

Basic Level Category Structure Emerges Gradually across Human Ventral Visual Cortex

Marius Cătălin Iordan¹, Michelle R. Greene¹, Diane M. Beck², and Li Fei-Fei¹

Abstract

■ Objects can be simultaneously categorized at multiple levels of specificity ranging from very broad (“natural object”) to very distinct (“Mr. Woof”), with a mid-level of generality (basic level: “dog”) often providing the most cognitively useful distinction between categories. It is unknown, however, how this hierarchical representation is achieved in the brain. Using multivoxel pattern analyses, we examined how well each taxonomic level (superordinate, basic, and subordinate) of real-world object categories is represented across occipitotemporal cortex. We found that, although in early visual cortex objects are best represented

at the subordinate level (an effect mostly driven by low-level feature overlap between objects in the same category), this advantage diminishes compared to the basic level as we move up the visual hierarchy, disappearing in object-selective regions of occipitotemporal cortex. This pattern stems from a combined increase in within-category similarity (category cohesion) and between-category dissimilarity (category distinctiveness) of neural activity patterns at the basic level, relative to both subordinate and superordinate levels, suggesting that successive visual areas may be optimizing basic level representations. ■

INTRODUCTION

Humans can distinguish between thousands of object categories in the real world with impressive speed and accuracy. Understanding how the brain represents categories across visual cortex is a key step in elucidating the complex cognitive mechanism by which categorization is achieved.

The mapping of category information across human visual cortex has been a major effort of modern neuroimaging studies, uncovering specific cortical regions specialized for broad stimulus categories such as faces, scenes, objects, and bodies (Downing, Jiang, Shuman, & Kanwisher, 2001; Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997; Malach et al., 1995), as well as organizational principles corresponding to broad attribute dimensions, including animacy (Konkle & Caramazza, 2013; Connolly et al., 2012; Kriegeskorte et al., 2008; Chao, Haxby, & Martin, 1999) and real-world object size (Konkle & Caramazza, 2013; Konkle & Oliva, 2012). Furthermore, many studies have demonstrated that category information is recoverable from distributed representations (Huth, Nishimoto, Vu, & Gallant, 2012; Eger, Ashburner, Haynes, Dolan, & Rees, 2008; Haynes & Rees, 2005; Cox & Savoy, 2003; Haxby et al., 2001). However, most previous studies have glossed over a fundamental property of real-world categories: Specifically, any particular object may belong to multiple categories simultaneously, ranging from very broad (“natural object,” “animal”) to very distinct (“pug,” “Mr. Woof”). Indeed, it

is yet unknown how this hierarchical representation is achieved in the brain.

We thus focus our investigation on assessing how category representations at different taxonomic levels (subordinate, basic, superordinate) change over the span of the human ventral visual cortex. Although, under certain conditions, category levels are flexible and may change with context, typicality, and degree of expertise (Mace, Joubert, Nespoulous, & Fabre-Thorpe, 2009; Tanaka & Taylor, 1991; Jolicoeur, Gluck, & Kosslyn, 1984), most often, human observers categorize objects faster and more accurately at a mid-level of specificity (i.e., basic level; Mack, Wong, Gauthier, Tanaka, & Palmeri, 2009; Murphy & Brownell, 1985; Mervis & Crisafi, 1982; Horton & Markman, 1980; Anglin, 1977; Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976; Brown, 1958). Thus, in our work, we restricted our analysis to sets of categories where these three levels are clearly differentiated behaviorally.

Concurrently, in characterizing the neural representation of this category hierarchy, we were inspired by Rosch et al.’s (1976) seminal work on categorization, which argued that a good category simultaneously maximizes within-category similarity (cohesiveness) and between-category dissimilarity (distinctiveness). In our work, we applied this principle to multivoxel fMRI patterns as a concrete measure of the strength of category representations across visual cortex. In particular, we ran two fMRI experiments in which participants were shown objects from hierarchies comprising three behaviorally normed taxonomic levels (superordinate, basic, and subordinate), and we employed several multivoxel pattern

¹Stanford University, ²University of Illinois at Urbana-Champaign

analyses (MVPAs) to characterize the similarity and dissimilarity of activity patterns across these separate levels. Here, high cohesion (positive correlation between activity patterns) would indicate that information content is similar within that particular category. Similarly, high distinctiveness (zero or negative correlation between activity patterns) would indicate that categories are distinguishable from one another; therefore, categories are more separable in that space.

In visual cortex, because two subordinate level exemplars (e.g., two pugs) should be most visually similar to each other, one might predict that categories adhere most strongly to a subordinate level representation. On the other hand, one might also expect superior superordinate level adherence (e.g., natural vs. man-made objects) because these categories might best reflect organization at the coarse scale of fMRI voxels. Finally, a wealth of behavioral evidence points to a mid-level of generality (basic level: “dog”) as being privileged in providing the most cognitively useful distinction between categories: Objects are learned and recognized faster at this intermediate level than at all other levels (Mack et al., 2009; Tanaka & Taylor, 1991; Murphy & Wisniewski, 1989; Murphy & Brownell, 1985; Jolicoeur et al., 1984; Mervis & Crisafi, 1982; Horton & Markman, 1980; Anglin, 1977; Rosch et al., 1976; Brown, 1958). This suggests that we may see evidence for superior basic level representations in visual cortex.

Thus, a subgoal of our work is to ask whether a particular behaviorally relevant taxonomic level is better represented in visual cortex. Here, we show that, for a set of object categories that exhibit a clear basic level advantage, category representations change as a function of taxonomic level as we move up the visual cortical hierarchy, progressively favoring the basic level relative to other levels of specificity. Thus, although objects are best represented at the subordinate level in early visual cortex, the basic level matches the quality of this representation in high-level object-selective regions as well as dominates superordinate representations throughout visual cortex. This provides evidence that basic level structure may be an emergent property of the human visual system.

METHODS

Experiment 1: Two Superordinate Categories—Natural and Man-made

To investigate how categories are represented across multiple levels of specificity, we ran a functional imaging experiment in which participants were shown objects from a three-tiered taxonomy (superordinate, basic, and subordinate levels), and we employed several MVPAs to characterize the similarity of activity patterns across these separate levels. To verify that our putative taxonomic levels are representative of real-world category organization, we first ran two behavioral experiments that assess

the perceptual and semantic differences in recognizing and categorizing objects across these taxonomic levels.

Stimuli

We constructed a three-tiered taxonomic hierarchy comprising two superordinate level (natural and man-made), four basic level (dog, flower, plane, and shoe), and 32 subordinate level categories. These included eight breeds of dogs: Komondor, Chihuahua, Pug, Malamute, Mastiff, Schnauzer, Welsh Corgi, and Schipperke; eight types of planes: airliner, biplane, fighter, delta plane, stealth, glider, gyroplane, and seaplane; eight types of flowers: blue daisy, ice poppy, sunflower, orchid, chrysanthemum, cosmos, violet, and toadflax; and eight types of shoes: slippers, cowboy boots, running shoes, pumps, loafers, flip-flops, clogs, and cleats. We had 32 instances of each of our 32 subordinate level categories for a total of 1024 color photographs collected from the ImageNet online database (Deng et al., 2009). Photographs were tightly cropped in a square region around the object of interest, resized to 400 × 400 pixels, and included their natural background (Figure 1A).

Behavioral Experiment: Match-to-category Multi-level Verification

Participants. Twelve participants (seven women, aged 18–30 years, including one of the authors) took part in the experiment. All participants had normal or corrected-to-normal vision, were financially compensated (except for the participating author), and provided informed written consent in compliance with procedures approved by the Stanford University institutional review board.

Materials. Stimuli were presented on a 21-in. CRT monitor, approximately 30 cm away from the observer. Images were shown centrally, subtending 16° × 16° visual angle. The experiment was implemented in MATLAB (www.mathworks.com), using the Psychophysics toolbox extension (Brainard, 1997; Pelli, 1997).

Experimental procedure. Each observer viewed 1024 images for 200 msec each, followed by a category query term. Query terms matched the image’s category on half of the trials and were drawn from a random other category on the other half of the trials. Query terms were drawn equally from superordinate level (e.g., “natural” or “man-made”), basic level (“plane,” “dog,” “flower,” “shoe”), or subordinate level (e.g., “Chihuahua” or “Chrysanthemum”) category. Participants were instructed to respond as quickly and accurately as possible as to whether the query term matched the image they had just seen. Performance feedback (accuracy and RT) was displayed at the end of each trial. Immediately before

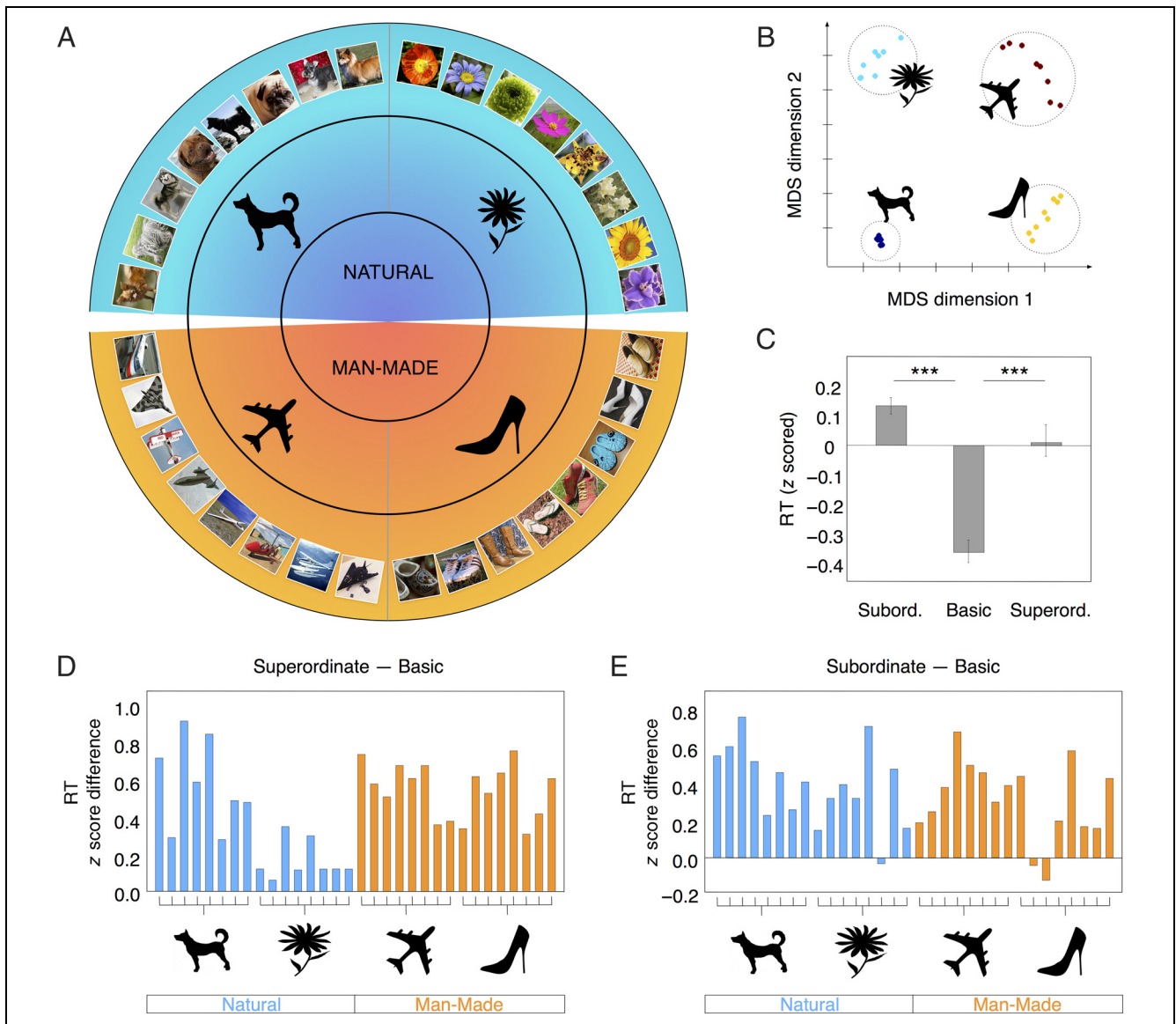


Figure 1. Experiment 1: stimulus set and behavioral results. (A) The stimulus set was organized according to a three-level taxonomic hierarchy comprising 32 subordinate level (most specific, outside layer), four basic level (middle layer), and two superordinate level (most general, center) categories. Each subordinate category consisted of 32 color photographs, with a representative image shown. Objects varied in color and pose. (B) Same-different subordinate level categorization behavioral experiment. We applied classical MDS to the perceptual distance between subordinate categories measured as z scored RTs. In a two-dimensional solution, the four basic level categories formed separate clusters. The first MDS dimension separates natural and man-made categories (superordinate level). The second MDS dimension separates dogs and shoes from flowers and planes. (C–E) Match-to-category behavioral experiment. (C) Participants verified category membership significantly faster at the basic level than at the superordinate or subordinate levels. (D) RT difference between basic and superordinate categorization conditions. Positive values indicate basic level advantage. Participants identified all stimulus categories faster at the basic level than at the superordinate level. (E) RT difference between basic and subordinate categorization conditions. Positive values indicate basic level advantage. Participants identified almost all stimulus categories faster at the basic level than at the subordinate level. There are only three exceptions: “sunflowers,” “clogs,” and “cowboy boots,” perhaps reflecting the atypicality of these stimuli. *** $p < .001$. Error bars: 95% confidence interval.

the experimental trials, participants were shown example images of each of the 32 subordinate categories, along with each of the three valid category labels affixed to that category.

Data analysis. RTs less than 200 msec and greater than 2 sec were discarded from analysis (1% of data, no more than 5% from any one participant). One participant was

discarded because of high numbers of rejected trials (46%) and errors (37%). RTs were transformed into z scores. To test for a basic level advantage, we examined the RTs for verifying an image as a member of a superordinate, basic, or subordinate level category, both overall and for each basic level category in particular. We also computed a measure of basic level advantage for each of the 32 subordinate level categories, defined as the RT

difference (in z scores) of basic level categorization compared to subordinate and superordinate level categorization.

Behavioral Experiment: Same-Different Subordinate Level Categorization

Participants. Twelve participants (five women, aged 18–30 years) took part in the experiment. All participants had normal or corrected-to-normal vision, were financially compensated, and provided informed written consent in compliance with procedures approved by the Stanford University institutional review board. One participant also took part in the fMRI experiment.

Materials. Stimuli were presented on a 21-in. CRT monitor, approximately 30 cm away from the observer. Images were shown side by side, each subtending $16^\circ \times 16^\circ$ visual angle, with 3° between them. The experiment was implemented in MATLAB (www.mathworks.com), using the Psychophysics toolbox extension (Brainard, 1997; Pelli, 1997).

Experimental procedure. Each observer viewed 1024 trials, with 512 trials showing pairs of images drawn from the same subordinate level category and 512 trials showing image pairs from two different subordinate level categories (16 pairs per subordinate per taxonomic level, randomly drawn for each participant). Participants were instructed to respond as quickly and accurately as possible whether both images were from the same subordinate category. Image pairs remained on the screen until response, and RT and accuracy feedback were given after each response.

Data analysis. RTs less than 200 msec and greater than 2 sec were discarded from analysis (2% of data, no more than 11% from any one participant). RTs were transformed into z scores relative to each participant's mean RT. We computed the average time required to reject a pair of images as being from the same subordinate level category and used this as a category distance measure in the context of a classical multidimensional scaling (MDS) analysis (criterion: metric stress).

fMRI Experiment

Participants. Ten volunteers (two women, aged 23–28 years, including author M. C. I.) with no past history of psychiatric or neurological disorders and normal or corrected-to-normal vision participated in this experiment. Participants gave informed written consent in compliance with procedures approved by the Stanford University institutional review board. Except for the participating author, all participants received financial compensation.

Scanning parameters and preprocessing. Imaging data were acquired with a 3-T G.E. Healthcare scanner (Fairfield, CT). A gradient-echo, echo-planar sequence was used to obtain functional images (volume repetition time = 2 sec, echo time = 30 msec, flip angle = 80° , matrix = 128×128 voxels, field of view = 20 cm, 29 oblique 3-mm slices with 1-mm gap, in-plane resolution = 1.56×1.56 mm). We also collected a high-resolution ($1 \times 1 \times 1$ mm voxels) structural scan (spoiled gradient recall; repetition time = 5.9 msec, echo time = 2.0 msec, flip angle = 11°) in each scanning session. The functional data were spatially aligned to compensate for motion during acquisition, and each voxel's intensity was converted to percent signal change relative to the temporal mean of that voxel using the AFNI software package (afni.nimh.nih.gov/afni). To perform our analyses, we computed the average voxel activity for each block. We did not use a general linear model (GLM) analysis and did not perform any smoothing.

Experimental procedure. Images were presented centrally subtending $21^\circ \times 21^\circ$ visual angle and were superimposed on an equiluminant gray background. We used a back-projection system (Optoma Corporation, Fremont, CA) operating at a resolution of 1024×768 pixels at 75 Hz. Participants performed eight runs, with 16 blocks per run and eight images per block. Each block consisted of a 500-msec fixation cross presented centrally, followed by eight consecutive stimulus presentations from the same subordinate level category, with a 12-sec gap between the blocks. Each image was presented for 160 msec, followed by a 590-msec blank gray screen. Participants were asked to maintain fixation at the center of the screen and respond via button press whenever an image was repeated (1-back task, 0–2 repetitions per block). Over the course of the experiment, each participant viewed four blocks from each of the 32 subordinate level categories, for a total of 128 blocks. The order of blocks, the number of repetitions in each block, and the images in each block were counterbalanced across runs and between participants.

ROIs. The positions and extents of each participant's functional ROIs (lateral occipital complex [LOC], trans-occipital sulcus [TOS], parahippocampal place area [PPA], retrosplenial cortex [RSC], and fusiform face area [FFA]) were obtained using standard localizer runs conducted in a separate fMRI session. Participants observed two runs, each with 12 blocks drawn equally from six categories: child faces, adult faces, indoor scenes, outdoor scenes, objects (abstract sculptures with no semantic meaning), and phase-scrambled objects. Blocks were separated by 12-sec fixation cross periods and comprised 12 image presentations, each of which consisted of images presented for 900 msec, followed by a 100-msec fixation cross. Each image was presented exactly once, with the exception of two images during each block that were

repeated twice in a row. Participants were asked to maintain fixation at the center of the screen and respond via button press whenever an image was repeated. To avoid any issues related to intrinsic variability in signal reliability across our participant pool, we selected fixed-volume ROIs across all our participants. The volume of each region in cubic millimeters was chosen conservatively, based on sizes previously reported in the literature, accounting for resolution differences between studies (Walther, Caddigan, Fei-Fei, & Beck, 2009; Golarai et al., 2007): LOC = 500 voxels, TOS = 200 voxels, PPA = 300 voxels, RSC = 200 voxels, and FFA = 100 voxels. LOC was defined as the top 500 voxels bilaterally near the inferior occipital gyrus that responded to an objects > scrambled objects GLM contrast. PPA was defined as the top 300 voxels bilaterally near the parahippocampal gyrus that responded to a scenes > objects GLM contrast. TOS was defined as the top 200 voxels bilaterally near the TOS that responded to a scenes > objects GLM contrast. RSC was defined as the top 200 voxels bilaterally near RSC that responded to a scenes > objects GLM contrast. FFA was defined as the top 100 voxels bilaterally near the fusiform gyrus that responded to a faces > objects GLM contrast. All ROIs were identified bilaterally, except for some participants' FFA (right hemisphere only: 3/10 for Experiment 1, 5/17 for Experiment 2).

To determine the locations of early visual areas V1, V2, V3v, and hV4, we used a standard retinotopic mapping protocol in a separate experiment, in which a checkerboard pattern undergoing contrast reversals at 5 Hz moved through the visual field in discrete increments (Sayres & Grill-Spector, 2008). First, a wedge subtending an angle of 45° from fixation was presented at 16 different polar angles for 2.4 sec each. Next, an annulus subtending 3° of visual angle was presented at 15 different radii for 2.4 sec each. Each participant passively observed two runs of six cycles in each condition, yielding 512 time points per participant. The locations and extents of early visual areas were delineated on a flattened cortical surface for each participant, using a horizontal-versus-vertical meridian general linear test, which gave the boundaries between retinotopic maps.

We aligned the positions of the ROIs to the experimental sessions using the AFNI software package (afni.nimh.nih.gov/afni), by first aligning the structural scans between sessions with submillimeter precision and then applying the alignment transformation to the ROI positions. Percent signal change was then extracted for each voxel in each ROI, and these vectors were submitted to the similarity and classification analyses described next.

fMRI Data Analysis

Within-category similarity (cohesion) and between-category similarity (distinctiveness). These analyses are defined identically to quantities used in Kriegeskorte

et al. (2008): Cohesion is within-category similarity; distinctiveness is between-category dissimilarity. For each category at each taxonomic level (subordinate, basic, superordinate), we computed category cohesion as the average correlation between neural patterns elicited by within-category pairs of blocks (four per subordinate category, 32 per basic category, 64 per superordinate category) at that taxonomic level. For example, at the basic level, cohesion for “dogs” is defined as the average correlation between voxel activations for any two blocks where any type of dog was shown. Similarly, we computed category distinctiveness as the average correlation between neural patterns elicited by between-category pairs of blocks at each taxonomic level. For example, at the basic level, distinctiveness for “dogs” is defined as average correlation between voxel activations for a block where dogs were shown and another block where, for example, flowers were shown. We performed each of these analyses for each participant and ROI separately. To show that the effects we obtain are not solely because of low-level image features, we also computed cohesion and distinctiveness in an analogous fashion for image descriptor features extracted from our stimulus images: color histograms, GIST (Oliva & Torralba, 2001), HOG (Dalal & Triggs, 2005), and SIFT (Lowe, 2004).

Category boundary effect. To quantify the interplay between cohesion and distinctiveness and how they give rise to category distinctions, we also defined the category boundary effect identically to Kriegeskorte et al. (2008) as the difference between cohesiveness and distinctiveness across a taxonomic level, averaged across all categories from that level. This quantity provides a measure of how well categories are separated at each taxonomic level. For each ROI, we also compute category boundary effect differences between the basic level versus the subordinate and superordinate level representations. These analyses were also repeated for the image descriptor feature representations of our stimuli.

Correlation classifier. To assess the amount of information present in the neural patterns at each taxonomic level, we implemented a standard MVPA correlation classifier to predict stimulus categories from neural patterns of activation at all three levels in our taxonomy (subordinate, basic, and superordinate). For each participant, we performed cross-validation by using two of the eight runs for testing (one block from each subordinate category) and the remaining six runs for training (three blocks from each subordinate category). We averaged the results across cross-validation folds to obtain classification accuracies for each participant and ROI. To compare classification results between different taxonomic levels, we normalized the decoding accuracy using the formula $(x - c)/(1 - c)$, where x is the accuracy obtained at a given level and c is the chance value (c is 12.5% for the

subordinate level, 25% for the basic level, and 50% for the superordinate level). To control for the number of training examples at the basic and superordinate levels, we matched the number of training and testing points to those at the subordinate level (three blocks for training, one block for testing) by randomly sampling blocks 10,000 times with replacement. We performed two-tailed *t* tests to identify results that were significantly different from chance levels (defined above) and two-tailed *t* tests within each area to identify when decoding accuracy at the basic level is significantly greater than accuracy at the other levels in the taxonomy. We also obtained ROI confusion matrices by extracting subordinate level confusion matrices for each participant and averaging them together. A row of a confusion matrix records the probability of classifying the corresponding subordinate category as each of the 32 subordinate categories in the columns.

Experiment 2: Three Superordinate Categories—Vehicles, Furniture, and Musical Instruments

Experiment 1 used object categories that straddle the boundaries of two main dimensions of selectivity known to affect the responses to objects in occipitotemporal cortex: animacy (Connolly et al., 2012) and real-world size (Konkle & Caramazza, 2013). Furthermore, by including naturalistic backgrounds together with our objects of interest in Experiment 1, it is possible that this factor may influence the observed category grouping. To ensure this is not the case, as well as to demonstrate the generalizability of our results from Experiment 1 to additional categories, we constructed a new three-tiered taxonomic hierarchy comprising exclusively big, inanimate objects. We first generated a putative taxonomy comprising 36 subordinate level categories and used a match-to-category behavioral experiment to eliminate nine members with ambiguous category status (defined as weak basic level advantage over the subordinate). Similar to Experiment 1, we then used a same-different subordinate categorization behavioral experiment to further verify that our new putative taxonomic levels are representative of real-world category organization. Finally, we conducted a second fMRI experiment using the new stimuli and replicated our analyses from Experiment 1.

Stimuli

We constructed a new three-tiered taxonomic hierarchy comprising exclusively big inanimate objects: three superordinate level categories (vehicles, furniture, musical instruments), nine basic level categories (cars, airplanes, ships, chairs, beds, tables, drums, guitars, pianos), and 36 subordinate level categories (four types of each of the nine basic level categories listed above: cars = sports car, sedan, antique car, station wagon; airplanes = airliner, biplane, fighter, stealth plane; ships = ice breaker, cargo ship, battleship, cruise ship; chairs = folding chair, armchair,

straight chair, Eames chair; beds = canopy bed, sleigh bed, platform bed, bunk bed; tables = dining table, coffee table, pedestal table, folding table; drums = bass drum, snare drum, timpani, bongos; guitars = flamenco, Stratocaster, dreadnaught, Les Paul; pianos = grand piano, Hammond organ, upright piano, synthesizer). We had 40 instances of each of our 36 subordinate level categories for a total of 1440 color photographs collected from the ImageNet online database (Deng et al., 2009). Images were cropped tightly around each object of interest, and we replaced the original background with pixel-wise full-color 1/f noise. The resulting images were 400×400 pixels, ensuring that all images stimulated the same retinal area.

Behavioral Experiment: Match-to-category Multi-level Verification

The first aim of this behavioral experiment was to finalize our category taxonomy by assessing category status in general and basic level advantage in particular. This ensured that categories we included in our taxonomy are representative of the relationships present in real-world taxonomies. We tested the category taxonomy listed above and then eliminated members with ambiguous category status. The taxonomy was pruned of nine subordinate categories (one for each basic) by eliminating those subordinates with the lowest behavioral basic level advantage (see Data Analysis section: antique car, stealth plane, battleship, Eames chair, bunk bed, folding table, bongos, Les Paul guitar, synthesizer). We used the resulting taxonomy (27 subordinate categories; Figure 4A) for all subsequent analyses.

Participants. Ten participants (six women, aged 18–35 years, including authors M. C. I. and M. R. G.) participated in the first behavioral experiment. All volunteers had normal or corrected-to-normal vision and provided informed consent in compliance with procedures approved by the Stanford University institutional review board. Nonauthor participants were compensated for their time.

Materials and experimental procedure. Analogous to Experiment 1.

Data analysis. RTs less than 200 msec and greater than 2 sec were discarded from analysis (2% of data, no more than 10% of trials from any participant). RTs for correct trials (84% of trials) were transformed into *z* scores. To test for a basic level advantage, we examined the differences in RTs to correctly verify an image as a member of a superordinate, basic, or subordinate level category. We also defined basic level advantage to be the RT difference (in *z* scores) of basic level categorization compared to subordinate level categorization and used this metric to reject the subordinate level categories in each branch of the hierarchy with the weakest basic level effects. Only one of the remaining 27 basic level categories (biplane)

had a negative basic level advantage, possibly because this less typical plane is better categorized at the subordinate level (Jolicoeur et al., 1984).

Behavioral Experiment: Same–Different Subordinate Level Categorization

Participants. Twenty individuals (nine women, aged 18–35 years) with normal or corrected-to-normal vision participated in this experiment. None of the participants took part in the fMRI experiment or in the first behavioral experiment. All provided informed consent in compliance with procedures approved by the Stanford University institutional review board and were compensated for their time.

Materials and experimental procedure. Analogous to Experiment 1.

Data analysis. RTs less than 200 msec and greater than 2 sec were discarded from analysis (<1% of data, no more than 8% from any one participant). RTs were transformed into z scores. We computed the average time required to reject a pair of images as being from the same subordinate level category and used this as a category distance measure in the context of a classical MDS analysis (criterion: metric stress).

fMRI Experiment

Participants. Seventeen volunteers (four women, aged 23–31 years, including authors M. C. I. and M. R. G.) with no past history of psychiatric or neurological disorders and normal or corrected-to-normal vision participated in this experiment. Participants gave informed written consent in compliance with procedures approved by the Stanford University institutional review board. Except for the participating authors, all participants received financial compensation.

Scanning parameters, preprocessing, experimental procedure, and ROIs. The second fMRI experiment was conducted similarly to Experiment 1. Participants performed five runs, with 27 blocks per run and eight images per block. Over the course of the experiment, each participant viewed five blocks from each of the 27 subordinate level categories, for a total of 135 blocks. The order of blocks, the number of repetitions in each block, and the images in each block were counterbalanced across runs and between participants.

fMRI Data Analysis

Within-category similarity (cohesion) and between-category dissimilarity (distinctiveness), category boundary effect, and correlation classifier. Performed analogously to Experiment 1.

Statistical Analyses

For all our experiments, we used paired two-tailed t tests when comparing observed effects against chance and when establishing whether a significant difference exists between two observed effects. We used Kolmogorov–Smirnov tests to establish that no significant deviation from normality exists for the distributions of all effects to which t tests were applied. Because statistical tests are made on a single number derived from the pattern of voxels within an ROI per condition of interest and these conditions are relatively few, we did not correct for multiple comparisons within our ROI analyses.

We also used Friedman nonparametric tests to investigate whether trends exist in data where the dependent variable is ordinal but not continuously organized. All statistical tests were implemented in MATLAB.

RESULTS

Experiment 1: Two Superordinate Categories—Natural and Man-made

Behavioral Experiments

In our first experiment, we used a three-tiered taxonomic hierarchy comprising two superordinate level (natural, man-made), four basic level (dog, flower, plane, shoe), and 32 subordinate level categories (e.g., Chihuahua, stealth plane; Figure 1A).

To verify that our putative basic level categories reflect entry level concepts, we first conducted a match-to-category behavioral experiment. As predicted, participants were significantly faster to verify category membership at the basic level (662 msec, $SEM = 36$ msec) than at the superordinate (747 msec, $SEM = 43$ msec) or subordinate (782 msec, $SEM = 44$ msec) levels (Figure 1C; basic > superord.: $t(18) = 5.1, p < .001$; basic > subord.: $t(18) = 8.6, p < .001$). We also computed a measure of basic level advantage for each of the 32 subordinate level categories, defined as the RT difference (in z scores) of basic level categorization compared to subordinate and superordinate level categorization. All 32 categories showed a basic level advantage over the superordinate level (Figure 1D), and all except three categories (cowboy boots, clogs, and sunflowers) showed a basic level advantage over the subordinate level of the taxonomy (Figure 1E). These few exceptions most likely represent less prototypical exemplars of their basic level category (Jolicoeur et al., 1984).

To map categories in terms of their behavioral similarity, we next used a same–different subordinate level categorization experiment to measure the perceptual distance between all pairs of subordinate categories. Reasoning that images in similar categories will take longer to reject than images from dissimilar categories, we used RTs to pairs of images in the “different” condition to generate a distance metric between our subordinate categories. Consistent with prior work (Rosch

et al., 1976), participants found objects within the same basic category to be more similar to each other than to stimuli in other basic categories ($t(22) = 4.7, p < .001$). Furthermore, classical MDS applied to this distance metric revealed that, in a two-dimensional solution, the four basic level categories form separate clusters (Figure 1B), with the first MDS dimension separating the natural and man-made categories (superordinate level).

These results replicated Rosch et al.'s (1976) original findings for our object categories by demonstrating that our taxonomy exhibits a clear basic level advantage and as such is representative of hierarchically organized real-world categories.

Neural Category Boundaries Favor Basic Level Representations

Having verified the taxonomy behaviorally, we scanned participants viewing these same 32 categories to find out how neural category representations change across taxonomic levels and across human ventral visual cortex. Because task may influence entry level categorization (Harel, Kravitz, & Baker, 2014; Mace et al., 2009; Mack et al., 2009), we asked participants to perform a 1-back repetition task in the scanner (i.e., no explicit categorization task) used solely to ensure they maintained attention and alertness during the experiment. Our analyses focused on object- (LOC), scene- (PPA, RSC, TOS), and face-selective (FFA) regions as well as early visual cortex areas (V1, V2, V3v, hV4).

Our first task was to assess the strength of category representations at each taxonomic level in terms of their cohesion and distinctiveness. According to Rosch et al. (1976), categories form such that they concurrently maximize within-category similarity (cohesion) and between-category dissimilarity (distinctiveness). To quantify the interplay between cohesion and distinctiveness and how they give rise to category distinctions, we defined the category boundary effect (Kriegeskorte et al., 2008) as the difference between cohesiveness and distinctiveness across a taxonomic level, averaged across all categories from that level. We computed the category boundary effect for each taxonomic level (subordinate, basic, superordinate) in each brain ROI.

We found that the category boundary effect is generally higher at the subordinate and basic levels compared to the superordinate level across visual cortex, especially in higher visual areas (Figure 2A; subordinate > superordinate: V1, $t(9) = 2.5, p = .032$; V2, $t(9) = 2.5, p = .035$; V3v, $t(9) = 1.9, p = .089$; hV4, $t(9) = 1.7, p = .133$; LOC: $t(9) = 5.6, p < .001$; FFA: $t(9) = 4.0, p = .003$; PPA: $t(9) = 4.7, p = .001$; TOS: $t(9) = 2.1, p = .067$; RSC: $t(9) = 3.5, p = .007$; basic > superordinate: V1, $t(9) = 2.2, p = .058$; V2, $t(9) = 2.8, p = .022$; V3v, $t(9) = 2.8, p = .020$; hV4, $t(9) = 2.8, p = .021$; LOC: $t(9) = 7.6, p < .001$; FFA: $t(9) = 3.6, p = .006$; PPA: $t(9) = 6.5, p < .001$; TOS: $t(9) = 3.3, p = .009$;

RSC: $t(9) = 4.8, p = .001$). Moreover, the category boundary effect increased in LOC compared to early visual areas at all levels of the taxonomy (subordinate: LOC > V1, $t(9) = 5.7, p < .001$; LOC > V2, $t(9) = 7.3, p < .001$; LOC > V3v, $t(9) = 9.7, p < .001$; LOC > hV4, $t(9) = 5.7, p < .001$; basic: LOC > V1, $t(9) = 6.5, p < .001$; LOC > V2, $t(9) = 7.3, p < .001$; LOC > V3v, $t(9) = 8.3, p < .001$; LOC > hV4, $t(9) = 5.5, p < .001$; superordinate: LOC > V1, $t(9) = 4.7, p = .001$; LOC > V2, $t(9) = 5.4, p = .001$; LOC > V3v, $t(9) = 5.7, p = .001$; LOC > hV4, $t(9) = 2.5, p = .032$). Taken together, these results suggest that categories become more sharply distinguishable as we move up the visual hierarchy and that, throughout ventral visual cortex, activity patterns adhere better to subordinate and basic level categories than to the more general (superordinate) levels of representation.

To characterize the difference between our taxonomic levels more clearly, we looked at the difference between the category boundary effect at the basic level compared to the other two levels (Figure 2C and D). We found that category boundary is always higher at the basic level than the superordinate across early visual areas and LOC. Moreover, subordinate category boundary started out with advantage over the basic level (generally negative values for V1; Figure 2C), but this advantage disappeared as we move up the visual cortical hierarchy (generally positive values for LOC; Figure 2C). Interestingly, the basic level gained an advantage over both the subordinate and superordinate levels as we move up the visual hierarchy from V1 to LOC (increasing trends in category boundary effect difference from V1 to LOC for basic – subord.: $p < .001$, basic – superord.: $p < .001$; Friedman nonparametric tests).

Overall, our results suggest that the neural representation of object categories in occipitotemporal cortex is highly dynamic across the taxonomic spectrum. First, we find evidence supporting both of our initial predictions: The subordinate and basic levels are both strongly represented, with the former being especially emphasized in early visual cortex, whereas the latter becoming more prominent in object-selective LOC. Second, we uncover a gradual trade-off between the subordinate and basic levels, which appears to develop as we move up the visual hierarchy, with a basic level advantage arising in object-selective cortex.

Category Cohesion and Distinctiveness across Occipitotemporal Cortex

The category boundary effect provides an intuitive measure of how categories group at each taxonomic level. However, this effect comprises contributions from both cohesion and distinctiveness, which describe the similarity of object representations within and between categories, respectively. Historically, it has been hypothesized that basic categories provide the best behavioral differentiation between concepts because they combine

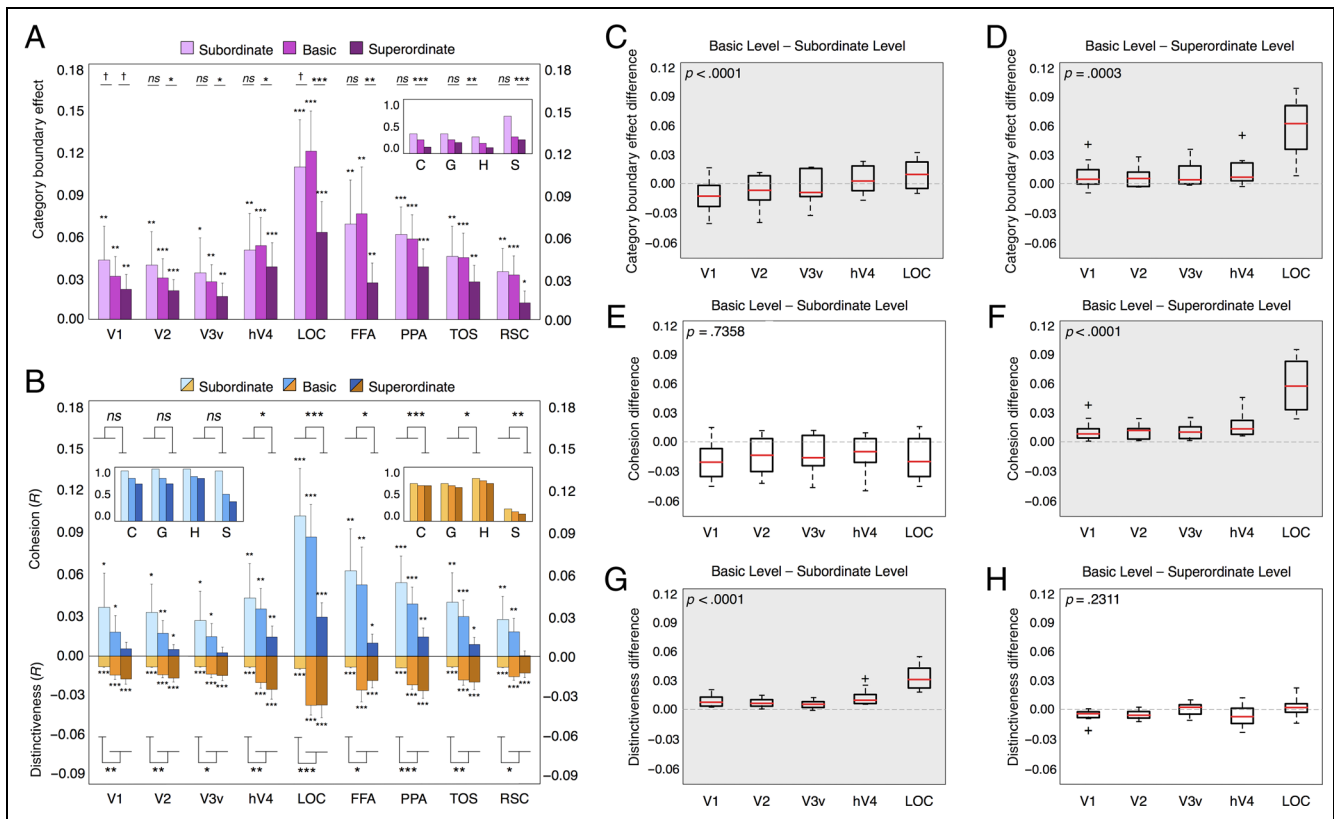


Figure 2. Experiment 1: neural category boundaries favor basic level representations. (A) Category boundary effect for neural activity patterns at each taxonomic level and in each ROI. Inset shows same analysis for image feature descriptors: C = color histograms; G = GIST features; H = HOG features; S = SIFT features. The neural representation of object categories in occipitotemporal cortex was highly dynamic across the taxonomic spectrum and was not fully explained by low-level image features. The subordinate and basic levels were together strongly represented, with the former being especially emphasized in early visual cortex, whereas the latter becoming more prominent in LOC. (B) Cohesion and distinctiveness for neural activity patterns at each taxonomic level and in each ROI. Inset shows same analyses for image feature descriptors. Cohesion generally decreased with taxonomic level and was significantly weaker at the superordinate level compared to the other two levels in all ROIs, which suggests that object representations become less homogenous within their category across visual cortex. Distinctiveness generally increased with taxonomic level and was significantly weaker at the subordinate level compared to the basic and superordinate levels, which suggests that object representations become better differentiated across categories in later visual areas. (C, D) Category boundary effect difference between basic level and subordinate and superordinate levels. We uncovered a gradual trade-off between the subordinate and basic levels, which appears to develop as we move up the visual hierarchy, with a trending basic level advantage arising in object-selective cortex. (E, F) Cohesion difference between basic level and subordinate and superordinate levels. (G, H) Distinctiveness difference between basic level and subordinate and superordinate levels. The category boundary difference appears to be driven by separate components of the category boundary effect, depending on taxonomic level. The trending advantage of the basic level over the subordinate in later visual areas was mainly because of the sharp increase in distinctiveness between early visual areas and LOC, whereas the clear advantage of the basic level over the superordinate was mainly because of the sharp increase in cohesion between early visual areas and LOC. * $p < .05$, ** $p < .01$, *** $p < .001$, † $p < .10$, ns = not significant. Error bars: 95% confidence interval. Shaded graphs indicate a significant increase from V1 to LOC.

the strengths but not the weaknesses of both subordinate and superordinate categories (Rosch, 1978): Members of subordinate categories, although very similar to each other (high cohesion), share too many features that overlap with members of other categories (low distinctiveness), and exemplars of superordinate categories, although very different from one another (high distinctiveness), share too few features in common with each other to successfully generalize across the entire category (low cohesion). To determine whether activity patterns in ventral visual cortex conform to this principle, we computed the average cohesion and distinctiveness of the activity patterns evoked by our stimuli for each taxonomic level.

We found that cohesion generally decreased with level of specificity across all ROIs (Figure 2B, top) and was significantly weaker at the superordinate level compared to the other two levels in the taxonomy in all high-level areas and hV4 (superordinate < basic and subordinate LOC: $t(9) = 7.3, p < .001$; FFA: $t(9) = 4.4, p = .005$; PPA: $t(9) = 6.9, p < .001$; TOS: $t(9) = 4.1, p = .009$; RSC: $t(9) = 4.8, p = .003$; hV4: $t(9) = 3.9, p = .011$). This result is consistent with the expectation that objects share more low-level features in common at the subordinate level (Kriegeskorte et al., 2008; Koustaal et al., 2001). Concurrently, between-category dissimilarity (distinctiveness) generally increased with taxonomic level (Figure 2B, bottom) and was significantly weaker at the

subordinate level compared to the basic and superordinate levels in all ROIs (subordinate < basic and superordinate LOC: $t(9) = 7.7, p < .001$; FFA: $t(9) = 4.7, p = .004$; PPA: $t(9) = 6.6, p < .001$; TOS: $t(9) = 5.2, p = .002$; RSC: $t(9) = 3.9, p = .011$; V1: $t(9) = 4.7, p = .003$; V2: $t(9) = 5.9, p < .001$; V3v: $t(9) = 4.1, p = .008$; hV4: $t(9) = 5.7, p = .001$). In other words, these results are in general agreement with the assertion that the basic level may be privileged because it strikes the best balance between category cohesion and distinctiveness (Rosch, 1978).

Although the general pattern of higher cohesion for subordinate and basic level categories and higher distinctiveness for basic and superordinate level categories held across our ROIs, the degree of cohesion and distinctiveness changed across visual areas. Interestingly, category cohesion increased in LOC compared to V1 at all levels of the taxonomy (LOC > V1: subord., $t(9) = 5.8, p < .001$; basic: $t(9) = 6.5, p < .001$; superord.: $t(9) = 4.9, p < .001$), suggesting that object representations become overall more homogenous within their category in later visual areas. Furthermore, distinctiveness increased in LOC compared to V1 at all levels of the taxonomy (LOC > V1: subord., $t(9) = 3.5, p = .006$; basic: $t(9) = 6.5, p < .001$; superord.: $t(9) = 4.5, p = .002$), which suggests that object representations become better differentiated across categories in later visual areas. Thus, in keeping with Rosch et al.'s (1976) assertion that good object categories are represented such that they maximize within-category similarity and between-category dissimilarity, our results suggest that LOC appears to be producing stronger category representations than earlier visual areas.

Do these changes in cohesion and distinctiveness favor the basic level? To assess this, we compared cohesion and distinctiveness across both taxonomic levels and visual areas (Figure 2E–H). The advantage of the basic level over the subordinate in later visual areas was mainly because of the sharp increase in distinctiveness between early visual areas and LOC (Figure 2G; increasing trend in distinctiveness difference from V1 to LOC for basic – subord.: $p < .001$; Friedman nonparametric test). Cohesion, on the other hand, was fairly stable across the same visual areas (Figure 2E; no increasing trend in cohesion difference from V1 to LOC for basic – subord.: $p = .736$; Friedman nonparametric test). Conversely, the advantage of the basic level over the superordinate was mainly because of the sharp increase in cohesion between early visual areas and LOC (Figure 2F; increasing trend in cohesion difference from V1 to LOC for basic – superord.: $p < .001$; Friedman nonparametric test), whereas distinctiveness remained relatively unchanged (Figure 2H; no increasing trend in distinctiveness difference from V1 to LOC for basic – superord.: $p = .231$; Friedman nonparametric test). This pattern of results aligns well with both theoretical considerations of category as well as intuitions about subordinate and superordinate categories. As predicted, we show that a trade-off exists between

category cohesion and category distinctiveness at the two extremes of our taxonomy (subordinate and superordinate levels), with the basic level potentially striking the best balance between these two quantities by encompassing both strong within-category similarity and strong between-category dissimilarity. In short, our data suggest that the basic level simultaneously gains an advantage over both the subordinate and superordinate levels as we move up the visual hierarchy from V1 to LOC.

The Contribution of Low-level Visual Features

The changes in cohesion and distinctiveness across visual cortex suggest that LOC may be optimizing both of these two components of what constitutes a good category. To determine the extent to which the patterns of results obtained in LOC are captured by low-level image features, we computed category boundary effect, cohesion, and distinctiveness in an analogous fashion for image descriptor features extracted from our stimulus images: color histograms, GIST (Oliva & Torralba, 2001), HOG (Dalal & Triggs, 2005), and SIFT (Lowe, 2004).

We found that all image descriptor category boundaries clearly favored the subordinate level (Figure 2A, inset). As such, these boundaries were similar to early visual cortex representations, but they did not capture category representations in LOC. By contrast, neural patterns in LOC exhibited a trend for reversing the preference of subordinate and basic levels, favoring the latter (basic > subordinate LOC: $t(9) = 2.0, p = .072$).

Furthermore, we found that, for all our feature descriptors, cohesion has high positive values for all levels of the taxonomy. However, concomitantly, between-category similarity was also very high (Figure 2B, insets), indicating poor distinctiveness at the image descriptor level. In other words, a high degree of similarity exists between all our stimulus images in terms of their low-level features, irrespective of category, and across all levels of the taxonomy (i.e., distinctions between all categories are very slight). Thus, although image features may partly explain category cohesion, they do a poor job at characterizing the distinctiveness between object categories we observe in the neural data. This lack of distinctiveness makes low-level image features a poor candidate for explaining the results we obtained in LOC, which show the basic level gaining an advantage compared to the other two levels in our taxonomy.

Our results are consistent with the predictions put forth by Rosch et al. (1976) based on behavioral observations: Object categories are represented such that they maximize within-category similarity and between-category dissimilarity. This property is not solely due to low-level image features; it holds across multiple levels of category generality (subordinate, basic, superordinate) and is, in fact, enhanced as we move up the ventral visual

stream: Cohesion and distinctiveness increase in object-selective areas compared to early visual cortex.

Correlation Classification Shows Basic Level Advantage in LOC

Our analyses so far suggest that, to understand category organization in visual cortex, we must consider cohesion and distinctiveness together. Furthermore, the category boundary analysis used here and by others (Kriegeskorte et al., 2008) assumes that cohesion and distinctiveness combine linearly to give rise to category distinctions. This linearity assumption may not be strictly true, raising the possibility that we are underestimating (or overestimating) the degree to which the activity patterns adhere to a particular taxonomic level. Thus, to complement our category boundary analysis, we also used a data-driven

method that weighs cohesion and distinctiveness automatically, without any prior knowledge provided by the experimenters.

In particular, we implemented an MVPA correlation classifier to decode category identity from each ROI at each taxonomic level (subordinate, basic, superordinate). We found that the information present in voxel-level neural patterns was sufficient to distinguish between categories at all taxonomic levels and in all brain regions considered above chance: object-, scene-, and face-selective areas (LOC, FFA, PPA, RSC, TOS) as well as early visual areas (V1, V2, V3v, hV4; Figure 3A).

Critically, however, we also found that information about object category did not increase monotonically with category generality (taxonomic level) in all brain areas. In LOC (and, to a lesser extent, in FFA and RSC), accuracy was highest at the basic level, and we saw a sig-

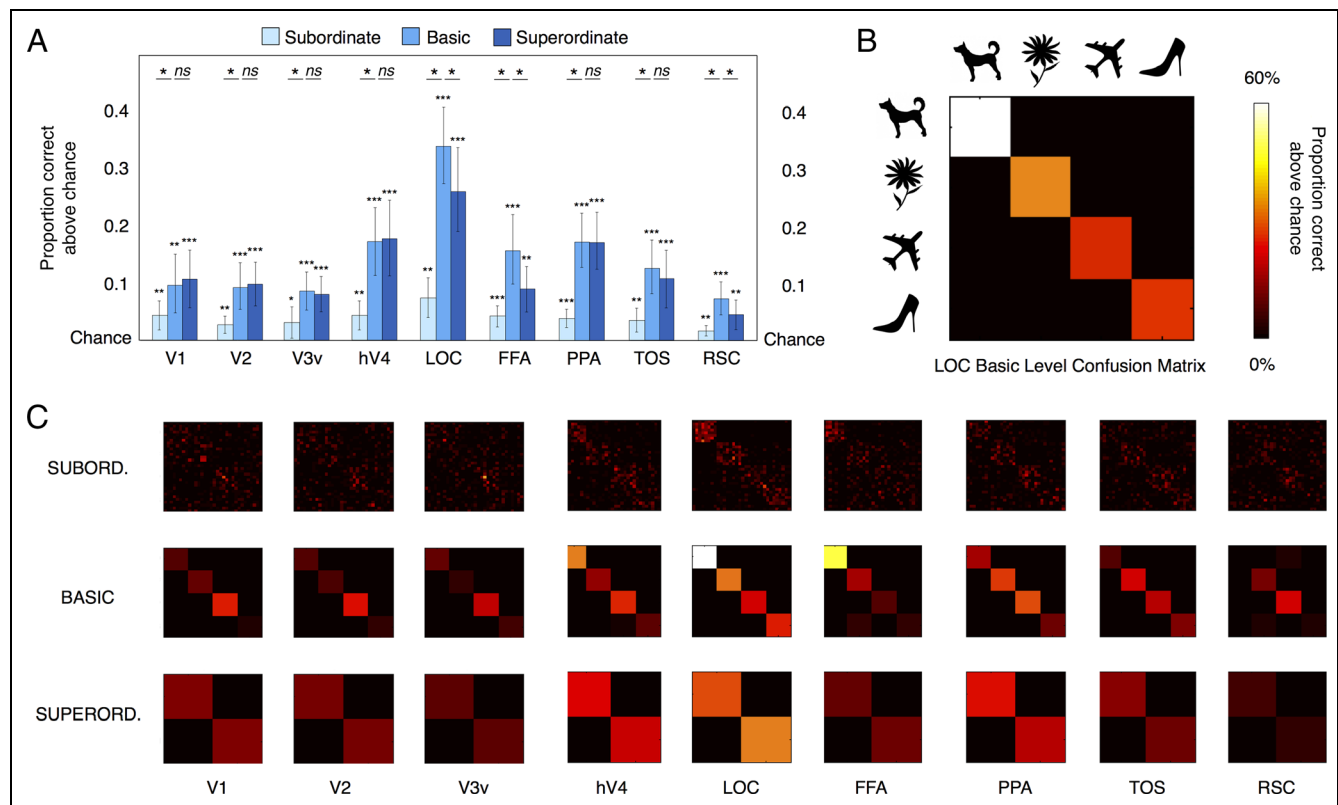


Figure 3. Experiment 1: MVPA classification reveals that object categories are most distinct at the basic level in LOC. (A) Proportion above chance of correct decoding responses for all levels of the taxonomy (chance is zero): subordinate, basic, and superordinate. Top insets denote whether differences between adjacent bars are significant. Category information was discernible significantly above chance at all taxonomic levels and in all ROIs, with higher visual areas generally showing larger values. Highest decoding accuracies were seen in object-selective LOC, but other high-level visual areas that are known to be scene- and face-selective (PPA, TOS, RSC, FFA) also contained category information at all levels. Decoding at the basic level was easier than at the subordinate and superordinate levels in LOC, RSC, and FFA (shaded), but not in any of the other brain areas considered. (B) Confusion matrix example: LOC basic level classification. Basic categories were ordered on the axes according to the pictograms: dogs, flowers, planes, and shoes. At the subordinate level, within each basic category, the eight corresponding subordinates were listed alphabetically. At the superordinate level, the “natural object” category was listed first, and the “man-made object” category was listed second. (C) Confusion matrices for decoding analysis in A: top = subordinate level; middle = basic level; bottom = superordinate level. In all regions, when classification errors did occur, the confusions were more likely to be within the same basic level than between basic levels (e.g., breeds of dogs were commonly confused with other breeds of dogs but not with types of flowers, shoes, or planes), with the effect most salient in LOC. The basic level matrices show that confusions become more common within the basic level as we move up the visual hierarchy. * $p < .05$, ** $p < .01$, *** $p < .001$, ns = not significant. Error bars: 95% confidence interval. SUBORD. = subordinate; SUPERORD. = superordinate.

nificant drop in decoding for both the subordinate and superordinate levels, compared to the basic level (LOC: basic > subord., $t(9) = 11.1, p < .001$; basic > superord., $t(9) = 4.5, p = .002$; FFA: basic > subord., $t(9) = 4.1, p = .003$; basic > superord., $t(9) = 3.0, p = .014$; RSC: basic > subord., $t(9) = 3.9, p = .004$; basic > superord., $t(9) = 2.6, p = .028$). Moreover, we found that, in all regions, when classification errors did occur, the confusions were more likely to be within the same basic level than between basic levels (i.e., breeds of dogs were commonly confused with other breeds of dogs but not with types of flowers, shoes, or planes; Figure 3B), with the effect most salient in LOC (within basic confusions > between basic confusions: LOC, $t(9) = 15.9, p < .001$; TOS, $t(9) = 5.6, p < .001$; PPA, $t(9) = 5.9, p < .001$; RSC, $t(9) = 4.2, p = .002$; FFA, $t(9) = 4.1, p = .003$; V1, $t(9) = 3.1, p = .013$; V2, $t(9) = 4.5, p = .001$; V3v, $t(9) = 4.9, p < .001$; hV4, $t(9) = 6.3, p < .001$).

The trends observed in the correlation classifier decoding results suggest that basic level categories are more clearly delineated at the voxel population level in object-selective areas, compared to the other two levels in our taxonomy. This result provides a quantitative validation to the intuition provided by the category boundary analysis that the basic level represents an optimal level of specificity in object taxonomy in object-selective cortex.

Finally, the basic level is most distinguishable in LOC using the MVPA analysis, but not using the category boundary effect analysis. This finding suggests that MVPA did not weigh cohesion and distinctiveness equally when assigning category labels to neural activations, and thus, cohesion and distinctiveness might not contribute equally to generating category boundaries in LOC.

Experiment 2: Three Superordinate Categories (Vehicles, Furniture, and Musical Instruments)—Removing the Contribution of Real-world Size, Animacy, and Natural Backgrounds

Behavioral Experiments

The stimulus set used in Experiment 1 comprised categories that straddle the boundaries of two main dimensions of selectivity known to affect the responses to objects in occipitotemporal cortex: animacy and real-world size. To ensure that these dimensions have no effect on our results as well as to demonstrate the generalizability of our results from Experiment 1 to additional categories, we constructed a new three-tiered taxonomic hierarchy comprising exclusively big and inanimate objects: three superordinate level categories (vehicles, furniture, musical instruments), nine basic level categories (cars, airplanes, ships, chairs, beds, tables, drums, guitars, pianos), and 36 subordinate level categories (four types of each of the nine basic level categories). In addition, to ensure that our effects were driven by objects and not by their naturalistic backgrounds, we superimposed our new stimuli on meaningless 1/f noise backgrounds.

To finalize our category taxonomy as well as to verify that our putative basic level categories reflect entry level concepts, we conducted a delayed match-to-category behavioral experiment, similar to the one used in Experiment 1. Our strategy was to test our initial category taxonomy and then eliminate members with ambiguous category status. To prune our taxonomy, we defined the basic level advantage to be the RT difference (in z scores) of basic level categorization compared to subordinate level categorization (Figure 4E). We then used this metric to reject the subordinate with the weakest basic level advantage of the four putative subordinate level categories in each basic (eliminating nine subordinate categories of the initial 36), resulting in 27 total subordinate level categories (Figure 4A). Only one of the remaining subordinates (biplane) had a negative basic level advantage, possibly because this less typical plane is better categorized at the subordinate level (Jolicoeur et al., 1984).

To test for the strength of the basic level advantage in our pruned taxonomy, we examined the differences in RTs to correctly verify an image as a member of a subordinate, basic, or superordinate level category. We observed strong basic level effects overall (Figure 4C): Participants were significantly faster to verify category membership at the basic level (566 msec, $SEM = 36$ msec) than at the superordinate level (623 msec, $SEM = 39$ msec; basic > superord.: $t(18) = 6.8, p < .001$). Similarly, basic level categorization was faster than subordinate level categorization (618 msec, $SEM = 36$ msec; basic > subord.: $t(18) = 6.2, p < .001$).

To map categories in terms of their behavioral similarity and dissimilarity, we next used a same-different subordinate level categorization experiment to measure the perceptual distance between all pairs of subordinate categories. Reasoning that images in similar categories will take longer to reject than images from dissimilar categories, we used RTs to pairs of images in the “different” condition to generate a distance metric between our subordinate categories. Consistent with prior work (Rosch et al., 1976), participants found objects within the same basic category to be more similar to each other than to stimuli in other basic categories ($t(74) = 39.0, p < .001$). Furthermore, classical MDS applied to this distance metric revealed that, in a two-dimensional projection, each of the nine basic level categories are clearly separated from one another (Figure 4B).

Similar to Experiment 1, these results replicated Rosch et al.’s (1976) original findings for our new set of object categories by demonstrating that our second taxonomy also exhibits a clear basic level advantage after removing the contribution of animacy, image backgrounds, and real-world size as described by others (Konkle & Caramazza, 2013; Konkle & Oliva, 2012).

Neural Category Boundaries Equally Favor Subordinate and Basic Level Representations

We scanned participants viewing these same three superordinate level categories to assess how neural category

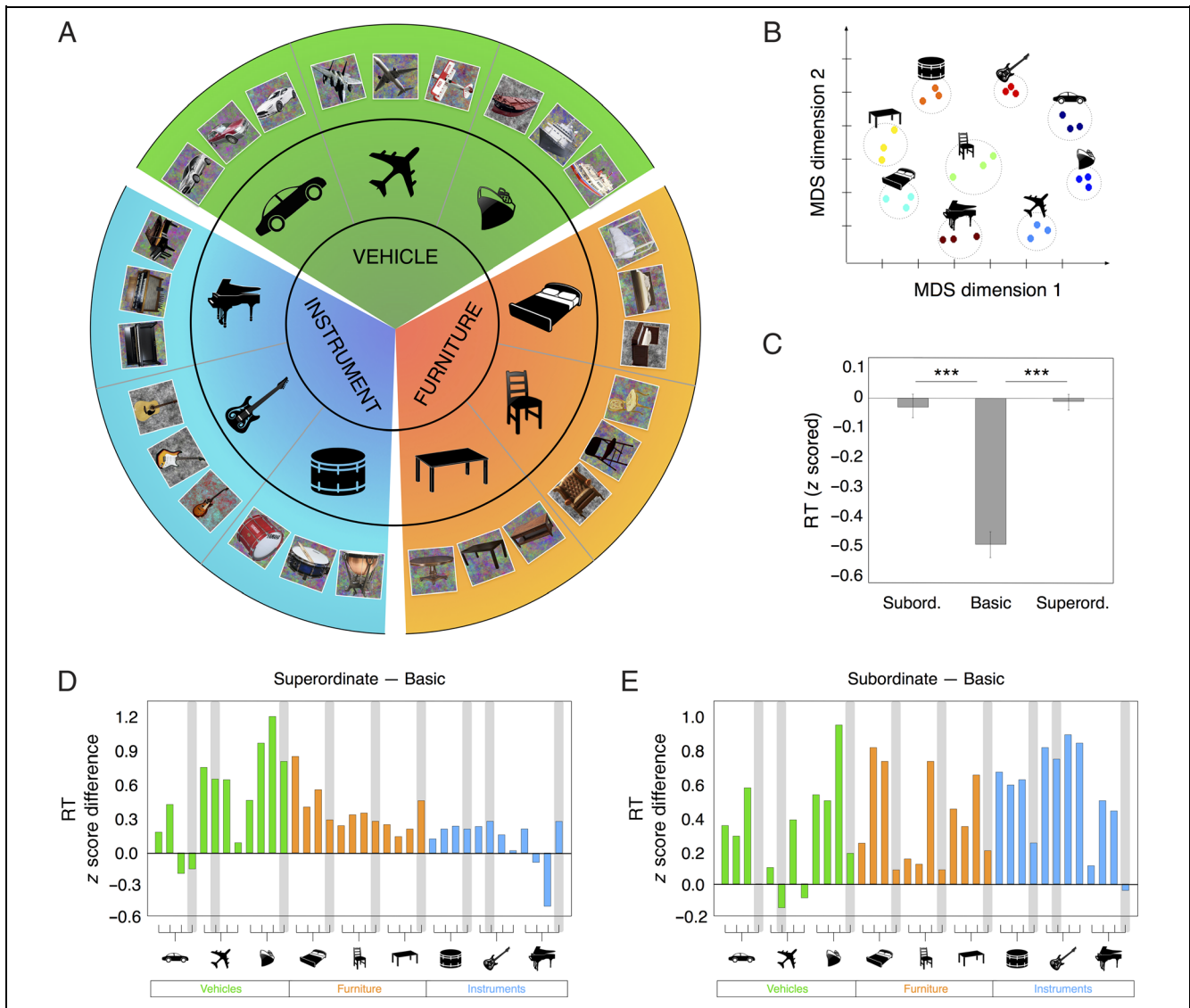


Figure 4. Experiment 2: stimulus set and behavioral results. (A) The stimulus set was organized according to a three-level taxonomic hierarchy comprising 27 subordinate level (most specific, outside layer), nine basic level (middle layer), and three superordinate level (most general, center) categories. Each subordinate category consisted of 40 color photographs, with a representative image shown. Objects varied in color and pose. (B) Same-different subordinate level categorization behavioral experiment. We applied classical MDS to the perceptual distance between subordinate categories measured as z scored RTs. In a two-dimensional solution, all nine basic level categories form separate clusters. (C–E) We used a match-to-category behavioral experiment to finalize our category taxonomy by assessing category status in general and basic level advantage in particular. We tested a larger category taxonomy (36 subordinate categories) and then eliminated members with ambiguous category status. (C) Participants verified category membership significantly faster at the basic level than at the superordinate or subordinate levels. (D) RT difference between basic and superordinate categorization conditions. Positive values indicate basic level advantage. Participants identified almost all stimulus categories faster at the basic level than at the superordinate level. (E) RT difference between basic and subordinate categorization conditions. Positive values indicate basic level advantage. Participants identified almost all stimulus categories faster at the basic level than at the subordinate level. We used this metric to reject the subordinate with the weakest such effect of the putative four subordinate level categories in each basic level (shaded categories were eliminated). Finally, only 1 of the remaining 27 basic level categories (biplane) had a negative basic level advantage, possibly because this less typical plane is better categorized at the subordinate level (Jolicoeur et al., 1984). *** $p < .001$. Error bars: 95% confidence interval. Subord. = subordinate; Superord. = superordinate.

representations change across taxonomic levels and across human ventral visual cortex. As in Experiment 1, participants performed a 1-back repetition task in the scanner (i.e., no explicit categorization task). Again, our analyses focused on object- (LOC), scene- (PPA, RSC, TOS), and face-selective (FFA) regions as well as early visual cortex areas (V1, V2, V3v, hV4).

Our first task for the new taxonomy was to reassess the strength of category representations at each taxonomic level. As such, we computed the category boundary effect for each taxonomic level (subordinate, basic, superordinate) and each brain ROI. We found that, as in Experiment 1, the category boundary effect was largest at the subordinate level in early visual areas, but this trend

disappeared in higher visual areas compared to the basic level (Figure 5A; subordinate > basic: V1, $t(16) = 5.7$, $p < .001$; V2, $t(16) = 4.2$, $p < .001$; V3v, $t(16) = 3.8$, $p = .002$; hV4, $t(16) = 1.4$, $p = .186$; LOC, $t(16) = 0.3$, $p = .754$; FFA, $t(16) = 0.7$, $p = .525$; PPA, $t(16) = 2.6$, $p = .018$; TOS, $t(16) = 0.1$, $p = .920$; RSC, $t(16) = 0.6$, $p = .583$; subordinate > superordinate: V1, $t(16) = 3.5$, $p = .003$; V2, $t(16) = 3.0$, $p = .008$; V3v, $t(16) = 2.7$, $p = .016$; hV4, $t(16) = 1.5$, $p = .161$; LOC, $t(16) = 2.1$, $p = .053$; FFA, $t(16) = 0.6$, $p = .533$; PPA, $t(16) = 0.7$, $p = .501$; TOS, $t(16) = 2.5$, $p = .022$; RSC, $t(16) = 1.3$, $p = .203$). Moreover, the category boundary effect increased in LOC com-

pared to V1 at all levels of the taxonomy (LOC > V1: subord., $t(16) = 2.9$, $p = .011$; basic, $t(16) = 4.1$, $p < .001$; superord., $t(16) = 2.6$, $p = .021$). These results again suggest that categories become more sharply distinguishable as we move up the visual hierarchy, and furthermore, early visual areas appear to favor subordinate distinctions, whereas in later areas this difference disappears between subordinate and basic levels.

This trend was, in fact, an enhanced version of our findings in Experiment 1: When comparing the difference between category boundaries at the basic level versus the other two levels, it became clear that the relative

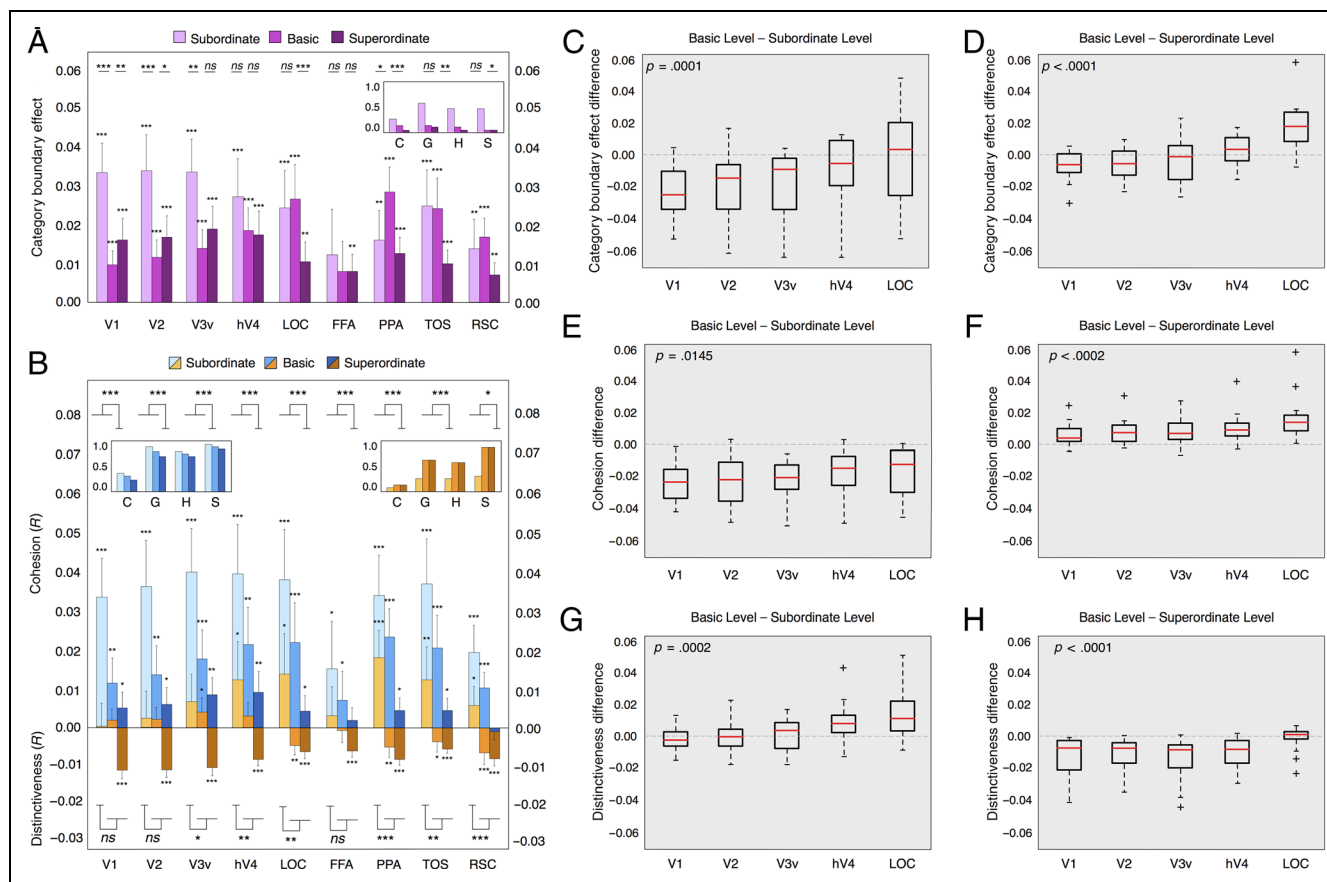


Figure 5. Experiment 2: After controlling for animacy, real-world size, and naturalistic backgrounds, neural category boundaries still show that basic level representations gain an increasing advantage as we move up the ventral visual stream. (A) Category boundary effect for neural activity patterns at each taxonomic level and in each ROI. Inset shows same analysis for image feature descriptors: C = color histograms; G = GIST features; H = HOG features; S = SIFT features. Early visual areas favored subordinate distinctions, whereas, in later areas, this difference disappeared between subordinate and basic levels. (B) Cohesion and distinctiveness for neural activity patterns at each taxonomic level and in each ROI. Inset shows same analyses for image feature descriptors. Cohesion generally decreased with taxonomic level and was significantly weaker at the superordinate level compared to the other two levels in all ROIs, which suggests that object representations become less homogenous within their category across visual cortex. Distinctiveness generally increased with taxonomic level and was significantly weaker at the subordinate level compared to the basic and superordinate levels in all ROIs, except for FFA, V1, and V2. (C, D) Category boundary effect difference between basic level and subordinate and superordinate levels. We observed an enhanced version of our findings in Experiment 1: When comparing the difference between category boundaries at the basic level versus the other two levels, it becomes apparent that the basic level gains an advantage over both the subordinate and superordinate levels as we move up the visual hierarchy from V1 to LOC. (E, F) Cohesion difference between basic level and subordinate and superordinate levels. (G, H) Distinctiveness difference between basic level and subordinate and superordinate levels. In contrast to Experiment 1, the category boundary difference appears to be driven by both components of the category boundary effect. The advantage of the subordinate level over the basic level disappeared in later visual areas, mainly because of the sharp increase in distinctiveness between early visual areas and LOC, whereas the advantage of the basic level over the superordinate level remained strong because of an increase in both cohesion and distinctiveness between early visual areas and LOC. * $p < .05$, ** $p < .01$, *** $p < .001$, ns = not significant. Error bars: 95% confidence interval. Shaded graphs indicate a significant increase from V1 to LOC.

difference between the basic and subordinate levels decreased much more sharply and ultimately disappeared as we move up the visual hierarchy from V1 to LOC. Simultaneously, the difference between basic and superordinate levels strongly increased along the visual hierarchy (Figure 5C and D; increasing trends in category boundary effect difference from V1 to LOC for basic – subord.: $p < .001$; basic – superord.: $p < .001$; Friedman nonparametric tests). In addition, category boundary was generally higher at the basic level than the superordinate throughout visual cortex, and interestingly, subordinate category boundary started out with advantage over the basic level (generally negative values for V1; Figure 5C), but this advantage disappeared as we moved up the visual cortical hierarchy (zero and slightly positive values for LOC; Figure 5C).

Overall, the second experiment confirms our initial results: The subordinate and basic levels are both strongly represented, with the former being especially emphasized in early visual cortex whereas the latter gaining an equally strong representation in LOC. Moreover, we notice a gradual trade-off between the subordinate and basic levels, which becomes apparent as we move up the visual hierarchy.

Category Cohesion and Distinctiveness across Occipitotemporal Cortex

Next, we replicated the analyses that investigate each component of the category boundary effect separately (cohesion and distinctiveness). Again, we found that cohesion decreased with taxonomic level across all ROIs (Figure 5B, top), such that it was significantly weaker at the superordinate level compared to the other two levels in the taxonomy in all ROIs (superordinate < basic and subordinate V1: $t(16) = 6.9, p < .001$; V2: $t(16) = 6.2, p < .001$; V3v: $t(16) = 6.9, p < .001$; hV4: $t(16) = 6.5, p < .001$; LOC: $t(16) = 6.0, p < .001$; FFA: $t(16) = 2.5, p = .026$; PPA: $t(16) = 7.1, p < .001$; TOS: $t(16) = 6.4, p < .001$; RSC: $t(16) = 6.3, p < .001$). Concurrently, between-category dissimilarity (distinctiveness) generally increased with taxonomic level (Figure 5B, bottom), such that it was significantly weaker at the subordinate level compared to the basic and superordinate levels in all ROIs, except for FFA, V1, and V2 (subordinate < basic and superordinate V1: $t(16) = 1.5, p = .142$; V2: $t(16) = 1.9, p = .080$; V3v: $t(16) = 2.6, p = .018$; hV4: $t(16) = 3.1, p = .007$; LOC: $t(16) = 3.3, p = .005$; FFA: $t(16) = 1.6, p = .130$; PPA: $t(16) = 6.4, p < .001$; TOS: $t(16) = 3.5, p = .003$; RSC: $t(16) = 4.2, p < .001$). In other words, Experiment 2 confirms our initial findings: The ventral visual cortex is optimizing category representations, and object categories are represented such that they maximize within-category similarity and between-category dissimilarity, with the basic level striking the best balance between category cohesion and distinctiveness.

Furthermore, in contrast to Experiment 1 where cohesion increased in LOC compared to V1 at all levels of the

taxonomy, in Experiment 2, we observed this effect only at the basic level but not at the subordinate or superordinate levels (LOC > V1: subord., $t(16) = 1.2, p = .249$; basic, $t(16) = 2.9, p = .012$; superord., $t(16) = 0.6, p = .551$), suggesting that object representations become overall more homogenous within their basic category in later visual areas. Note that this phenomenon cannot be explained by animacy, real-world size, or image backgrounds, as our stimulus set in this experiment did not vary across these factors. As in Experiment 1, distinctiveness increased in LOC compared to V1 at all levels of the taxonomy (LOC > V1: subord., $t(16) = 3.3, p = .005$; basic, $t(16) = 5.7, p < .001$; superord., $t(16) = 4.1, p < .001$), which suggests that object representations become better differentiated across categories in later visual areas, regardless of taxonomic level. In other words, basic level category representations benefit from both increased cohesion and distinctiveness as we move up the ventral visual stream, whereas subordinate and superordinate categories only exhibit increased distinctiveness, suggesting a potential advantage for the basic level in higher visual areas.

To further investigate whether changes in cohesion and distinctiveness favor the basic level, we compared these quantities across both taxonomic level and visual areas (Figure 5E–H). The advantage of the basic level over the subordinate level in later visual areas was again mainly because of the sharp increase in distinctiveness between early visual areas and LOC (Figure 5G; basic – subord. distinctiveness increase from V1 to LOC: $p < .001$; Friedman nonparametric test). Interestingly, however, cohesion also exhibited a slight increase as we moved up the visual stream, albeit much less so than distinctiveness (Figure 5E; basic – subord. cohesion increase from V1 to LOC: $p = .015$; Friedman nonparametric test). This suggests that, although the contribution of cohesion to the difference between subordinate and basic level representations is small, this component nonetheless exerts a quantifiable influence in the category representations we observed.

Whereas, in Experiment 1, the advantage of the basic level over the superordinate was mostly because of an increase in cohesion, here, the same advantage was because of an increase in both cohesion and distinctiveness between early visual areas and LOC (Figure 5F and H; increasing trends in cohesion and distinctiveness difference from V1 to LOC for cohesion basic – superord.: $p < .001$, distinctiveness basic – superord.: $p < .001$; Friedman nonparametric tests). It is possible that, in Experiment 1, we were unable to detect this emerging distinctiveness advantage for the basic level over the superordinate because our “natural object” category included both animate and inanimate stimuli, which were overall more distinctive and thus obscured a more subtle change between levels.

Overall, our results replicate our findings in Experiment 1, which show that a trade-off exists between

category cohesion and category distinctiveness at the two extremes of our taxonomy (subordinate and superordinate levels), with the basic level potentially striking the best balance between these two quantities by encompassing both strong within-category similarity and strong between-category dissimilarity. In short, our data suggest that the basic level simultaneously gains an advantage over both the subordinate and superordinate levels as we move up the visual hierarchy from V1 to LOC.

The Contribution of Low-level Visual Features

Similar to Experiment 1, we sought to show that the patterns of results obtained in LOC were not attributed to low-level image features. As such, we computed category boundary effect, cohesion, and distinctiveness in an analogous fashion for image descriptor features extracted from our stimulus images: color histograms, GIST (Oliva & Torralba, 2001), HOG (Dalal & Triggs, 2005), and SIFT (Lowe, 2004). Here, we found an enhanced version of our findings from Experiment 1: Descriptor category boundaries strongly favored the subordinate level, thus more closely capturing early visual cortex representations (Figure 5A, inset). By contrast, neural patterns in LOC, TOS, PPA, and RSC exhibited a trend for reversing the preference of subordinate and basic levels, favoring the latter.

Furthermore, we once again found that, for all our feature descriptors, both cohesion and distinctiveness had high positive values for all levels of the taxonomy. This implies that a high degree of similarity exists between all our stimulus images in terms of their low-level features, even among categories that were highly distinctive in our neural data. Thus, although image features may partly explain cohesion, they do a poor job at characterizing the distinctiveness between object categories we observe in the neural data.

Correlation Classification Shows Basic Level Advantage in LOC

Finally, as we did in Experiment 1, we used a more data-driven approach to assess category boundaries by implementing an MVPA correlation classifier to decode category identity from each ROI at each taxonomic level (subordinate, basic, superordinate). We found that the information present in voxel-level neural patterns was sufficient to distinguish above-chance between categories at all levels in the hierarchy and in all brain regions considered: object-, scene-, and face-selective (LOC, FFA, PPA, RSC, TOS) areas, as well as early visual areas (V1, V2, V3v, hV4; Figure 6A).

Critically, however, we again found that information about object category did not increase monotonically with category generality (taxonomic level) in all brain areas. In LOC, accuracy was highest at the basic level, and we saw a significant drop in decoding for both the subordinate and superordinate levels, compared to the

basic level (LOC: basic > subord., $t(16) = 2.4, p = .031$; basic > superord., $t(16) = 4.4, p < .001$). Moreover, we found that, in all regions, when classification errors did occur, the confusions were more likely to be within the same basic level than between basic levels (i.e., types of cars were commonly confused with other types of cars but not with types of ships, for example; Figure 6B), with the effect most salient in LOC (within basic confusions > between basic confusions: V1, $t(16) = 5.3, p < .001$; V2, $t(16) = 5.7, p < .001$; V3v, $t(16) = 6.3, p < .001$; hV4, $t(16) = 5.1, p < .001$; LOC, $t(16) = 5.5, p < .001$; FFA, $t(16) = 4.4, p < .001$; TOS, $t(16) = 6.3, p < .001$; PPA, $t(16) = 7.7, p < .001$; RSC, $t(16) = 6.9, p < .001$).

Our correlation classifier decoding results mirror the findings from Experiment 1, which suggest that the basic level represents an optimal level of specificity in object taxonomy in object-selective cortex. Furthermore, we again see evidence that MVPA did not weigh cohesion and distinctiveness equally when assigning category labels to neural activations, because decoding produces a stronger advantage for the basic level than the category boundary analysis. This suggests that cohesion and distinctiveness might not contribute equally to generating category boundaries in LOC.

Together, our two experiments show that category representations change as a function of taxonomic level across the span of the human ventral visual processing stream: Initially, subordinate categories are more distinguishable in early visual areas, but this advantage diminishes in later areas, and this is because of changes in both category cohesion and distinctiveness between visual areas. Most importantly, by testing two separate taxonomies, each representative of real-world hierarchical organization of objects, we show that this effect is robust, generalizable, not fully explained by low-level visual features, and persists after eliminating image backgrounds and removing the contribution of animacy and real-world size.

DISCUSSION

Our work establishes a link between the neural representation of object categories in occipitotemporal cortex and human object taxonomy. We achieve this by showing that, for two category taxonomies that exhibit a clear behavioral basic level advantage, category representations change as a function of taxonomic level as we move up the ventral visual cortical hierarchy. This provides evidence that basic level structure may be an emergent property of the human visual system.

Consistent with the tenets of categorization theory (Rosch et al., 1976), patterns in high-level visual cortex adhere to the principle of simultaneously maximizing within-group similarity and between-group dissimilarity. Moreover, our results provide the first neural support for the hypothesis that the basic level strikes the best balance between these two measures, whereas the subordinate and superordinate levels appear to each optimize

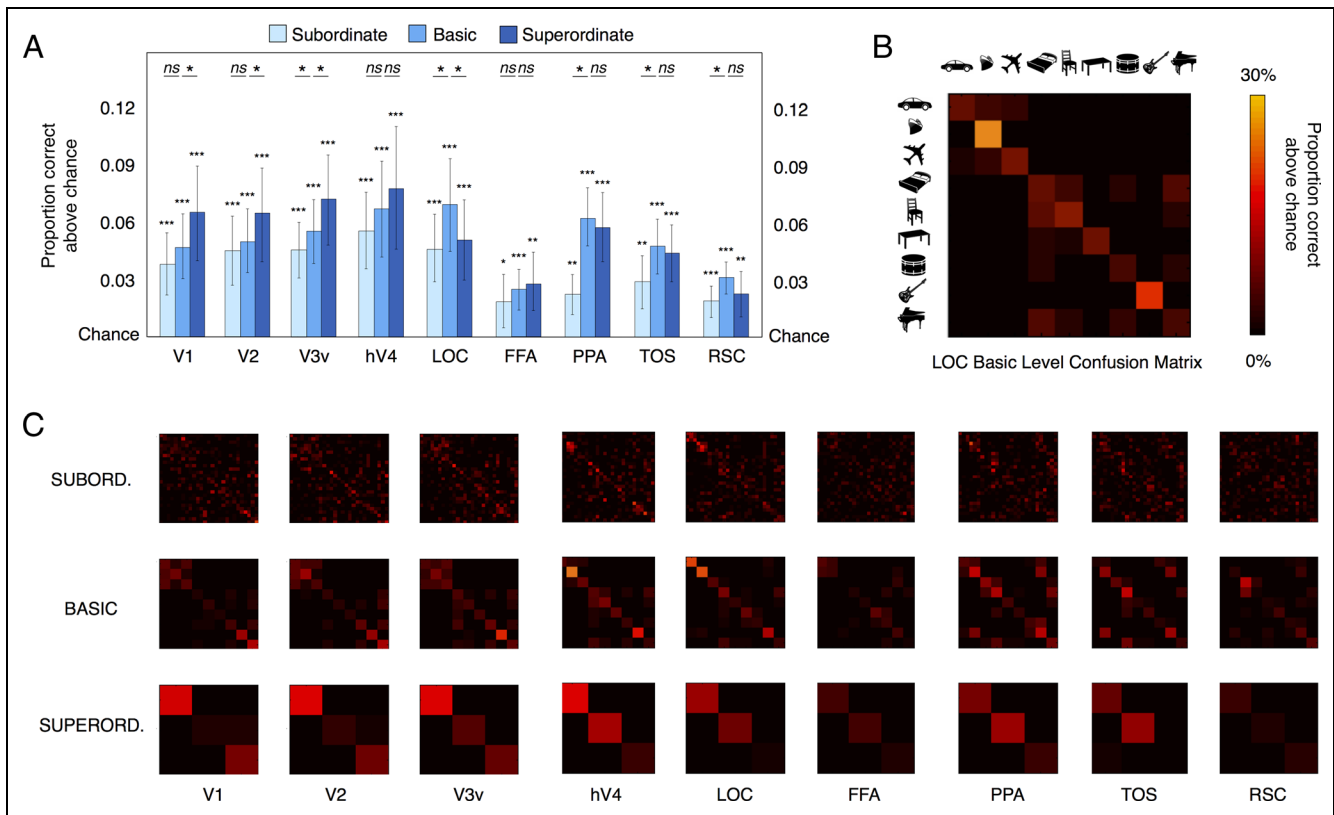


Figure 6. Experiment 2: After controlling for animacy, real-world size, and naturalistic backgrounds, MVPA classification reveals that object categories are most distinct at the basic level in LOC. (A) Proportion above chance of correct decoding responses for all levels of the taxonomy (chance is zero): subordinate, basic, and superordinate. Top insets denote whether differences between adjacent bars are significant. Category information was discernible significantly above chance at all taxonomic levels and in all ROIs. Decoding accuracy at the basic level was higher than both at the subordinate and superordinate levels in LOC, but not in any of the other brain areas considered. (B) Confusion matrix example: LOC basic level classification. Basic categories were ordered on the axes according to the pictograms: cars, ships, planes, beds, chairs, tables, drums, guitars, and pianos. At the subordinate level, within each basic category, the three corresponding subordinates were listed alphabetically. At the superordinate level, the “vehicle” category was listed first, the “furniture” category was listed second, and the “musical instrument” category was listed last. (C) Confusion matrices for decoding analysis in A: top = subordinate level; middle = basic level; bottom = superordinate level. In all regions, when classification errors did occur, the confusions were more likely to be within the same basic level than between basic levels (e.g., types of cars were commonly confused with other types of cars but not with ships or beds), with the effect most salient in LOC. The basic level matrices show that confusions become more common within the basic level as we move up the visual hierarchy. * $p < .05$, ** $p < .01$, *** $p < .001$, *ns* = not significant. Error bars: 95% confidence interval. SUBORD. = subordinate; SUPERORD. = superordinate.

similarity along one dimension over the other (Rosch, 1978). Moreover, our data underscore the importance of considering the joint contribution of both aspects that give rise to the concept of a category in visual cortex: Within-category similarity (cohesion) may be an intuitive candidate for what makes a good category, but our work shows that, in fact, distinctiveness is just as important in establishing neural category boundaries and actually varies more sharply between early visual areas and object-selective cortex than cohesion. Most importantly, this organizational principle emerges gradually as we move up the visual cortical hierarchy and is not present in either low-level image features or early visual cortex activations (Figures 2 and 5). This suggests that objects in the world do not group naturally by basic level category in terms of their appearance, but instead, successive levels in the visual system may be optimizing basic level categorizations.

Previous studies have reported that information decoding in early visual areas using a linear classifier is at

chance levels when retinal location, viewing angle, or size is altered (Cichy, Chen, & Haynes, 2011; Eger, Ashburner, et al., 2008; Eger, Kell, & Kleinschmidt, 2008). Perhaps surprisingly, our results show a predilection for early visual areas to group objects strongly at the subordinate level, with this grouping diminishing gradually in favor of the basic level only in later visual processing regions. This effect can be well understood if we consider that objects within the same subordinate level category share more low-level features in common with each other than with members of other (subordinate, basic, or superordinate) categories, as evidenced by the low-level feature analyses in Figures 2A, B and 5A, B (insets). Thus, given that subordinates share more overall low-level features in common, we expect to observe greater subordinate level category cohesion, especially in early visual areas. High cohesion here may also be partially explained by the fact that our stimuli were all presented centrally, allowing the low-level features to overlap despite the localized

information processing and the small receptive fields in these areas (Cichy et al., 2011; Eger, Ashburner, et al., 2008; Eger, Kell, et al., 2008). Consequently, our results do not imply that fine-grained category distinctions are most strongly represented in early visual cortex; instead, early visual cortex is simply the region where low-level features best drive similarity of activity patterns. In fact, decoding performance in early visual cortex indicates that subordinate categories are less distinguishable than the other two, presumably reflecting their low distinctiveness. Altogether, this suggests that the principle of maximizing within-category similarity and between-category dissimilarity is necessary but not sufficient for a good category representation: For example, in early visual areas, we see strong category boundaries, but they are likely because of low-level features.

Our results support the hypothesis that fine-grained categories become more separable in higher visual areas at the scale of neural response afforded to us by fMRI. This trend is illustrated best in Figure 5B: Initially, activity patterns elicited by subordinates are not distinguishable (distinctiveness near zero in V1), but they become increasingly anticorrelated (significantly positive distinctiveness in hV4 and LOC). This indicates that fine-grained distinctions increase with complexity of visual processing and that the high category boundary effect values observed for subordinate categories in early visual areas are mainly driven by high cohesion because of low-level feature overlap. Finally, although low-level features of our stimuli may, in part, contribute to the overall trend we observe for subordinate categories, prior evidence suggests that, indeed, visual features may be inextricably linked to categorical representations (Fairhall, Anzellotti, Pajtas, & Caramazza, 2011; Kellenbach, Wijers, & Mulder, 2000).

Anatomically, prior evidence suggests that large-scale smooth selectivity gradients for semantic category groupings (Huth et al., 2012) and object attributes, such as animacy (Connolly et al., 2012; Kriegeskorte et al., 2008; Chao et al., 1999) and real-world size (Konkle & Oliva, 2012), underlie object category responses in the human visual system. By leveraging similarity in cortical activity patterns, our work complements this view by revealing what may be an important principle of categorization in the brain: Fine-grained representations trade off with more general basic level representations after early visual areas. By analyzing the similarity between the patterns of category responses, we uncovered a tendency for object-selective cortex (LOC) to amplify basic level category boundaries compared to those at other taxonomic levels. Although this tendency is strongest in LOC, other high-level areas exhibit similar trends compared to early visual cortex (albeit much less so than LOC). These include both scene-selective (PPA, TOS, RSC) and face-selective (FFA) areas. The fact that object-related activity behaves similarly in these high-level visual areas, including those that are not typically associated with object processing (PPA,

TOS, RSC), suggests that these areas may share common computations—computations whose byproduct is to clarify and separate categories.

The behavioral basic level advantage is mainly supported by evidence that most objects are categorized faster at the basic level (Mack et al., 2009; Tanaka & Taylor, 1991; Murphy & Wisniewski, 1989; Murphy & Brownell, 1985; Jolicoeur et al., 1984; Smith, Balzano, & Walker, 1978; Rosch et al., 1976; but not for domain-level naming: Taylor, Devereux, Acres, Randall, & Tyler, 2012) and that basic level labels are used nearly exclusively when people freely name an object (Rosch et al., 1976). Our results offer a plausible neural explanation for these aspects of the basic level perceptual advantage. Under our proposed model, the basic level advantage arises because of cortical computations that increase the efficacy of basic level category boundaries between early visual cortex and object-selective cortex. If LOC primarily enhances category representations between objects at the basic level, then areas that use its afferents as input (temporal: McClelland & Rogers, 2003; or frontal: Freedman & Miller, 2008; Miller, Freedman, & Wallis, 2002) would require less computation and thus less time to extract or construct categorical information at the basic level of specificity. Information about basic category is easily linearly separable in LOC, whereas further computations would be required to access subordinate and superordinate representations. Consequently, basic level information is mostly available from polling object-selective areas at little additional computational cost and thus voluntarily expressed faster, which is consistent with prior behavioral findings (Rosch et al., 1976). Consequently, our results are also consistent with the hypothesis that an enhanced basic level advantage for neural patterns of activity might arise at a postperceptual level of representation, such as in high-level semantic areas (e.g., posterior middle temporal gyrus, inferior temporal gyrus) that likely represent and build amodal representations of object categories (Clarke & Tyler, 2014; Bruffaerts et al., 2013; Fairhall & Caramazza, 2013). Indeed, we believe the search for such an area and representation constitutes an interesting avenue for future study.

Although the basic level advantage is a well-accepted phenomenon, there is some controversy surrounding its robustness: Some behavioral studies report that either the subordinate or superordinate level is accessed first, rather than the basic level of specificity (Taylor et al., 2012; Mace et al., 2009; Mack et al., 2009; Tanaka & Taylor, 1991; Jolicoeur et al., 1984). In our behavioral experiments, we found a strong basic level advantage for virtually all categories we investigate in terms of speeded categorizations, thus confirming that the entry level for our taxonomy lies at the basic level. Nonetheless, the real world contains several orders of magnitude more categories embedded in a much deeper hierarchical tree than the three-tiered taxonomy we used. Thus, the results reported here do not preclude the

possibility that a carefully picked stimulus set (e.g., containing less typical members of basic categories; Jolicoeur et al., 1984), a different task (e.g., ultrafast categorization; Mace et al., 2009), or a set of participants who possess expertise in the categories being tested (Tanaka & Taylor, 1991) may change the level of the taxonomy at which neural patterns may group object stimuli. Furthermore, our results are highly generalizable across two separate hierarchies where the superordinate level is defined at different specificity distances from the basic level (arguably natural and man-made are farther from the basic level than vehicles, musical instruments, and furniture). We are agnostic, however, whether other possible superordinates may fare differently against our basic level categories. Nevertheless, we would then predict that such effect would also be reflected in behavior. As such, all the above manipulations provide interesting avenues of further inquiry.

More broadly, our data suggest an alternative hypothesis to the view that categorical distinctions emerge mainly from processing in anterior temporal or frontal areas of the brain (Freedman & Miller, 2008; McClelland & Rogers, 2003; Miller et al., 2002), a view also mirrored by models that strongly encapsulate vision from cognition (Riesenhuber & Poggio, 2000; Phyllyshyn, 1999; Fodor, 1993). Instead, our work shows that clear category separations emerge gradually as early as occipitotemporal regions and in the absence of an explicit categorization task, suggesting that categorization may be part of visual processing. This view is consistent with recent behavioral results that show that categories alter perception (Gilbert, Regier, Kay, & Ivry, 2006), even when categorization is task irrelevant (Lupyan, Thompson-Schill, & Swingley, 2010).

The basic level advantage is a pervasive phenomenon that captures something fundamental about human cognition. As such, it has influenced many fields of knowledge, ranging from psychology and neuroscience to molecular biology, engineering, and the humanities. In fact, Rosch's original finding was cited over 4000 times across these disciplines. Our work provides a long overdue understanding of why the basic level might be privileged: The human brain appears to build basic level categories over successive visual areas. Such an understanding is key to answering the broader question about how the human brain extracts and organizes information from our visual world.

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Reprint requests should be sent to Marius Cătălin Iordan, Computer Science Department, Stanford University, 353 Serra Mall, Rm. 240, Stanford, CA 94305, or via e-mail: mci@cs.stanford.edu.

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