Neural specialization for 'visual' concepts emerges in the absence of vision

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Abstract

Vision provides a key source of information about many concepts, including 'living things' (e.g., *tiger*) and visual events (e.g., *sparkle*). According to a prominent theoretical framework, neural specialization for different conceptual categories is driven by sensory features, e.g., living things are neurally dissociable from navigable places because living things concepts depend more on visual features. We tested this framework by comparing the neural basis of 'visual' concepts across sighted (n=22) and congenitally blind (n=21) adults. Participants judged the similarity of words varying in their reliance on vision while undergoing fMRI. We compared neural responses to living things nouns (birds, mammals) and place nouns (natural, manmade). In addition, visual event verbs (e.g., 'sparkle') were compared to non-visual events (sound emission, hand motion, mouth motion). People born blind exhibited distinctive univariate and multivariate responses to living things in a temporo-parietal semantic network activated by nouns, including the dorsal precuneus (PC). To our knowledge, this is the first demonstration that neural selectivity for living things does not require vision. We additionally observed preserved neural signatures of 'visual' light events in the left middle temporal gyrus (LMTG). Across a wide range of semantic types, neural representations of sensory concepts develop independent of sensory experience.

Introduction

An influential view dating back to British empiricism proposes that concepts originate in our first-person sensory experience with the world. John Locke famously argued that a person born blind could never understand 'visual' concepts, such as *rainbow*, based on definition or verbal description alone because, "that definition, how exact and perfect soever, would never make a blind man understand it; because several of the simple ideas that make that complex one, being such as he never received by sensation and experience, no words are able to excite them in his mind" (Locke, 1690). Related theoretical frameworks in psychology and cognitive neuroscience describe that conceptual knowledge originates in sensory representations, and that by extension, the neural basis of concepts is shaped by the sensory modality that was used to acquire them (Barsalou, 1999; Barsalou et al., 2003; Pulvermüller, 1999; Zwaan, 2004; Gallese & Lakoff, 2005). One prediction that emerges from these proposals is that neural specialization for different conceptual categories, e.g., living vs. nonliving things, depends on sensory experience.

Studies of 'visual' concepts in people born blind offer a strong test of the contribution of sensory experience to conceptual representation. Vision is an important source of information about multiple important conceptual categories, including living things (e.g., animals, plants), visual events (e.g., 'sparkle', 'glow'), and colors (Barsalou, 1999; Richter & Zwaan, 2009; Cutsforth, 1932, 1951; Humphreys & Forde, 2001; Striem-Amit et al., 2018). In the case of living things, watching animals such as elephants and blue jays offers information about their shape, color, texture, and behavior. Inspired in part by such observations, classic neuropsychological theories attributed semantic deficits for living things to damaged visual knowledge (Allport, 1985; Warrington & Shallice, 1984; Farah & McClelland, 1991; Gaffan & Heywood, 1993; Moss et al., 1997; Tranel et al., 1997; Martin et al., 2000; cf. Caramazza &

Shelton, 1998; Caramazza & Mahon, 2003). According to these theories, visual features play a privileged role in concepts of living things, and as a result, damage to visual knowledge disproportionately impairs the living things category (Warrington & McCarthy, 1987; Humphreys & Forde, 2001).

Consistent with the idea that vision shapes living things concepts, knowledge of the appearance of living things differs across sighted and congenitally blind people. Semantic similarity judgments about plants (fruits and vegetables) are informed by color knowledge in sighted but not blind participants. By contrast, judgments about tools are indistinguishable across groups (Connolly et al., 2007). Congenitally blind people also disagree with sighted people and with each other about animal colors and rate large animals (e.g., 'bear', 'rhinoceros') as less familiar than sighted people (Kim et al., 2019). Together, this evidence supports the view that sighted people rely on vision to learn about living things.

Some recent neuroimaging studies comparing blind and sighted people appear to support the view that selective neural responses to 'living things' are different or absent in people who are born blind (Mahon et al., 2009; He et al., 2013; Bi et al., 2016). In sighted people, living things (including animals and people) elicit distinct neural responses in ventral occipito-temporal cortices (VOTC) as compared to places (e.g., 'desert') (Kanwisher et al., 1997; O'Craven & Kanwisher, 2000; Grill-Spector et al., 2004; Konkle & Carmazza, 2013; Aguirre et al., 1998; Epstein & Kanwisher, 1998; Weiner et al., 2017). Responses to living things are more lateral and places more medial in VOTC. While place selectivity has been observed in VOTC of blind adults, attempts to identify selective responses to living things have yielded mixed results (Mahon et al., 2009; Wolbers et al., 2011; He et al., 2013; Bi et al., 2016; van den Hurk et al., 2017; Ratan Murty et al., 2020; Mattioni et al., 2020). However, even in sighted people, VOTC

responses to animals and people are observed only for images and not for words (Devlin et al., 2002; Mahon et al., 2009; Lewis et al., 2005; Adam & Noppeney, 2010; He et al., 2013; see Bi et al., 2016 for a review).

In sighted people, modality-independent (i.e., both images and words) but specialized responses to living things are found in temporo-parietal cortex (Fairhall & Caramazza, 2013a; 2013b; Fairhall et al., 2014; Deen & Freiwald, 2022). Specifically, responses to living vs. nonliving things can be decoded using multivariate analyses in precuneus (PC), inferior lateral temporal cortex, and posterior temporo-parietal cortex, and a classifier trained on images generalizes its performance to words, suggesting amodal representations (Fairhall & Caramazza, 2013a; Elli et al., 2019). Selectivity for living vs. nonliving things follows a dorsal-to-ventral gradient in the PC, whereby dorsal portions of the PC exhibit a preference for living things (e.g., people) compared to nonliving things (e.g., places), while the ventral PC prefers nonliving things to living things (Fairhall & Caramazza, 2013b; Fairhall et al., 2014; Deen & Freiwald, 2022). Whether this dorsal specialization for living things requires vision to emerge is not known. We test this question in the current study by comparing neural responses to living things nouns in congenitally blind and sighted adults.

The second ‘visual’ category examined in the current study is light events (e.g., ‘sparkle’). Unlike living things, light events can only be perceived through direct visual experience. Behaviorally, sighted and congenitally blind adults make similar semantic judgments about light events. For example, both groups distinguish light events based on periodicity (flash vs. shine) and intensity (glow vs. shine) (Landau & Gleitman, 1985; Lenci et al., 2013; Bedny et al., 2019). However, the behavioral data leave open the possibility that sighted and blind people provide similar responses to linguistic stimuli while drawing upon different underlying

conceptual representations (e.g., visual vs. verbal representations, respectively). Neural data offer one way to test whether the conceptual representations that support behavior are similar or different across blind and sighted people.

Previous studies with sighted and blind people have implicated the left middle temporal gyrus (LMTG) in representing event concepts. The LMTG responds preferentially to verbs that refer to events, such as ‘run’ and ‘think’, compared to nouns, such as ‘tiger’ and ‘house’ (e.g., Damasio & Tranel, 1993; Martin et al., 1995; Kable et al., 2002; 2005; Noppeney et al., 2003; Davis et al., 2004; Bedny & Thompson-Schill, 2006; Bedny et al., 2012; Elli et al., 2019). The LMTG also responds more to nouns that refer to events (e.g., ‘hurricane’) than nouns that refer to entities (e.g., ‘strawberry’), suggesting that the representations supported by this region are not purely grammatical (Bedny et al., 2014; Lapinskaya et al., 2016). Recent studies have also found that neighboring regions of the temporal lobe respond to abstract features of visually perceived events (e.g., social interaction, intention) and exhibit high cross-modal decoding accuracy for linguistic and visual events (Isik et al., 2017; Wurm & Caramazza, 2019). The LMTG is therefore a hub for event meaning. Here we test whether neural representations of purely visual events (i.e., light emission verbs) in the LMTG develop differently in the absence of vision.

One prior study examined the neural basis of ‘visual’ concepts in blindness, testing ‘visual’ weather/scene words (e.g., ‘rainbow’) and color words (e.g., ‘blue’), and focusing on the anterior temporal lobe (ATL) (Striem-Amit et al., 2018). The results revealed more overlapping responses for ‘visual’ and abstract concepts (e.g., ‘freedom’) in the anterior temporal lobe (ATL) of early blind compared to sighted people. One possible conclusion from these data is that ‘visual’ categories are neurally distinctive in blindness. However, the degree to which these findings apply broadly across the semantic system is unclear. Unlike weather and color words,

living things and events elicit robust and distinctive neural signatures in sighted people, making it possible to test whether the emergence of these signatures depends on vision (e.g., Fairhall & Caramazza, 2013a; Deen & Freiwald, 2022; Bedny et al., 2014; Elli et al., 2019). Together, living things and light events also span a wide range of conceptual types. Animals are concrete entities situated in space and encoded in most languages by nouns, while light emission events are situated in time and encoded in most languages by verbs (Talmy, 1975; Langacker, 1987; Frawley, 1992). By testing these specific yet diverse semantic types, we offer a broad perspective on the contribution of vision to the neural instantiation of concepts.

In the current study, we used individual-subject univariate and multivariate approaches to compare neural representations of 'visual' categories across sighted and congenitally blind people. We first localized brain regions that exhibited a preference for entities vs. events in individual participants. Within entity- and event-preferring networks, we compared 'visual' categories to non-visual control categories, i.e., conceptual types from the same class (entity or event) for which vision is thought to play a less important role. Congenitally blind and sighted participants performed semantic similarity judgments on words from four entity/noun categories (living: birds, mammals; nonliving: manmade places, natural places) and four event/verb categories (visual: light, nonvisual: sound, hand action, mouth action). Using place nouns as our nonliving things category additionally enabled us to test for previously documented place selectivity in the medial VOTC of blind and sighted people (i.e., parahippocampal place area (PPA); Epstein & Kanwisher, 1998; Wolbers et al., 2011; He et al., 2013; van den Hurk et al., 2017; Mattioni et al., 2020).

A secondary goal of the current study was to examine responses to spoken words in the visual cortices of sighted and congenitally blind adults. Prior studies find responses to sentences

and words in occipital cortices of congenitally blind people and to some degree even sighted people (Röder et al., 2002; Amedi et al., 2003; Bedny et al., 2011; Lane et al., 2015; Kanjlia et al., 2016; Bola et al., 2017; Seydell-Greenwald et al., 2020). We used univariate and multivariate methods to test the sensitivity of visual cortices to word meanings in both populations.

Methods

Participants

Twenty-one congenitally blind adults (13 females, age range 18-67 years, M = 39.14 ± 13.81 SD) and twenty-two sighted age and education matched controls (16 females, age range: 19-62 years, M = 37.55 ± 13.25 SD) participated in the experiment (Supplementary Table 1). Blind participants lost their sight due to pathologies of the eyes or optic nerve, anterior to the optic chiasm (i.e., not due to brain damage), and had at most minimal light perception since birth. Throughout the experiment, all participants (sighted and blind) wore a light exclusion blindfold to match their visual input. Sighted and blind participants were screened for cognitive and neurological disabilities (self-report). Participants gave written informed consent and were compensated $30 per hour. The study was reviewed and approved by the Johns Hopkins Medicine Institutional Review Boards.

Four additional blind participants were scanned but excluded from the final sample because they were older than 70 years of age (n=2), they were not blind since birth (n=1), or they gave similarity judgments different from those of the group (n=1, correlation with the group lower than 2.5 SDs from the average for both verbs and nouns).

Stimuli and procedure

While undergoing functional magnetic resonance imaging (fMRI), participants heard pairs of words and judged how similar the two words were in meaning on a scale from 1 (not at all similar) to 4 (very similar), indicating their responses via button press. Word stimuli consisted of 18 words in each of 8 semantic categories (Figure 1, Supplementary Table 2, see Appendix 1 for full list of stimuli): 4 categories of entities/nouns (birds, e.g., 'the crow'; mammals, e.g., 'the fox'; manmade places, e.g., 'the barn'; natural places, e.g., 'the swamp'), and 4 categories of events/verbs (light emission, e.g., 'to sparkle'; sound emission, e.g., 'to squeak'; hand-related actions, e.g., 'to pluck', mouth-related actions, e.g., 'to bite'). Word pairs were presented in blocks of 4 and were grouped by semantic category within blocks. Each word appeared only once within a block. Blocks were 16 s long and were separated by 10 s of rest. The experiment included a total of 144 blocks evenly divided into 8 runs.

The word stimuli for the current study were previously validated in a separate experiment with sighted participants (Elli et al., 2019) and are described in detail there. Here we reiterate essential points for clarity. Words were matched across semantic categories in syllable length (based on the CMU Pronouncing Dictionary; Weide, 1998), phonological neighborhood size (using N-Watch; Davis, 2005), familiarity, and concreteness based on ratings collected on Amazon Mechanical Turk (AMT). We did not match nouns and verbs on imageability. Verbs are inherently less imageable than nouns (Bird et al., 2001; 2003). Matching them would therefore result in unrepresentative class members and make it impossible to study the most 'visual' nouns (living things) and verbs (light emission), which was the goal of the current study. A separate group of AMT participants also rated all possible pairs of words in the experiment according to their semantic similarity to verify that entities/nouns and events/verbs did not differ from each other in their overall semantic distance (Elli et al., 2019).

To facilitate MVPA decoding analyses, we created two non-overlapping subsets of words that were exclusively presented in either even or odd runs. This enabled us to train the classifier on one set of words and test it on a different set of words, ensuring that any above-chance classification effects reflect differences in the neural patterns associated with semantic categories and not word forms. For instance, the classifier trained to distinguish 'glow' from 'bang' was then tested on its ability to distinguish 'sparkle' from 'boom.' Words in each semantic category were divided into two non-overlapping sets of 9 words. Within each set, we created all the possible pairs within a category (e.g., 'the seagull – the parrot', 36 pairs per set per category). There were no cross-category pairs.

Behavioral data analysis

Due to a response box malfunction, 19/21 blind and 19/22 sighted participants contributed to behavioral data analysis. In-scanner similarity judgments were first standardized (z-scored to mean=0 ± 1SD) within each participant to account for individual differences in Likert scale use, and then standardized within grammatical class (i.e., events/verbs, entities/nouns) to a [0,1] range (i.e., $x = \frac{x - x_{min}}{x_{max} - x_{min}}$).

To assess agreement in semantic judgments across blind and sighted groups, we correlated item-wise ratings within each semantic category using Spearman's rho (ρ) rank correlations. This analysis asks whether blind and sighted participants agree regarding which pairs within a semantic category are most similar in meaning. To compare group agreement across semantic categories, we averaged ratings for a given pair across participants within a group and then correlated ratings across groups. To measure the variability among participants within groups, we computed within-group coherence (i.e., the agreement among blind and

among sighted participants) by correlating each participant to their group mean in a leave-one-participant-out correlation procedure (i.e., $\rho = \mathrm{corr}(s_i, N - s_i)$). We tested whether blind and sighted groups differed across semantic categories in within-group coherence using two-tailed independent samples Student's t-tests and ANOVAs on Fisher-Z transformed single-subjects' ρ values. All Spearman's rank correlations were computed on participants' standardized ratings using the Hmisc package in R (Harrell & Dupont, 2014).

fMRI data acquisition

MRI structural and functional data of the whole brain were collected using a 3 Tesla Phillips scanner with a 32-channel head coil. We collected T1-weighted 3D-MPRAGE structural images using a pulse sequence in 170 sagittal slices with 1mm isotropic voxels (TE/TR=7.0/3.2ms, FoV=240x240 mm, 288x272 acquisition matrix, scan duration=5:59'). We collected T2*-functional BOLD images using parallel transverse ascending echo planar imaging (EPI) sequences in 36 axial slices with 2.5 x 2.5 x 2.5 mm voxels (TE/TR=30/2000ms, FoV=192x172mm, 76x66 acquisition matrix, 0.5mm gap, flip angle=70º, scan duration=8:04').

fMRI data analysis

Univariate analysis

Prior to preprocessing and analyzing the data, we trimmed the first 4 TRs of runs 6-8 in one congenitally blind participant (CB_24). This was necessary to remove a sharp, abrupt movement at the beginning of the runs that prevented the correct alignment of structural and functional images.

Data were analyzed using FSL, Freesurfer, the Human Connectome Project workbench, and custom in-house software written in Python (Dale, Fischl, & Sereno, 1999; Smith et al.,

2004; Glasser et al., 2013). Functional data were motion corrected using FSL's MCFLIRT algorithm (Jenkinson et al., 2002), high pass filtered to remove signal fluctuations at frequencies longer than 128 seconds/cycle, mapped to the cortical surface using Freesurfer, spatially smoothed on the cortical surface (6mm FWHM Gaussian kernel), and prewhitened to remove temporal autocorrelation. Covariates of no interest were included to account for confounds related to white matter, cerebral spinal fluid, and motion spikes.

Each of the noun and verb categories was entered as a separate predictor in a general linear model (GLM) after convolving with a canonical hemodynamic response function and its first temporal derivative. Each run was modeled separately, and runs were combined within-subject using a fixed-effects model (Dale et al., 1999; Smith et al., 2004). Group-level random-effects analyses were cluster-corrected at $p<0.01$ family-wise error rate (FWER) using a nonparametric permutation test.

ROI definition

We defined individual subjects' functional ROIs in a three-step procedure. First, we defined group-level search spaces based on each group's whole-brain results for the verbs vs. nouns contrast in the left hemisphere. Then, we merged the search spaces defined in the blind and sighted groups to create group-unbiased search spaces encompassing the activation observed in both group maps. Finally, individual ROIs were defined for each subject by selecting in each search space the top 300 active vertices for the verbs>nouns (verb ROI) or nouns>verbs (noun ROIs) contrasts.

For each participant, we defined four entity-responsive ROIs (nouns>verbs) in the left precuneus (LPC), left inferior parietal lobule (LIP), left lateral inferior temporal cortex (LlatIT),

and left medial ventral temporal cortex (LmedVT), and one event-responsive ROI (verbs>nouns) in the left middle temporal gyrus, which extended in the superior temporal gyrus and inferior aspect of the parietal cortex (LMTG+). We selected these regions because they exhibited greater activation for either verbs or nouns in univariate analysis and were found to respond more to event or entity words in previous studies (see Crepaldi et al., 2013, for a review). Although the left inferior frontal gyrus also responded more to verbs than nouns, we previously found that it showed weak and category-invariant decoding in sighted adults (Elli et al., 2019). Therefore, we did not use this ROI in the current study.

Following past work demonstrating occipital activation during language processing in blind individuals (Röder et al., 2002; Amedi et al., 2003; Bedny et al., 2011, 2012, 2015; Lane et al., 2015), we defined in each participant two ROIs in occipital cortex: left and right V1-V2 (BA17-18) from the PALS-B12 Brodmann area atlas included in FreeSurfer (Van Essen, 2005).

MVPA ROI analysis

We used MVPA (PyMVPA toolbox; Hanke et al., 2009) to assess the extent to which patterns of activity in entity- and event-responsive ROIs encode differences in semantic category within each grammatical class.

For each ROI in each participant, we trained a linear support vector machine (SVM) classifier to separately decode among the 4 verb categories and the 4 noun categories (chance 25%). We obtained the z-scored beta parameter of the GLM associated with each vertex for each semantic category in each run (2 grammatical classes * 4 categories per class = 8 total observations per run). To eliminate run effects, we then normalized (mean=0, SD=1) the z-scored beta values assigned to each vertex with respect to the mean signal for that vertex across

all 8 semantic categories. This normalization procedure was carried out separately within each run, before restricting the dataset to either the verb or the noun categories, depending on the analysis (i.e., MVPA for verb and noun categories was conducted separately).

We used a two-folds (even/odd) cross-validation split: the classifier was trained on half of the data (e.g., even runs) and tested on the other half (e.g., odd runs). Classification accuracy was then averaged across the two even/odd splits. Note that since even and odd runs contained different verb and noun pairs, the classifier was trained and tested on different, non-overlapping subsets of words.

Within each of the entity- and event-responsive ROIs, we used one-tailed Student's t-tests to test the classifier's accuracy against chance (25%), and two-tailed independent samples Student's t-test to compare the accuracy for verbs and nouns. We used repeated measures ANOVAs to test for interactions between groups, ROIs, and grammatical class (nouns/verbs). We evaluated significance using a combined permutation and bootstrapping approach (Schreiber & Krekelberg, 2013; Stelzer, Chen, & Turner, 2013). In this approach, t- and F-statistics obtained for the observed data are compared against an empirically generated null distribution of statistical values for each test (see Elli et al., 2019 for details on the permutation testing and bootstrapping steps). We report the t- and F-values obtained for the observed data and the nonparametric permuted P-values, which correspond to the proportion of shuffled analyses that generated comparable or higher t/F values. The same approach was used to assess the statistical significance of decoding accuracies within the two occipital ROIs.

Next, to evaluate how well the classifier performed on pairwise distinctions among verbs and among nouns (e.g., birds vs. mammals), we inspected the confusion matrices generated by the classifier. The confusion matrices yield the classification and misclassification frequencies

for any pair of categories, which can be compared using a signal detection theory framework (Swets, Tanner Jr, & Birdsall, 1961; Green & Swets, 1966; Haxby, Connolly, & Guntupalli, 2014). Within each ROI, we assessed the discriminability between 1) living things vs. place nouns across the entity-responsive network and 2) light verbs vs. all other verb categories in the LMTG by computing the nonparametric estimate of discriminability (Pollack & Norman, 1964; Grier, 1971; Stanislaw & Todorov, 1999). An A′ of 0.5 corresponds to chance performance, whereas 1.0 indicates perfect discriminability. Because A′ values did not follow a normal distribution, we used one-sample Wilcoxon signed rank tests to compare A′ values to chance performance, and a repeated measures permutation ANOVA (5,000 permutations) using the permuco package in R (Frossard & Renaud, 2021) to test for interactions between groups, ROIs, and classification error type in entity-responsive brain regions.

Results

Behavioral results

The similarity judgments of the blind and sighted people were significantly correlated across groups for every semantic category, but some categories were more similar across groups than others (Figure 1). Correlations across groups were highest for mouth verbs (ρ^2=0.87), and lowest for birds (ρ^2=0.37) and mammals (ρ^2=0.47). When we measured coherence among individuals within a group, we likewise observed some between-group differences. An ANOVA comparing within-group agreement revealed a semantic category by group interaction, whereby blind and sighted participants' judgments differed more within-group for some semantic categories compared to others (Figure 2, nouns group x noun semantic category interaction, $F_{(3,111)}$=3.47, $p<0.02$; group x verb semantic category interaction $F_{(3,111)}$=2.79, p=0.04). Specifically, there was

lower agreement for birds and mammals among blind than sighted people (birds: blind $\rho=0.19 \pm 0.18$ SD; sighted $\rho=0.44 \pm 0.19$; mammals: blind $\rho=0.38 \pm 0.22$; sighted $\rho=0.62 \pm 0.14$).

Birds and mammals were also the categories for which there was the largest difference in average similarity judgments between blind and sighted people. That is, people born blind tended to rate birds and mammals as more similar to each other than people who are sighted (marginal group x semantic category interaction, $F_{(3,111)}=2.58$, $p=0.06$). Relative to the sighted, blind participants also provided higher noun similarity ratings overall (Supplementary Figure 1A; repeated measures ANOVA, 2 groups (sighted, blind) x 4 noun semantic categories (birds, mammals, manmade pl., natural pl.): main effect of group, $F_{(1,37)}=7.46$, $p=0.01$). There were no group effects or group by condition interactions in reaction time data (Supplementary Figure 1B; see Appendix 2 for details). These results are consistent with the notion that vision influences within category semantic similarity judgments for living things.

fMRI results

Selective responses to living things (birds and mammals) in dorsal precuneus do not require visual experience

Both groups exhibited preferential univariate responses to nouns over verbs in parietal and temporal regions previously associated with concrete entities, including the posterior parietal, lateral inferior temporal, and medial occipito-temporal cortices as well as the precuneus (Supplementary Figure 2). MVPA revealed that living things were decodable from places throughout this entity-responsive network in both sighted and blind participants, including in the PC (sighted: $V = 210$, $p = 0.00005$, blind: $V = 173$, $p = 0.0009$). Inspection of the confusion matrices showed that in both groups, birds were more likely to be confused with mammals than with places (repeated measures ANOVA, 2 groups (sighted, blind) x 2 error types (bird-mammal,

bird-place) x 4 ROIs (LPC, LIP, LlatIT, LmedVT): main effect of error type $F_{(1,41)}$=32.04, permuted p = 0.0002), although this effect was smaller in the blind than in the sighted (error type x group interaction $F_{(1,41)}$=10.60, permuted p = 0.003). This result confirms the robust dissociation of living things within the entity-responsive network of blind people.

The whole-brain univariate contrast between living things and nonliving things revealed that living things (birds and mammals) activated a dorsal sub-region of the PC in both sighted and blind participants (Figure 3A sighted; B blind). The dorsal 'living things' response observed in the blind group overlapped with previously reported responses to living things in dorsal PC of sighted participants (Fairhall et al., 2014). This result suggests that the emergence of a preferential response to living things in the dorsal PC does not require visual experience.

Consistent with prior findings, preferential responses to place nouns were observed in an inferior portion of PC in sighted participants and emerged in the same location at a more lenient statistical threshold in the blind group ($p<0.01$, uncorrected). This inferior PC region overlaps with the location of the retrosplenial cortex, part of the 'place' processing network (Ino et al., 2002; Rauchs et al., 2008; Epstein, 2008). In both groups, preferential responses to places were also observed in medial VOTC, near but somewhat anterior to the canonical location of the parahippocampal place area (PPA) (Weiner et al., 2017). PPA-like activation in the blind group extended posteriorly into early visual cortices. The same medial VOTC region showed a larger preference for places over living things in the sighted group relative to the blind group (group-by-condition interaction, Figure 6B). The only other group-by-condition interaction for the living things vs. places contrast was observed in early visual areas and is discussed in detail below.

Responses to visual 'sparkle' verbs in LMTG are similar across blind and sighted people

A univariate whole-brain analysis revealed a preference for verbs over nouns in left middle temporal gyrus (LMTG) of blind and sighted participants (Figure 4). We used individual-subject ROI analysis to compare LMTG responses to 'visual' light emission verbs and other verb categories across groups. Light verbs elicited a similar degree of activation across blind and sighted groups in the LMTG (Figure 4; repeated measures ANOVA, 2 groups (sighted, blind) x 4 verb categories (hand, mouth, light, sound): group x verb category interaction, $F_{(3,123)}=1.14$, $p=0.34$; main effect of group, $F_{(3,123)}=0.06$, $p=0.81$; main effect of semantic category, $F_{(3,123)}=7.16$, $p<0.001$). This result suggests that univariate responses to 'visual' and other verbs in the LMTG are not affected by visual experience.

Consistent with the idea that the LMTG is sensitive to fine-grained semantic and/or grammatical distinctions among verbs, multivariate patterns of activity in LMTG distinguished between semantic categories of verbs in blind ($t_{(20)}=3.91$, permuted $p=0.0004$) and sighted ($t_{(21)}=3.88$, permuted $p=0.0003$) participants. There were no differences in decoding accuracy between the groups (repeated measures ANOVA, 2 groups (sighted, blind): main effect of group, $F_{(3,123)}=0.94$, $p=0.34$; Supplementary Figure 4). In the blind group, the LMTG was the only region that showed higher decoding for verbs than nouns ($t_{(20)}=-2.68$, permuted $p=0.01$). In the sighted, decoding for verbs and nouns was not different in the LMTG ($t_{(21)}=-0.28$, permuted $p=0.78$), whereas it was higher for nouns in LPC and LmedVT (Supplementary Figure 4; Supplementary Table 4). To verify that the decoding pattern of the LMTG was significantly different from that of the other ROIs, a 3-way repeated measures ANOVA was used to test for an ROI by grammatical category interaction (2 groups (sighted, blind) x 5 ROIs (LMTG, LPC, LIP, LlatIT, LmedVT) x 2 grammatical classes (entities/nouns, events/verbs)). The ANOVA revealed an ROI x grammatical class interaction but no 3-way interaction with group (two-way ROI x

grammatical class interaction, $F_{(4,164)}=6.40$, permuted $p<0.0001$; 3-way interaction $F_{(4,164)}=1.31$, permuted $p=0.26$). This analysis thus confirms that verbs and nouns are decodable to different degrees across regions and that this pattern is similar across blind and sighted groups.

Next, we compared classifier error patterns to probe the 'representational space' of the LMTG across groups. Consistent with the idea that the LMTG of blind and sighted people shares a similar representational space, the confusion matrices for the blind and sighted groups were significantly correlated (Figure 5B; $r(30)=0.55$, $p=0.03$). This correlation suggests the same verb categories that are more similar and thus more confusable for the sighted group are also more similar and more confusable for the blind group.

Finally, we examined the classification of visual verbs separately. We found that light verbs could be distinguished from hand verbs (blind: $V = 158$, $p = 0.0009$, sighted: $V = 170$, $p = 0.0001$) in both groups. In the blind group, light verbs were also distinguishable from both sound verbs ($V = 92$, $p = 0.007$) and mouth verbs ($V = 127$, $p = 0.009$). In the sighted group, light verbs were not distinguishable from sound verbs ($V = 86$, $p = 0.65$) and were marginally distinguishable from mouth verbs ($V = 113$, $p = 0.046$). Together, these results suggest that visual verbs are distinguishable from other verb categories in the LMTG of both blind and sighted people.

Differences in responses to words in occipital networks of blind and sighted people

Group differences in univariate responses to verbs vs. nouns emerged exclusively within occipital cortices. On the medial, ventral, and dorsal surfaces of the occipital pole, particularly in the right hemisphere, sighted participants exhibited greater deactivation for nouns compared to verbs, whereas blind participants exhibited equivalent above-baseline activity for both nouns and

verbs (Figure 6A). Group differences in univariate responses to living things vs. places also emerged in occipital cortices. On the medial, ventral, and dorsal surfaces of the left occipital pole, blind participants exhibited increased responses to places over living things, with above baseline responses to both word types, whereas sighted participants exhibited deactivation for both living things and places (Figure 6B). As discussed above, a small region in the medial VOTC also showed a larger preference for places in the sighted. These results suggest that unlike frontal, temporal and parietal cortices, occipital cortices do not show similar word category preferences across blind and sighted groups. The same occipital areas that 'prefer' place words in the blind group show greater deactivation for places in the sighted, while the same areas that show deactivation for entities in the sighted show above rest responses to both entities and events in the blind. Furthermore, sighted participants showed systematic deactivation in occipital areas (e.g., for entities) but no above-rest activity for any word category. By contrast, several early occipital areas showed above-rest responses to entities and events in the blind group.

Multivariate ROI analysis revealed weak decoding among entities and among events in visual cortices in both groups (Supplementary Figure 6). In low-level visual regions defined using a Brodmann area atlas (V1-V2; BA17-18), we observed above-chance decoding in the right hemisphere of blind participants (noun categories: $t_{(20)}$=2.51, permuted p=0.009; verb categories: $t_{(20)}$=2.33, permuted p=0.01) and marginal decoding in the left hemisphere of sighted participants for nouns (noun categories: $t_{(21)}$=1.56, permuted p=0.07, verb categories: $t_{(20)}$=0.45, permuted p=0.34). Despite above-rest univariate responses to verbs and nouns in early visual

cortices of blind people, these regions do not appear to robustly encode finer-grained distinctions among semantic categories in either the blind or the sighted.

Discussion

Preserved specialization for living things in semantic network of people born blind

Vision offers an important source of information about living things (Allport, 1985; Warrington & Shallice, 1984; Farah & McClelland, 1991; Gaffan & Heywood, 1993; Moss et al., 1997; Tranel et al., 1997; Martin et al., 2000; Warrington & McCarthy, 1987; Humphreys & Forde, 2001). Consistent with this idea, we found that within-category semantic similarity judgments for birds and mammals (e.g., 'crow' vs. 'dove') differed between blind and sighted people, more so than judgments about places (e.g., 'swamp' vs. 'bay'). For birds in particular, blind and sighted judgments were least correlated, and blind participants provided numerically higher similarity ratings for this category compared to sighted participants. The somewhat collapsed nature of blind individuals' similarity ratings for birds suggests that the sighted population we studied uses information about visual appearance when judging bird similarities. This finding is consistent with prior evidence that sighted adults living in industrialized societies rely heavily on surface-level information (e.g., visual appearance) when making within category similarity judgments about living things. By contrast, experts and members of cultural groups that live in closer contact with nature tend to rely more on abstract causal information, such as behavioral and ecological patterns (Boster & Johnson, 1989; López et al., 1997; Proffitt, Coley, Medin, 2000; Bailenson et al., 2002; Medin & Atran, 2004). Therefore, we might predict more similar judgments among blind and sighted bird experts.

Despite behavioral differences among sighted and blind adults, we observed robust neural specialization for living things in congenitally blind adults. Multivariate analysis revealed that spatial patterns of activity for living things and places were distinguishable in both groups throughout a network of entity-responsive regions, including left precuneus (PC), inferior parietal lobule (LIP), lateral inferior temporal cortex (LlatIT), and medial ventral temporal cortex (LmedVT). These results parallel findings from past studies with sighted adults (Fairhall et al., 2014; Elli et al., 2019). In univariate analysis, selective responses to living things emerged in the dorsal PC of both blind and sighted participants. The dorsal PC has previously been implicated in the representation of living things, particularly people-related concepts (Fairhall & Caramazza, 2013a; 2013b; Fairhall et al., 2014; Deen & Freiwald, 2022). Together, our findings suggest that neurally dissociable responses to living things emerge independent of vision.

Unlike in the current study, prior work with blind adults failed to find selectivity for living things. However, as noted in the introduction, these past studies focused on responses in ventral occipito-temporal cortex (VOTC) (Mahon et al., 2009; He et al., 2013; Bi et al., 2016; van den Hurk et al., 2017; Mattioni et al., 2020). Even in sighted people, selective responses to living things in VOTC have almost exclusively been observed during image viewing (see Bi et al., 2016 for a review). One explanation for this pattern of results is that the VOTC represents form-based visual information relevant to visual recognition of categories such as human faces, animals, and scenes (Levy et al., 2001; Hasson et al., 2002; Arcaro et al., 2009; Rajimehr et al., 2011; Nasr et al., 2014; Long et al., 2018). In contrast, the temporal-parietal entity-responsive networks observed in the present study, including the PC, are thought to represent abstract conceptual information. Our results demonstrate that neural specialization for living things in higher-order conceptual networks is present in people born blind. We therefore conclude that,

contrary to previous claims, the development of neural specialization for living things does not require visual experience.

As in past experiments, we also observed a PPA-like response to place nouns in the medial VOTC of both sighted and blind people (Wolbers et al., 2011; He et al., 2013; van den Hurk et al., 2017; Mattioni et al., 2020). This finding corroborates past work with blind individuals, suggesting that specialized responses to places in the VOTC emerge independent of vision. In the sighted group, this PPA-like response was located anterior to the 'perceptual' PPA response typically found for images of places and was therefore consistent with anterior conceptual/memory-related responses observed for place words in previous studies (Fairhall et al., 2014; Häusler et al., 2022; see also Baldassano et al., 2013; Silson et al., 2016). In the blind group, the medial VOTC place response was more spatially distributed and variable across participants, extending into posterior occipital cortex. An open question is whether PPA-like responses in people born blind encode conceptual or perceptual information.

In summary, the emergence of similar neural signatures of living things and places in sighted and congenitally blind individuals suggests that neural specialization for these categories does not depend on visual experience.

Preserved responses to light events in LMTG of people born blind

Unlike many other conceptual categories, light events (e.g., 'sparkle', 'glow') can be perceived only through the visual modality. Despite this, we observed similar neural responses to light emission verbs among sighted and congenitally blind adults. In both blind and sighted people, 'visual' light emission verbs elicited higher activity compared to nouns and a similar level of activity when compared to sound emission and hand/mouth action verbs in the LMTG. Many

prior studies have implicated the LMTG in the comprehension of words that refer to events, including action verbs (e.g., ‘run’) as well as event nouns (e.g., ‘hurricane’) and mental state verbs (Martin et al., 1995; Damasio & Tranel, 1993; Kable et al., 2002; 2005; Davis et al., 2004; Bedny & Thompson-Schill, 2006; Bedny et al., 2014). In the current study, activity patterns in the LMTG of blind adults also distinguished light verbs from other verb categories, including sound emission verbs (e.g., ‘squeak’) and hand/mouth action verbs (e.g., ‘pluck’, ‘bite’).

These results are consistent with prior evidence for preserved neural representations of motion verbs in the LMTG of congenitally blind individuals (Noppeney et al., 2003; Bedny et al., 2012) and point to the amodal nature of event representations in the LMTG (for discussion see Martin et al., 1995; Kable et al., 2002; Tranel et al., 2003; Kemmerer et al., 2008; Noppeney, 2008; Pulvermüller & Fadiga, 2010; Kemmerer & Gonzalez-Castillo, 2010). It remains possible that sighted individuals activate visual representations when thinking about light emission verbs under certain task conditions. However, the LMTG does not appear to store such representations. The presence of similar neural signatures of light emission verbs among blind and sighted adults is consistent with the observation that both groups provide highly similar behavioral judgments for light emission verbs, as reported in this and prior work (Lenci et al., 2013; Bedny et al., 2019). Moving beyond the prior literature, the current results suggest that these similar behavioral judgments are also supported by similar underlying neural machinery.

Our findings do not rule out the possibility that there are neural differences for some categories not tested here. As noted in the introduction, one previous study reported that for blind people color and visual weather (e.g., ‘rainbow’) words elicit neural signatures more characteristic of abstract than concrete nouns in the anterior temporal lobe (ATL) (Striem-Amit et al., 2018). The semantic networks studied in the current study do not show a clear dissociation

between concrete and abstract words, and we did not include abstract words as stimuli in the current study. However, our evidence suggests that for a broad range of semantic types, from concrete entities to visual events, neural representations are invariant to large scale changes in sensory experience.

Occipital plasticity in congenitally blind adults

In the current study, occipital cortices exhibited the largest group differences, both in terms of baseline activation levels and the direction of category-specific effects. The same left dorsal and ventral occipital regions that showed a preference for place nouns in the blind group were deactivated by both living things and places in the sighted. Additionally, the dorsal, ventral, and medial surfaces of the occipital pole were deactivated more for entities than events in sighted individuals, whereas the same regions showed equivalent above-baseline activity for both entities and events in the blind. These univariate differences are consistent with prior evidence for functional reorganization in the occipital cortices of people born blind (e.g., Röder et al., 2002; Bedny et al., 2011; Collignon et al., 2013; see Pascual-Leone et al., 2005; Merabet & Pascual-Leone, 2010; Bedny, 2017 for reviews). They also suggest that at a coarse spatial scale, there are differences in neural responses to entity and event words in the occipital cortices of both blind and sighted people. The direction of these effects differs across groups, and in sighted people these differences reflect deactivation below rest.

Despite the above-baseline activity for nouns and verbs observed in blind occipital cortex, multivariate decoding of more fine-grained semantic distinctions among entity and event categories revealed weak decoding in low-level ‘visual’ cortices of blind people. This was in contrast to the robust decoding we observed in fronto-temporal semantic networks of both groups. One prior study found that TMS stimulation applied to the occipital pole impairs verb

generation in people born blind, inducing mostly semantic errors (Amedi et al., 2004). It is possible that conceptual representations are more spatially diffuse and/or less systematic in occipital cortices of blind people, leading to weaker decoding. Another possibility is that occipital cortex contributes to sentence-level rather than word-level processing in blindness (Lane et al., 2015; Kanjlia et al., 2016; Loiotile et al., 2020). Whether occipital networks of blind adults are behaviorally relevant in language tasks is an open question that requires further investigation (see Siuda-Krzywicka et al., 2016 for an example of a related approach with sighted individuals).

Conclusion

To our knowledge, the current study is the first to demonstrate that neural selectivity for living things develops in the absence of visual experience. We also find that purely visual semantic categories (e.g., ‘sparkle’) elicit similar neural signatures across blind and sighted people. For a wide range of seemingly sensory conceptual categories, distinctive neural signatures develop independent of sensory experience.

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Figures

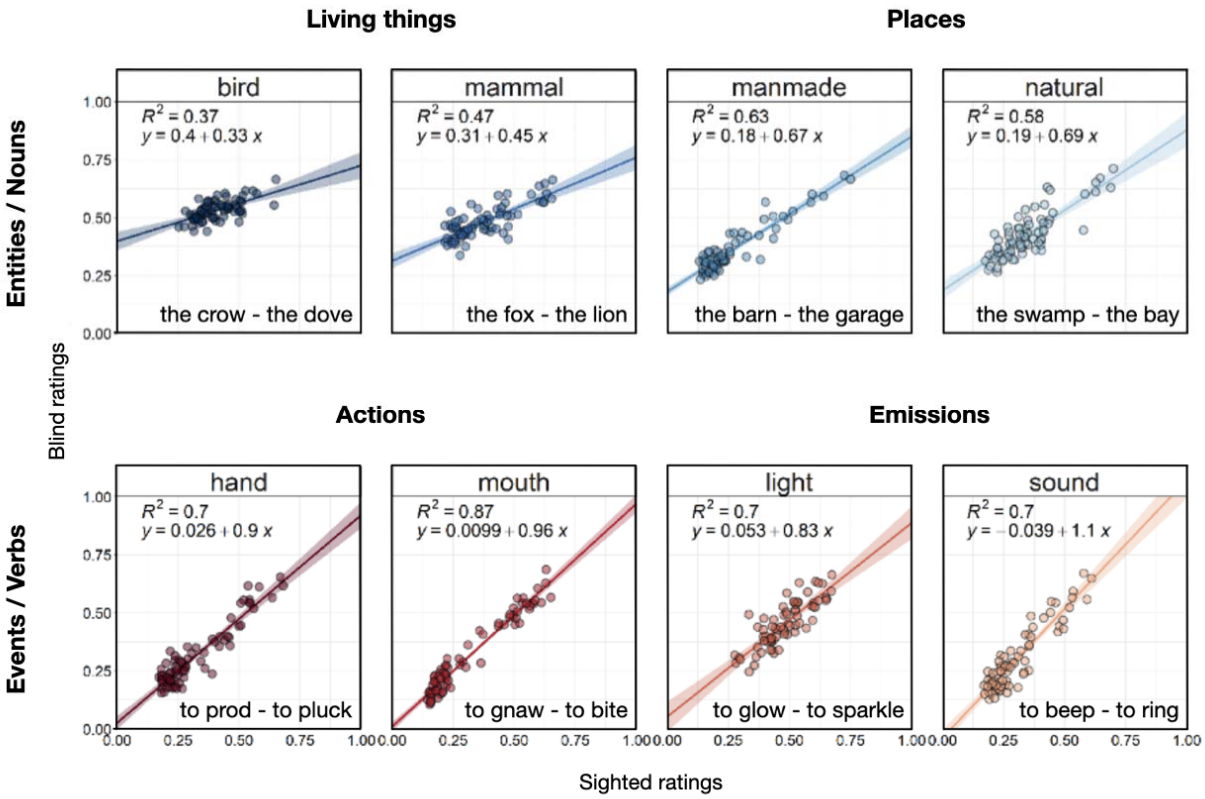

Figure 1: Item-wise correlations (Spearman's rho ρ) between blind and sighted average group ratings. Confidence intervals (95%) are indicated via shading.

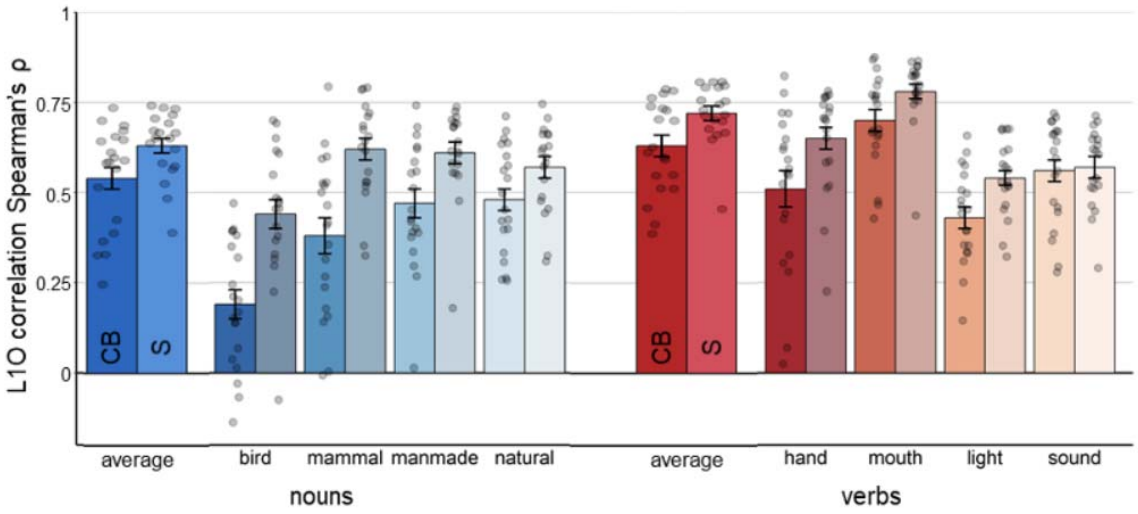

Figure 2: In-scanner behavioral results by semantic category: Leave-one-out within-group correlations (Spearman's ρ). Error bars: ± standard error of the mean.

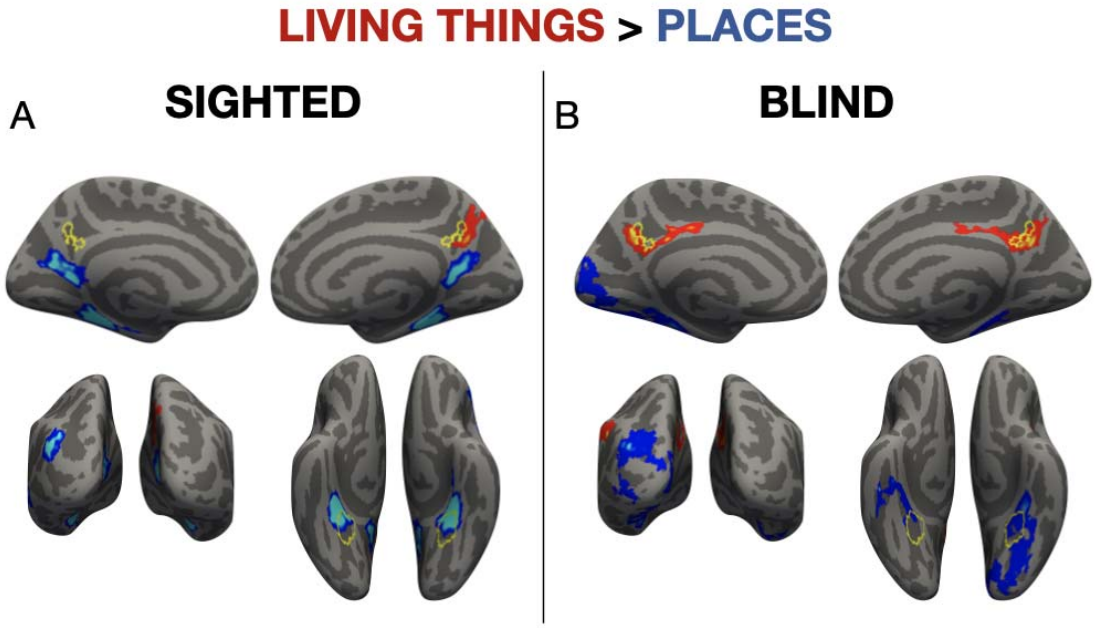

Figure 3: Whole-brain results for living things>places: (A) Sighted; (B) Blind. Group maps are shown p<0.01 with FWER cluster-correction for multiple comparisons. Voxels are color coded on a scale from p=0.01 to p=0.00001. The average PPA location from separate cohort of sighted subjects (Weiner et al., 2017) is overlaid on the place noun response observed in the current study. The two overlap in both groups, with the focus of the place noun response located more anteriorly. The average precuneus location from a separate cohort of sighted subjects (Fairhall & Caramazza, 2013) is overlaid on the living things response observed in the current study. These also overlap in both blind and sighted participants. Increased activation for living things over places is observed in the left dorsal precuneus in sighted participants at a lower statistical threshold ($p < 0.05$ uncorrected). See Supplementary Figure 3 for full whole-brain results.

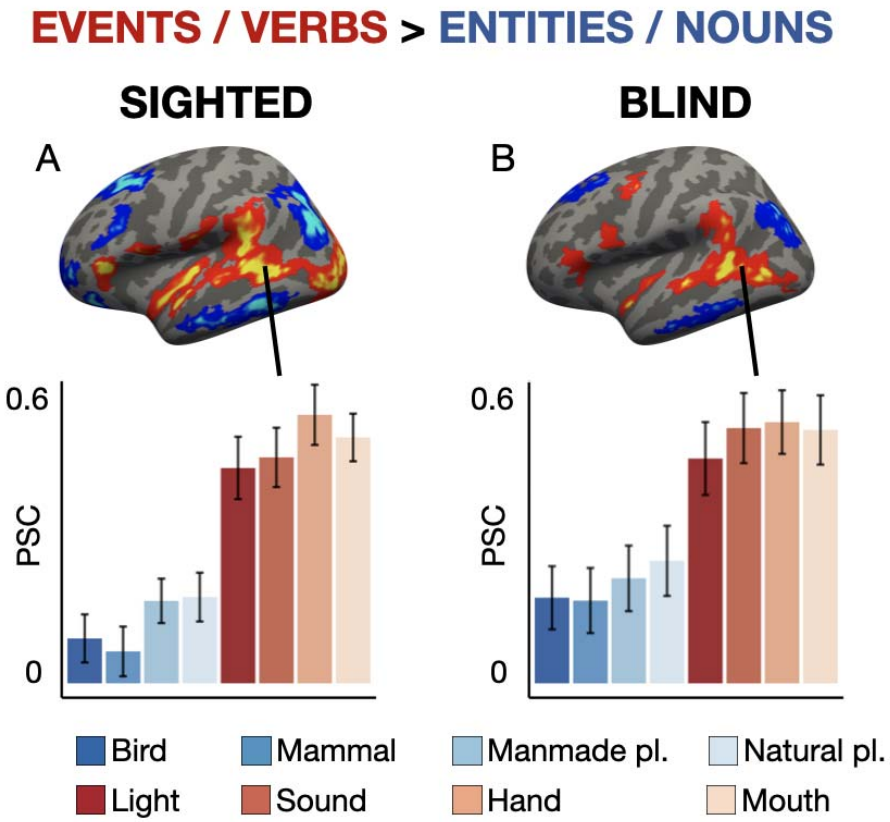

Figure 4: Whole-brain results for events/verbs > entities/nouns on the left lateral surface: (A) Sighted; (B) Blind. Group maps are shown at p<0.01 with FWER cluster-correction for multiple comparisons. Voxels are color coded on a scale from p=0.01 to p=0.00001. (C) Peak percent signal change (PSC) from the 5% most active vertices for verbs>nouns in the LMTG (left: sighted; right: blind). See Supplementary Figure 2 for full whole-brain results.

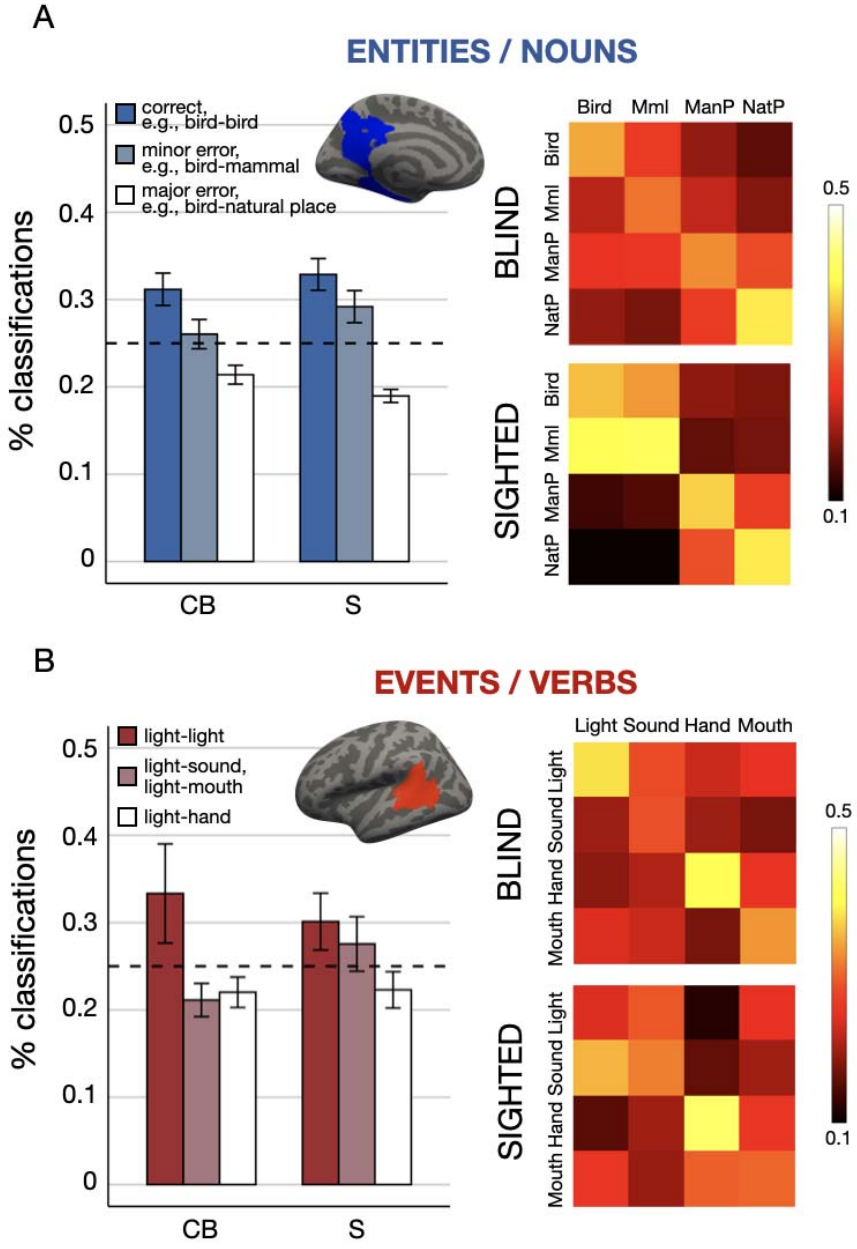

Figure 5: Classifier responses and confusion matrices for entity categories in the LPC (A) and for event categories in the LMTG (B). Bar graphs display the correct responses and errors for classification of living things vs. places (LPC) and light vs. all other verb categories (LMTG) within each participant group. Note that in the two lightest bars reflect the number of errors made in both directions (e.g., "light-sound" = mean of light (real) – sound (predicted) and sound (real) – light (predicted)). Chance: 25%. Confusion matrices (columns = real, rows = predicted) display the percentage of correct responses (diagonals) and errors (off diagonals) for classification of the relevant categories in each ROI. See Supplementary Figure 5 for results from all ROIs. Key: Mml = mammal, ManP = manmade place, NatP = natural place.

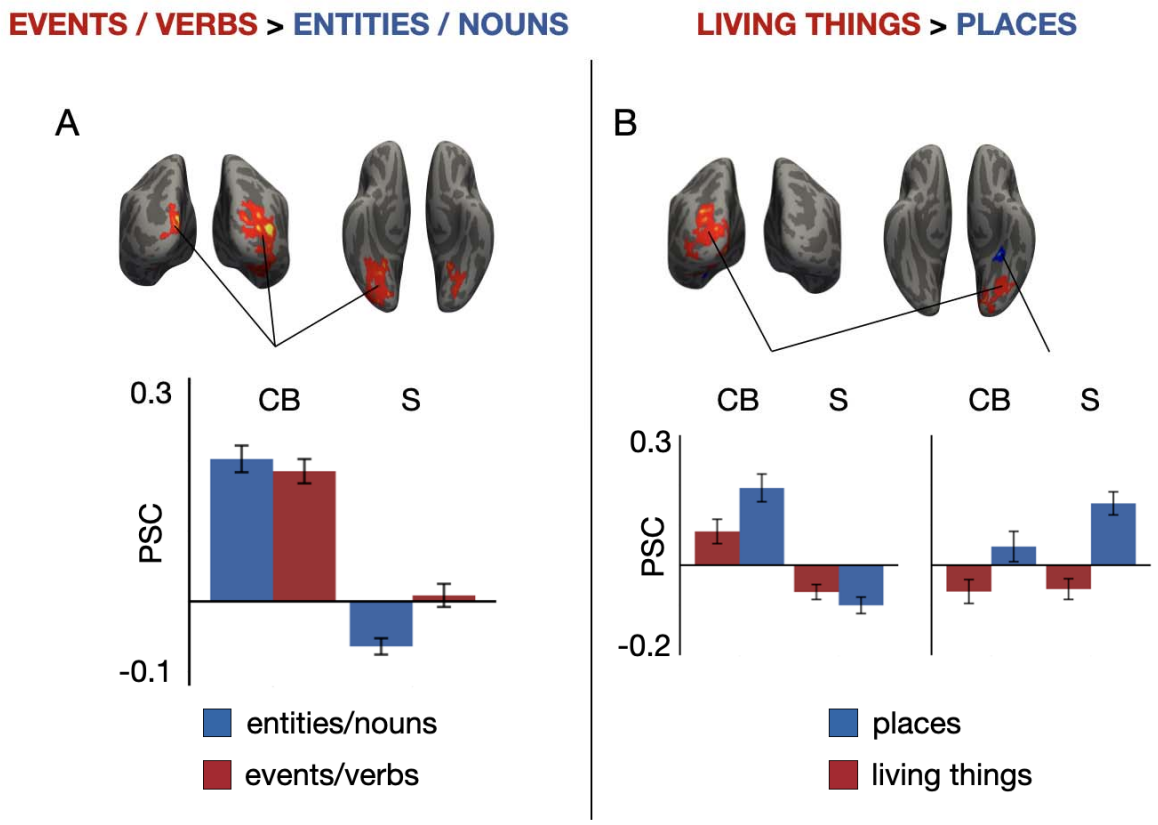

Figure 6: Group-by-condition interactions of univariate responses in occipital cortices. Group maps are shown p<0.01 with FWER cluster-correction for multiple comparisons. Voxels are color coded on a scale from p=0.01 to p=0.00001. (A) Peak percent signal change averaged across all occipital regions in which group-by-grammatical class (events vs. entities) interactions were observed. (B) Peak percent signal change in occipital regions in which group-by-noun category (living things vs. places) interactions were observed (occipital pole, anterior medial VTC).

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