub3**	113	127	2	1.6
	Sub4	-	-	-	-	**Sub4**	-	-	-	-
	Sub5	57	32	0	0	**Sub5**	-	27	-	-
	Sub6	54	-	-	-	**Sub6**	53	-	-	-
	Sub7	44	-	-	-	**Sub7**	74	-	-	-
	Sub8	118	-	-	-	**Sub8**	84	75	0	0
	Sub9	63	40	0	0	**Sub9**	114	66	0	0
	Sub10	91	-	-	-	**Sub10**	97	-	-	-
	Sub11	87	17	0	0	**Sub11**	114	36	0	0
	Sub12	51	-	-	-	**Sub12**	97	-	-	-
			average % overlap:		**0.00**			**average % overlap:**		**0.27**
				sem	**0.00**				**sem**	**0.27**
Hand, ORS (SetB)	**Sub1**	38	28	0	0	**Sub1**	67	29	0	0
	Sub2	122	11	0	0	**Sub2**	48	22	0	0
	Sub3	73	10	0	0	**Sub3**	113	36	0	0
	Sub4	-	-	-	-	**Sub4**	-	-	-	-
	Sub5	57	66	0	0	**Sub5**	-	13	-	-
	Sub6	54	-	-	-	**Sub6**	53	11	0	0
	Sub7	44	31	0	0	**Sub7**	74	-	-	-
	Sub8	118	59	0	0	**Sub8**	84	26	0	0
	Sub9	63	47	0	0	**Sub9**	114	30	0	0
	Sub10	91	24	0	0	**Sub10**	97	-	-	-
	Sub11	87	14	0	0	**Sub11**	114	20	0	0
	Sub12	51	46	0	0	**Sub12**	97	42	0	0
			average % overlap:		**0.00**			**average % overlap:**		**0.00**
				sem	**0.00**				**+/-**	**0.00**

Supplemental Table 3: Analysis of voxel overlap between the occipital-partietal reachspace-preferring region and other classic lateral-dorsal ROIs. The superior parietal reachspace region is not shown, as they did not overlap with any ROIs.



Supplemental Figure 5: All Experiment 1 ROIs viewed in single-subjects. The color legend is as follows: yellow for objects, blue for reachspaces, green for scenes, pink for faces, orange for hands.

Supplemental Figure 6, Part 1: Experiment 3 stimuli. A) reachspaces images with the background removed in Photoshop, yielding images of multiple objects in realistic spatial arrangements; B) reachspaces images with background removed and the remaining objects scrambled to disrupt their spatial arrangement; C) 6 objects with large real-world size (e.g. trampoline, dresser) arranged in a 3x2 grid one a white background.

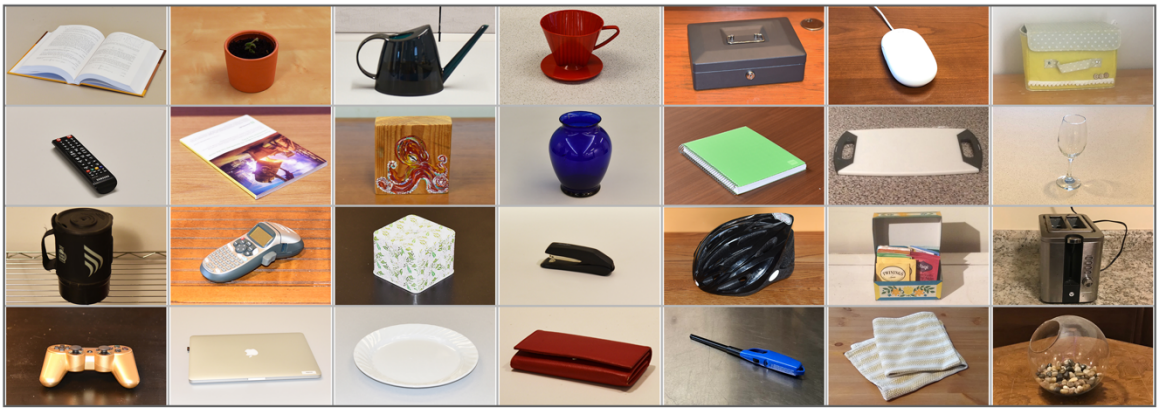


Supplemental Figure 6, Part 2: Experiment 3 stimuli, continued. D) 6 objects with small real world size (e.g. mug, watch) arranged in a 3x2 grid a white background (presented at the same visual size as the large object condition); E) reachable environments with all objects removed except the support surface; F) reachspaces containing only a single object on the support surface.

G.

H.

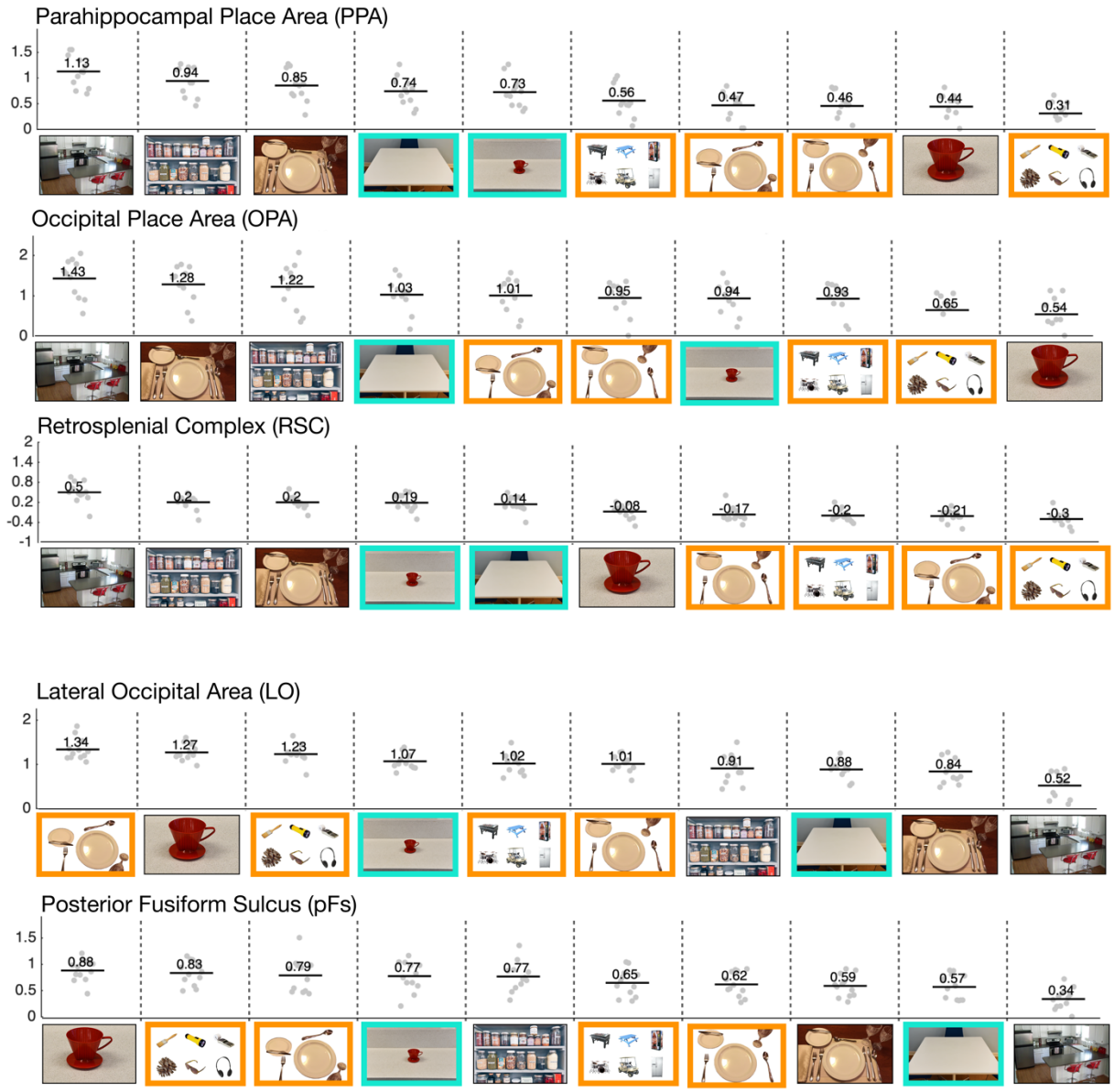
I.



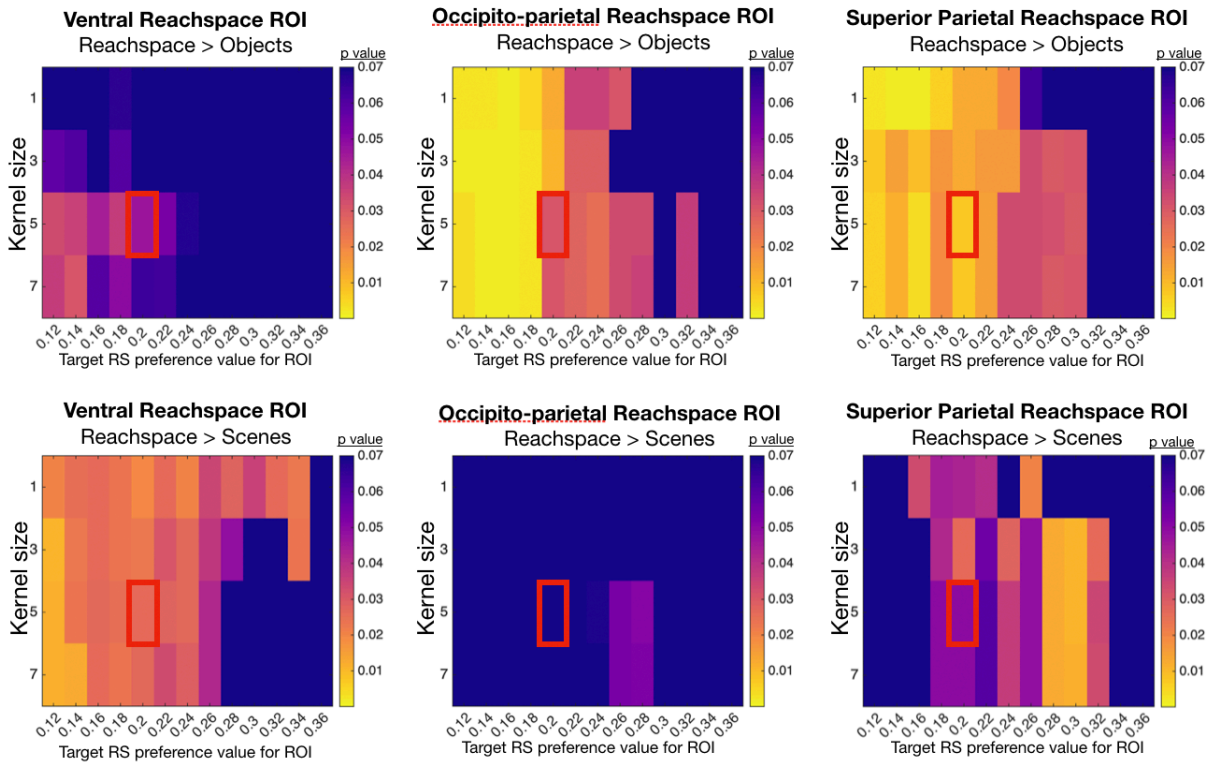
Supplemental Figure 6, Part 3: Experiment 3 stimuli, continued. G) vertical reachspaces, where the disposition of objects was vertical rather than horizontal (e.g. shelves, peg-boards); H) regular (i.e. horizontal) reachspaces; I) objects (i.e. close-up views of single objects on their natural background).

J.

Supplemental Figure 6, Part 4: Experiment 3 stimuli, continued. J) Scene images.



Supplemental Figure 7: Experiment 3 results for scene- and object-selective ROIs. Results for each ROI are sorted from high to low.



Supplemental Figure 8: Visualization of how Experiment 1 results vary as the automatic ROI-selection parameters are varied. For Experiment 2, reachspace-preferring ROIs were selecting using a semi-automatic procedure (see Methods). Parameters such as the size of the smoothing kernel and the reachspace-preference threshold value were determined a priori, based on analyses run in a separate set of data. Results in the main text were extracted from ROIs defined using a 5-voxel smoothing kernel and requiring a reachspace preference of 0.2 betas. Here, we display how the statistics significance of the preference for reachspaces over objects (top row) and scenes (bottom row) would have changed with different parameters. In each graph, the rows vary the size of the smoothing kernels applied to the statistical maps computed from the conjunction contrast RS>O & RS>S, from 1 to 7 voxels. The columns vary the threshold for the beta value of reachspace preference we required of the final ROI, from 0.12 to 0.36. The color in each cell shows the statistical significance of the comparison indicated in the title. The red square shows the cell corresponding to the parameters used in the main text.