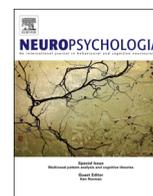




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journal homepage: www.elsevier.com/locate/neuropsychologiaConceptual size representation in ventral visual cortex[☆]Shai Gabay^{a,b,*}, Eyal Kalanithroff^{c,d}, Avishai Henik^e, Nurit Gronau^a^a Department of Psychology & Cognitive Science Studies, The Open University, Raanana, Israel^b Department of Psychology and the Institute of Information Processing and Decision Making, University of Haifa, Haifa, Israel^c Anxiety Disorders Clinic and the Center for OCD and Related Disorders, New York State Psychiatric Institute, New York, NY, United States^d Department of Psychiatry, Columbia University Medical Center, New York, NY, United States^e Department of Psychology and Zlotowski Center for Neuroscience, Ben-Gurion University of the Negev, Beer-Sheva, Israel

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ABSTRACT

Recent findings suggest that visual objects may be mapped along the ventral occipitotemporal cortex according to their real-world size (Konkle and Oliva, 2012). It has been argued that such mapping does not reflect an abstract, conceptual size representation, but rather the visual or functional properties associated with small versus big real-world objects. To determine whether a more abstract conceptual size representation may affect visual cortical activation we used meaningless geometrical shapes, devoid of semantic or functional associations, which were associated with specific size representations by virtue of extensive training. Following training, participants underwent functional magnetic resonance imaging (fMRI) scanning while performing a conceptual size comparison task on the geometrical shapes. In addition, a size comparison task was conducted for numeral digits denoting small and big numbers. A region-of-interest analysis revealed larger blood oxygenation level dependent (BOLD) responses for conceptually 'big' than for conceptually 'small' shapes, as well as for big versus small numbers, within medial (parahippocampal place area, PPA) and lateral (occipital place area, OPA) place-selective regions. Processing of the 'big' visual shapes further elicited enhanced activation in early visual cortex, possibly reflecting top-down projections from PPA. By using arbitrary shapes and numbers we minimized visual, categorical, or functional influences on fMRI measurement, providing evidence for a possible neural mechanism underlying the representation of abstract conceptual size within the ventral visual stream.

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1. Introduction

Several large-scale organizing principles have been proposed for the representation of stimuli in the ventral temporal cortex. One such principle is the retinotopic eccentricity of visual stimuli, where stimuli occupying central retinal locations activate mainly lateral temporal areas encompassing face and word-selective regions, while more eccentric stimuli requiring peripheral vision activate mainly medial temporal areas encompassing place/scene-selective regions¹ (Levy et al. (2001), Malach et al. (2002) but also see Troiani et al. (2012)). A different yet associated suggestion is that objects are organized along the visual cortex according to

their apparent size. Using perspective cues that create a distance illusion for stimuli of equal retinal size, Cate et al. (2011) demonstrated that object-selective regions (e.g., lateral occipital cortex, LO) and scene-selective regions (parahippocampal place area, PPA) are preferentially activated by stimuli perceived as small or large, respectively (see also Amit et al. (2012)). Stimuli perceived as large due to perspective distance cues were also found to be represented within a wider cortical region in early visual areas (e.g., V1) (Murray et al., 2006), suggesting that top-down neuronal projections (possibly originating at the PPA) may affect early perceptual processing stages (Fang et al., 2008; Murray et al., 2006; Sperandio et al., 2012).

Interestingly, recent evidence has demonstrated that activation in ventral occipitotemporal regions is not only affected by an object's perceived size, but also by its real-world size as determined by stored semantic knowledge (Konkle and Oliva (2012), see also He et al. (2013)). An image of a peach, for instance, elicits stronger activation in lateral ventral temporal regions than an image of a piano (both occupying equal retinal size), while an opposite activation pattern is observed in medial temporal regions. Critically, these cortical areas were found to be almost unaffected by conceiving the objects in an atypical size (e.g., imagining a peach is

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¹ We use the terms "place-" and "scene-selective" regions interchangeably, to describe the parahippocampal place area (PPA) and the occipital place area (OPA).

large or a piano is small). Consequently, [Konkle and Oliva \(2012\)](#) proposed that the spatial topography of objects in the ventral visual cortex does not represent an abstract representation of conceptual size, such as the stored semantic knowledge that an object is big or small. Rather, it represents the functional or visual properties that are correlated with small and big real-world objects. For instance, small objects are typically graspable and manipulable, while big objects tend to be heavy and non-manipulable. Consequently, small objects can be carried and used as effectors, whereas big objects provide support for the body or serve as landmarks in the environment. In addition, small and big objects may vary in their global shape and in their low-level visual features ([Konkle and Caramazza, 2013](#); [Konkle and Oliva, 2012](#)). It is these features and functional characteristics of stimuli, rather than their conceptual size *per se*, which are represented in ventral visual cortex, according to the authors.

However, lifetime experience with everyday objects may undermine an attempt to manipulate their conceived size independently of semantic and functional knowledge associated with the objects. Thus, for example, a peach imagined as large may still be conceptualized as a fruit which is picked, grasped and eaten. Namely, the real-world size of an object may be an inseparable part of its long-term memory representation (e.g. [Gabay et al. \(2013\)](#) and [Konkle and Oliva \(2011\)](#)), and it may be difficult to uncouple size properties from other semantic and functional object properties (see also [Amit et al. \(2012\)](#)). In order to allow a more “pure” assessment of conceptual size effects on cortical activation, one may need to control for stimulus identity by using novel, meaningless stimuli.

In the present study, participants were extensively trained to assign specific conceptual sizes to arbitrary, geometrical shapes of equal retinal size. Participants learned the ‘size’ of the shapes by using images of real-world animals (e.g., a cat, a tiger, an elephant, all presented in equal retinal size) as reference points. That is, they learned the relative size of a shape with respect to a smaller and/or a bigger animal (see detailed procedure in the methods [Section 2](#)). Prior to the beginning of the training phase, a ‘conceptual size scale’ was constructed, which participants were unaware of and to which they were never exposed. Animal categories were arranged on the scale according to their conceptual (i.e., real-world) size, interleaved with the geometrical shapes. During training, participants were asked in each trial which of two stimuli – an animal or a particular shape – were conceptually bigger. Participants learned the relative sizes of the shapes via trial and error (each participant completed at least 4 separate training sessions), until they reached a high performance level on a size-comparison test containing shapes only. Subsequently, they performed a conceptual size comparison task on the geometrical shapes while being scanned in a functional magnetic resonance imaging (fMRI) scanner. Importantly, the comparison task was limited to shape stimuli and animal images were excluded altogether at this stage. Note that it has been previously shown that while the ventral visual cortex is sensitive to the real-world size of objects, it is rather immune to the size of animals ([Konkle and Caramazza, 2013](#)). Any potential association with big or small animals during the shape comparison task, therefore, should not affect cortical activation elicited by the shapes.

To examine more closely the neural underpinnings of conceptual size representation we further ran an additional study in which participants were presented with Arabic digits denoting small or big numerical values. Note that digits signify size, or magnitude, via a symbolic representation which is clearly abstracted from object meaning or category. Obtaining size-related effects of digits in visual associative regions may provide an additional important evidence for a rather abstract conceptual size representation in the ventral cortex. In line with this view, recent

behavioral findings have shown that the conceptual size representation of objects may be associated with numerical value ([Gabay et al., 2013](#)). To avoid carry-over effects of the digits on the learned conceptual sizes of the shapes, a digit size comparison task was always conducted subsequent to the shape size comparison task.

To anticipate, our ROI analysis findings demonstrated that both medial (parahippocampal place area, PPA) and lateral (occipital place area, OPA) place-selective regions, as well as early visual cortex, were found to be more strongly activated by the presentation of conceptually ‘big’ than ‘small’ arbitrary shapes. Stronger activation in the right PPA and right OPA was also found for digits denoting large than for digits denoting small numerical value. Finally, the effect of the shape size in the EVC was positively correlated with activation differences in PPA.

2. Materials and methods

2.1. Participants

Ten participants (3 males, 7 females, mean age=23.6 years, $SD=1.65$, range=21–26 years) participated in the experiment for payment. All participants were right handed, reported normal or corrected-to-normal visual acuity, gave their informed consent to participate in the study, and had no known history of a neurological disorder. All experimental procedures were approved by the Helsinki Committee of Soroka Medical Center, Beer Sheva, Israel.

2.2. Materials and task procedures

2.2.1. Training phase: assigning a conceptual size to arbitrary shapes

Stimuli in the training phase consisted of six geometrical shape categories, each containing five stimulus exemplars. The stimulus exemplars within a certain shape category consisted of a basic shape (e.g., a triangle) and four additional tilted versions of the basic shape (e.g., a triangle tilted 22.5° to the right, a triangle tilted 45° to the right, and two corresponding triangles tilted to the left). All geometrical shapes were filled with a checker-board texture design, to allow activation of early visual regions during the fMRI test session. In addition to the six geometrical shape categories, the training phase contained five animal categories of different conceptual sizes (e.g., a cat, a dog, a horse, etc.), with each category consisting of five different exemplars (e.g., five different images of cats, five different images of dogs, etc.). The use of several exemplar stimuli for each shape and animal category was intended to allow maximal generalization during the training phase (see below), and a repetitive presentation of the different categories during the fMRI testing phase while minimizing signal suppression due to fMRI-adaptation effects for repeated exemplars (e.g. [Grill-Spector et al. \(1999\)](#)). All geometrical shapes and animal images subtended a visual angle of 3.8° by 6° (width and height, respectively). All stimuli were presented on a white background.

Prior to the beginning of the training phase, a ‘conceptual size scale’ was constructed. Animal categories were arranged on the scale according to their real-world (i.e., conceptual) size. Each geometrical shape category was assigned a specific conceptual size, according to its position on the scale (between two animals, see [Fig. 1a](#)). Note that the stimuli forming the conceptual scale belonged to the same superordinate category (i.e., animals/mammals), in order to minimize categorical and semantic differences that could be potentially associated with ‘small’ and ‘big’ shapes. There were two different scale matrix conditions, differing in the order of the geometrical shape categories along the scale (i.e., the scale matrices mirrored each other, such that the ‘biggest’ shape category in one matrix was the ‘smallest’ shape category in the other matrix). Participants were assigned to one of the two matrix conditions, with equal proportions of participants in each condition. That is, shape-size association was counterbalanced across participants, thus preventing a potential linkage of specific sizes with particular visual shape properties. In addition, the two shape categories (i.e., the three rightmost and the three leftmost shapes along the conceptual size scale) did not differ in their low-level image properties (i.e., their average pixel gray value was 173 and 179, $t(28)=1.14$, $p=.26$).

[Fig. 1b](#) presents the trial sequence in the training phase. Each trial began with the presentation of a central fixation cross (0.3°) for 1000 ms. Subsequently, a geometrical shape appeared for 1000 ms followed by an animal image presented for an additional 1000 ms. Note that the two stimuli were always taken from adjacent size categories along the conceptual size scale (e.g., a pentagon could either appear before a cat or a dog, but not before a horse). A 1000 ms blank screen appeared after disappearance of the animal image. Participants were instructed to determine as fast and accurately as possible which of the two images – the geometrical shape or the animal – was conceptually larger by pressing their left or

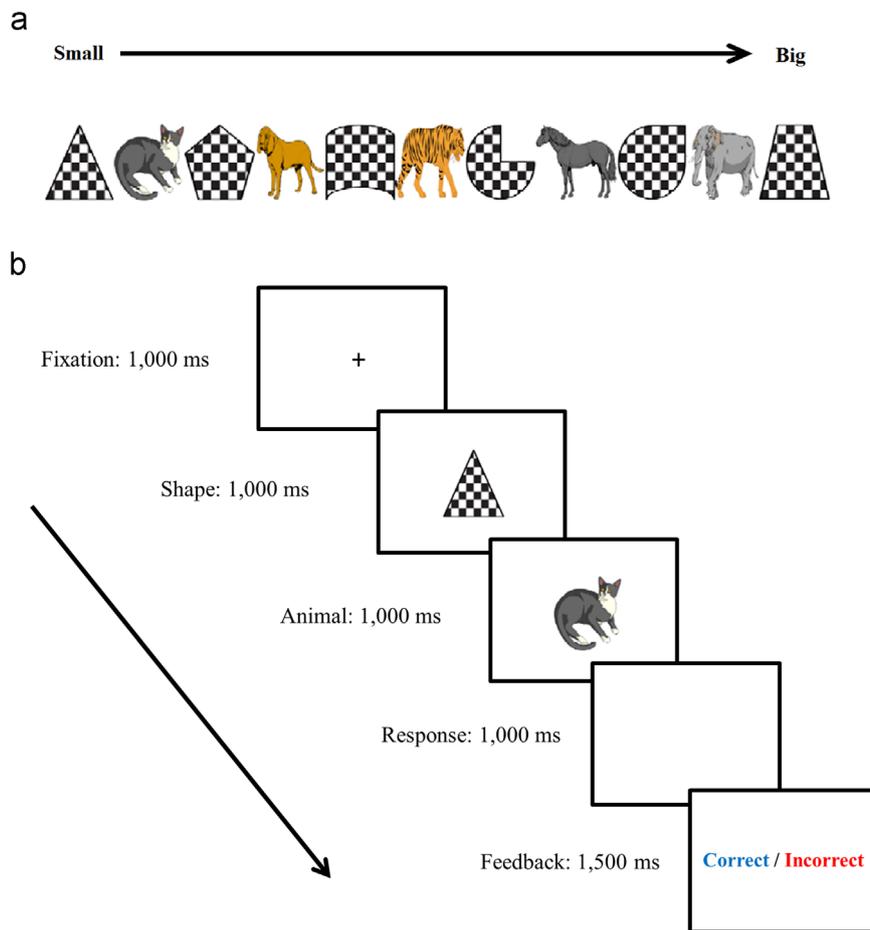


Fig. 1. (a) The five animal categories forming the conceptual (i.e., real-world) size scale, with the six geometrical shape categories organized along the scale. Participants were randomly assigned to two different scale matrix conditions that differed in the order of the geometrical shape categories along the scale. At no point were participants explicitly exposed to the conceptual size scale; hence, acquisition of shape size representation depended solely on trial and error training. (b) An example of a trial sequence during the training session. Participants were instructed to determine as fast and accurately as possible which of the two images (the geometrical shape or the animal) was conceptually larger and received feedback for their performance.

right index finger on the 'Q' and 'P' keys of a keyboard, respectively. A 1500 ms feedback display was presented following participant response (either a "correct" or an "incorrect" message). Critically, all animal and geometrical shape images were of equal retinal size, hence, size judgment could not rely on physical image dimensions. Note that participants were never explicitly exposed to the conceptual size scale (such as the one in Fig. 1a), and they were expected to learn the relative conceptual sizes of shapes through trial and error training in the animal comparison task.

Each participant completed at least four training sessions conducted on different days, with each session composed of 3 parts containing 5 blocks of 40 trials (yielding 600 trials altogether per training session). The amount of training sessions required for each participant was determined individually on the basis of the participant's performance on a shape-comparison test taken at the end of each session (see below). Participants were considered to be highly proficient with the shape sizes when they reached an accuracy level of at least 95% in three out of five consecutive training blocks within a single session. The amount of total training sessions per participant ranged between 4 and 5 (mean=4.1, $SD=0.31$), and the total time lapse between first and last training sessions ranged between 4 and 6 days (mean=4.8, $SD=0.4$).

Note that in order to simplify the learning process, during the first training session, the first block of trials contained only the basic exemplars for each geometrical shape and each animal category (as depicted in Fig. 1a). In the remaining blocks, all shape and animal exemplars were presented with equal proportions. Each training session ended with a test block of 120 trials, in which *only* geometrical shape exemplars were presented (i.e., animal images were excluded altogether). In each test trial, participants were presented with two geometrical shape exemplars of different conceptual sizes that appeared simultaneously, one to the left and one to the right of fixation. Participants were asked to determine as fast as possible which of the two shapes – the left or the right shape – was conceptually bigger by pressing their left or right index finger on the 'Q' and 'P' keys, respectively. In contrast to the training phase, pairs of shape images in the test phase were not restricted to adjacent size categories along the conceptual size scale.

2.3. fMRI conceptual size comparison task

After training was completed, participants underwent fMRI scanning. During scanning participants performed a size comparison task on the geometrical shapes (no animal images were presented at this stage). The task was constructed in a fast event-related design: Trials consisted of a pair of geometrical shape exemplars presented sequentially, each for 1000 ms (similar to the timing of the sequential presentation in the training phase), followed by a 1000 ms response interval. Participants were required to determine as fast as possible whether the second shape exemplar was conceptually smaller or bigger than the first shape exemplar (with equal percentage of trials for each response type), by pressing a key using the index finger of their left or right hand, respectively. Separate response gloves were used for each hand. Critically, the two shape exemplars always belonged to adjacent size categories along the conceptual size scale such that, regardless of the response to the second stimulus (smaller/bigger), both stimuli either denoted 'small' or 'big' shape categories (note that the identity of the first stimulus was restricted to the second or fifth shape category along the size scale; thus 'small' pair trials could potentially include two of the three leftmost shape categories on the scale, while the 'big' pair trials could include two of the three rightmost shape categories on the scale). By presenting either pairs of 'big' or 'small' categorical shapes, we could assess the blood oxygenation level dependent (BOLD) signal collapsed across both stimulus exemplars within a given trial and compare participants' BOLD responses to the two types of conceptual size trials (regardless of the required response for these trials). Participants completed five fMRI scans, each composed of 40 trials, for a total of 200 trials in the size comparison task (i.e., 100 trials per each size condition – 'small'/'big'). A jitter interval (2–8 s) was inserted between the trials to enable an efficient deconvolution analysis of the BOLD signal.

2.4. fMRI numeral size comparison task

Subsequent to the shape size comparison task, and following a short rest phase,

a number size comparison task was presented. For this task, the digits 2, 3 and 4 were used as “small” numbers, while the digits 5, 6 and 7 were used as “big” numbers (each digit appeared in one of five different fonts). The digits of both categories were characterized by similar low-level image properties (i.e., the average pixel gray value for small and big number categories was 212 and 210, respectively, $t(28)=0.08$, $p=.94$). Participants conducted a fast event-related size comparison task on the numbers, similar to the one conducted with the geometrical shapes. Namely, each trial consisted of a pair of digits presented sequentially, and participants were required to determine as fast as possible whether the second digit was smaller or bigger than the first one. Critically, both digits either denoted small or big numbers, allowing the averaging of fMRI signal for each of the size conditions (i.e., small/big) across response type. All other parameters were identical to those in the shape comparison task.

2.5. fMRI data acquisition and statistical analyses

fMRI scans were performed on a 1.5T Philips Intera scanner, equipped with a standard head coil, located at Soroka Medical Center, Beer Sheva, Israel. BOLD contrast was acquired using a gradient echo planner imaging sequence. Whole-brain coverage scans were conducted with 20 slices, 5 mm thickness, 0.5 mm gap, repetition time (TR)=2000 ms, field of view (FOV)= 210×210 mm², and a matrix size of 128×128 . High-resolution anatomical volumes were acquired with a T1-weighted three-dimensional (3D) pulse sequence ($1 \times 1 \times 1$ mm), to enable co-registration of the functional data. Data analysis was conducted using the BrainVoyager QX software package (Brain Innovation, Maastricht, Netherlands). The first four images of each functional scan were discarded. Preprocessing of functional scans included 3D motion correction, slice scan time correction, and removal of low frequencies, up to three cycles per scan (linear trend removal and high-pass filtering). The anatomical and functional images were transformed to the Talairach coordinate system using trilinear interpolation.

In the event-related size comparison tasks, the time-course for each condition was estimated using a deconvolution algorithm implemented in BrainVoyager. This algorithm produces estimates of the hemodynamic response at each TR (TR=2 s) during a 20 s window following trial onset. Beta weights of each experimental condition were estimated for each subject. Beta weights refer to the scaling of regressors in a GLM, in which the BOLD response is reconstructed.

To define areas of interest for the ROI analyses, each individual participant performed, subsequent to the shape and the numeral comparison tasks, a standard blocked-design functional localizer task. We used the general linear model (GLM) implemented in the BrainVoyager software to estimate the neural response as a box-car function for the block duration, convolved with a standard hemodynamic response function (sum of two gamma functions). The localizer task was conducted for defining typical “categorical” areas previously implicated in size computation, such as scene/place-selective regions shown to be sensitive to large stimuli (PPA and OPA, e.g., Amit et al. (2012), Cate et al. (2011), Levy et al. (2001), Mullally and Maguire (2011) and Troiani et al. (2012)) and an object-selective region (LO) shown to be sensitive to small stimuli (e.g., Amit et al. (2012), Cate et al. (2011), Park et al. (2014), but see Troiani et al. (2012)). In addition, we contrasted images of big and small objects, to define specific size-selective regions within ventral cortex (e.g., Konkle and Oliva (2012)). Finally, we localized early visual areas which are potentially affected (via feedback projections) by the processing of large stimuli in high-level cortical regions (e.g., Murray et al. (2006), Sperandio et al. (2012) see also Park et al. (2014)).

Altogether, the localizer task was composed of blocks of buildings, faces, big objects, small objects and scrambled objects. Scrambling was achieved by segmenting each object image into a mosaic composed of 900 elements, which then were randomly rearranged in order to create the meaningless scrambled images (both big and small object images were used). Each block contained 10 images that were presented for 800 ms with a 200 ms interval between images. A 6 s fixation break was inserted between the image blocks. One of the images within each block

was presented twice, successively, and participants were required to press a key when detecting a repetition (“1-back” task). Each image category was presented in seven separate blocks, resulting in 63 images per category. The order of the blocks was pseudo randomized. All images were achromatic, presented with a surrounding ellipse on a black background. For the small objects blocks, images of objects smaller than a shoe box were used (e.g. a hammer, computer mouse, key chain, remote control, ladybug, etc.). For the big objects blocks, images of objects which are typically larger than a carton box were used (e.g. an oven, chair, bench, bicycle, coat, etc.). The objects in both size categories were presented in equal retinal size (see object examples in Fig. 2).

Two place-selective regions, the parahippocampal place area (PPA) and the occipital place area (OPA) (also known as transverse occipital sulcus, TOS, see Dilks et al. (2013)), were defined by voxel clusters that exhibited significantly enhanced activity during presentation of building images compared to face images; An object-selective region within lateral occipital (LO) cortex was defined by contrasting all object blocks (big and small) to scrambled objects. In addition, a contrast of Big versus Small objects was utilized to determine size-preference regions within ventral cortex. This contrast elicited reliable activations in medial (parahippocampal cortex) and in lateral inferior (occipital temporal sulcus) areas within ventral cortex, corresponding to big and small objects, respectively. We term these areas “Big-PHC” and “Small-OTS”, following the terminology of Konkle and Oliva (2012). No reliable activations were seen for big versus small objects in LO. In addition, regions in the early visual cortex (EVC) were defined by a contrast of scrambled objects versus fixation (“rest”). Functional ROIs were defined for each hemisphere in each participant, after correcting for multiple comparisons by using a false discovery rate of $q(\text{FDR}) < 0.05$. In cases in which no significant activation was observed under these conditions, we used an uncorrected statistical threshold of $p < .05$ (For ROI’s average coordinates and maximal *T*-values, see Table 1).

For whole-brain group analyses, preprocessing of functional scans additionally included an 8 mm spatial smoothing. The whole-brain group contrasts were computed by using a random effect GLM analysis, corrected for multiple comparisons with a false discovery rate of $q(\text{FDR}) < 0.05$.

3. Results

We first describe the behavioral results obtained during the training phase sessions, and then we present the fMRI results of the two size comparison tasks.

3.1. Training phase results

All participants reached an accuracy rate above 95% in the shape-comparison test of the last three blocks of the last training session (mean=97.5%, $SD=0.01\%$). To evaluate the extent to which the conceptual size of shapes was perceived automatically following the training phase, we computed a Pearson correlation between the shape-to-shape distance (i.e., the distance along the size scale between the two shapes) and the reaction time (RT) for the correct responses in the shape-comparison test within the last training session. Note that in this test only geometrical shapes were presented (i.e., there were no animal images). A significant negative correlation was found ($r_p = -0.23$, $p < .001$), indicating that shorter RTs were obtained for trials containing larger distances between shapes. Importantly, this negative correlation was found both at the group level and at the individual level for each

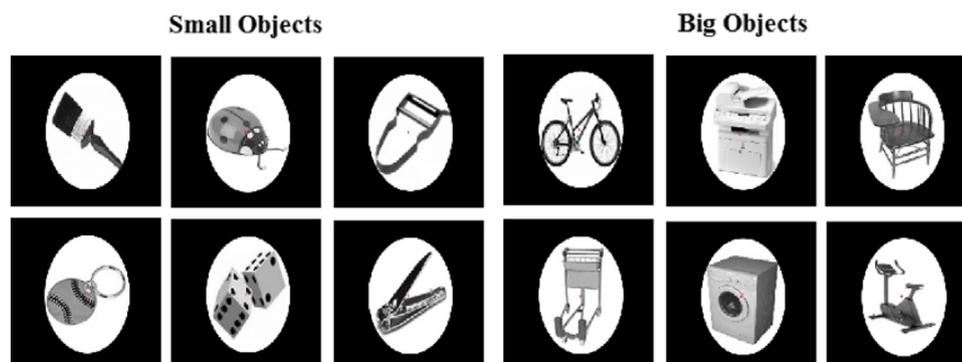


Fig. 2. Examples of small and big real-world objects used in the localizer task for defining size-preference regions within ventral cortex.

Table 1
ROI properties as reflected by the average Talairach coordinates of each ROI center of mass, and the average peak *t*-value within the ROI, across participants.

Left hemisphere				
	X	Y	Z	Peak t-value
PPA	−28.18	−53.80	−11.02	6.19
OPA	−32.71	−88.01	7.14	4.61
LO	−42.62	−78.40	−4.30	5.48
Big-PHC	−23.80	−46.50	−11.46	3.32
Small-OTS	−40.32	−45.05	−10.58	3.70
EVC	−21.88	−91.39	−7.31	12.06
Right hemisphere				
	X	Y	Z	Peak t-value
PPA	24.47	−50.63	−11.81	5.56
OPA	31.24	−87.19	13.07	4.58
LO	41.64	−79.60	−6.32	4.93
Big-PHC	25.61	−46.45	−13.54	3.51
Small-OTS	39.33	−44.51	−12.51	3.20
EVC	21.95	−90.15	−6.86	10.98

participant. This finding resembles the well known *distance effect* typically obtained with numbers (Cantlon et al., 2009; Feigenson et al., 2004; Moyer and Landauer, 1967), suggesting that the acquired conceptual size of the shapes reached a level of automaticity.

3.2. fMRI conceptual size effects

A random effect GLM group analysis was conducted in order to obtain a whole-brain activation map for the conceptual size factor. This analysis yielded no statistically significant activations when correcting for multiple comparisons ($FDR < 0.05$). We therefore focus on the ROI analyses, for which a three-way analysis of variance (ANOVA) was conducted in order to assess the influence of ROI (PPA, OPA, LO, Big-PHC, Small-OTS and EVC), hemisphere (left, right) and conceptual size (big, small) on the BOLD signal. Based on previous findings concerning size-sensitivity in ventral cortical regions, we hypothesized that scene-selective areas and areas specifically responsive to big objects (Big-PHC) would show greater activation for shapes conceived as big than for shapes conceived as small. Feedback projections from these regions may additionally result in higher responses to conceptually big shapes in early visual regions (e.g., Fang et al. (2008), Murray et al. (2006) and Sperandio et al. (2012)). In contrast, object-selective regions and regions specifically sensitive to small objects (Small-OTS) would show an opposite pattern of response.

Peak signal activation (i.e., beta weights at the time point of 6–8 s after trial onset)² was entered as the dependent measure into the ANOVA. Significant main effects of ROI ($F(5, 45) = 13.6, p < .01$) and hemisphere ($F(1, 9) = 11.0, p < .01$) were observed, indicating differences in activation level within the different ROIs, and greater overall activation in the right relative to the left hemisphere. In addition, the interaction between these two factors was significant ($F(5, 45) = 4.5, p < .01$). A significant main effect of conceptual size was also obtained ($F(1, 9) = 5.3, p < .05$) reflecting overall enhanced BOLD responses for shapes conceived as 'big' relative to shapes conceived as 'small', however, this main effect

was qualified by a statistically significant interaction of ROI with conceptual size ($F(5, 45) = 2.8, p < .05$). Critically, this latter interaction indicated that conceptual size modulated cortical activity differently in the different ROIs. All other interaction effects were non-significant (all $F_s < 1.2$).

In order to investigate more thoroughly the effects of conceptual size within the different ROIs, for each region we conducted a two-way ANOVA including hemisphere and conceptual size as factors. This analysis revealed a main effect of conceptual size in the PPA ($F(1, 9) = 5.4, p < .05$), the OPA ($F(1, 9) = 5.7, p < .05$), Big-PHC ($F(1, 9) = 6.8, p < .05$) and EVC ($F(1, 9) = 6.4, p < .05$). Fig. 3 (top) presents the average beta weights for the peak signal activation of conceptually 'small' and 'big' shapes within the various ROIs, collapsed across hemispheres. As mentioned earlier, the relatively enhanced cortical responses for conceptually big shapes in scene-selective regions such as the PPA and the OPA corroborate previous findings using perceptual (Cate et al., 2011) as well as conceptual (Konkle and Caramazza, 2013; Konkle and Oliva, 2012) size manipulations. In addition, the increased activation for 'big' shapes in Big-PHC (defined by contrasting big and small everyday objects) further highlights the importance of the PHC as a size-preference area (Konkle and Oliva, 2012). Moreover, the conceptual size effect seen in the EVC may reflect a possible feedback projection from high-level processing regions (e.g., PPA) to early processing regions, in accord with the perceived size effects (stemming from a Ponzo illusion) seen in V1 (Murray et al., 2006).

To further support our hypothesis regarding feedback projections from high-level processing regions to the EVC, we calculated for each participant the effect of conceptual size (i.e., the difference in beta weights between 'big' and 'small' shapes at the time point of 6–8 s after trial onset) in the PPA, OPA and Big-PHC, as well as in the EVC. We then computed a forward stepwise regression analysis designed to predict the effect of conceptual size at the EVC by the activation pattern at the other more high-level regions. This regression analysis showed that the activation profile of the PPA significantly predicted the activation pattern at the EVC ($\beta = 0.84, t(8) = 4.5, p < .01$). No other high-level regions were found to significantly contribute to the variance in EVC response.

It is important to note that PPA and Big-PHC partly overlap, yet they do not correspond to the exact same regions (see average coordinates of the two ROIs in Table 1). The differences in anatomical distribution and possibly in the sensitivity of these regions to the conceptual size manipulation, may account for the fact that only the former was predictive of the activation pattern at the EVC. Our findings suggest, thus, that the PPA may serve as a possible source for the enhanced activity seen with conceptually big relative to conceptually small objects in the early visual cortex. Interestingly (and somewhat surprisingly), our hypothesis concerning a preference for shapes conceived as small in regions previously implicated in processing of small objects (e.g., LO, Small-OTS) was not confirmed. Namely, these regions did not exhibit enhanced activity for conceptually small shapes relative to conceptually large shapes. We discuss this finding in the Discussion section.

3.3. fMRI numerical size effects

Statistical analyses similar to the ones conducted with the shapes were conducted for the digits denoting small and big numerical values in the number size comparison task. As in the previous whole-brain analysis, the random effect group activation map did not survive multiple comparison correction ($FDR < 0.05$), and therefore we focus on the ROI analyses. Peak signal activation (i.e., 6–8 s after trial onset) was entered as the dependent measure in the three-way ANOVA for the small and big digits. A significant main effect of ROI was observed ($F(5, 45) = 16.1, p < .01$), and in

² The BOLD response in all measured ROIs reached peak activation at a 6–8 s time point. This rather late peak may have resulted from the specific experimental parameters used in the size comparison task: each trial contained two successive events (two shapes/digits), each presented for 1 s. The offset of stimulus presentation after 2 s, in addition to the requirement to select a response only after the second stimulus presentation, presumably caused a small shift in the peak activation relative to the trial onset.

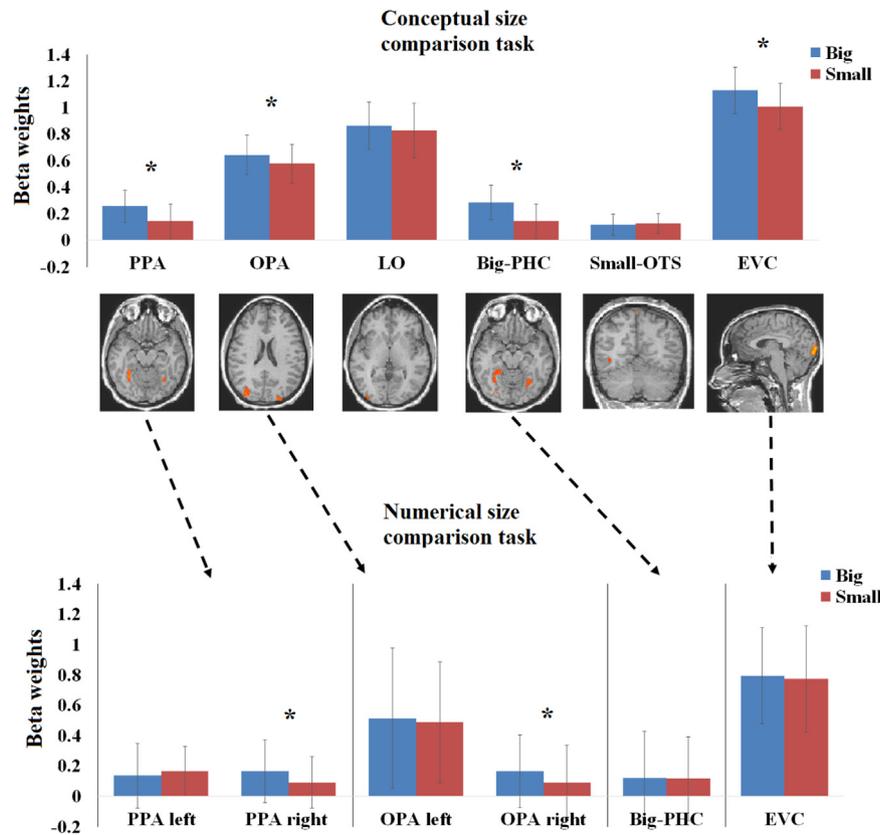


Fig. 3. Top: ROIs (of a representative participant) and beta weights for the BOLD signal at peak signal activation (averaged across participants) within the parahippocampal place area (PPA), occipital place area (OPA), lateral occipital cortex (LO), parahippocampal cortex responsive to big objects (Big-PHC), occipital temporal sulcus responsive to small objects (Small-OTS) and early visual cortex (EVC), as a function of shapes' conceptual size (collapsed across hemispheres). Asterisks represent statistical significance at $p < .05$ for the main effect of size in the two-way Anova conducted for each of the ROIs (see main text). Bottom: Beta weights for peak signal activation (averaged across participants) as a function of numerical size within ROIs showing a significant size effect in the shape comparison task. Activation in two place-selective regions (PPA, OPA) is shown separately for the two hemispheres. Asterisks in these regions represent a significant simple main effect of size within hemisphere ($p < .05$). Note that anatomical cortical slices are presented in Radiological convention, i.e., left of image represents right of participant's brain. Error bars represent 1 STD in all figures.

addition, a two-way interaction between ROI and hemisphere was significant ($F(5, 45) = 3.2, p < .05$). No other main effects or interaction effects were significant (all $F_s < 1.7, p > 0.2$). Namely, in contrast to the findings with the shape comparison task, no effects of numerical size or of the interaction between numerical size and ROI were significant.

We nevertheless wished to examine possible numerical size effects within the regions specifically found to be sensitive to conceptual size in the shape comparison task. That is, we conducted a two-way analysis ANOVA (including hemisphere and numerical size factors) only for those regions which demonstrated a significant modulation of activation by the shapes' conceptual size. Our results revealed no significant effects in any of the ROIs, aside from an interaction effect of numerical size by hemisphere found in the PPA ($F(1, 9) = 12.0, p < .01$). This interaction effect reflected higher activation for big than for small numbers in the right PPA ($F(1, 9) = 6.0, p < .05$) with no effect of size in the left PPA ($F(1, 9) < 1$). Similar results were found within the OPA, that is, a higher activation for big than for small numbers in the right OPA ($F(1, 9) = 6, p < .05$) with no effect of size in the left OPA ($F(1, 9) < 1$). The numerical size by hemisphere interaction in this region, though, failed to reach statistical significance ($F(1, 9) = 2.0, p = .18$) (the average beta weights of peak activation for both the PPA and the OPA are presented separately for each hemisphere in Fig. 3, bottom, while the beta weights for the other two ROIs are collapsed across hemispheres). Note that numbers are typically represented more dominantly in the right than in the left hemisphere (e.g., Cappelletti et al. (2010) and Hyde et al. (2010)), in accordance with the greater sensitivity to number magnitude in

the right hemisphere found in the present study.

4. Discussion

The present study examined the influence of conceptual size on cortical response in the ventral visual stream. Participants learned the conceptual sizes of arbitrary shapes through extensive trial and error training and were subsequently scanned while conducting a size comparison task on these shapes. In addition, a size comparison task was conducted for digits denoting small and big magnitudes. An ROI analysis demonstrated higher BOLD activation in regions typically referred to as place- or scene-selective, such as the PPA and the OPA, when processing conceptually big shapes compared to conceptually small shapes. When processing digits conveying big versus small numerical magnitudes, a similar pattern was observed in the right PPA and the right OPA. Taken together, our results emphasize the role of place- or scene-selective areas in object size computation. More specifically, we demonstrate that these regions can represent not only big real-world objects/scenes, but also meaningless shapes or symbolic stimuli conceived as big.

Previous studies have emphasized the role of the parahippocampal cortex, and specifically the PPA, in the encoding of large objects, by demonstrating a bias of this region towards stimuli encompassing a large retinal size (e.g., Troiani et al. (2012)), stimuli spanning peripheral retinal locations (Levy et al., 2001), or stimuli perceived as large via perspective depth information (e.g., Cate et al. (2011)). More relevant to the current study, recent

findings have demonstrated parahippocampal sensitivity to the real-world size of everyday objects (e.g., He et al. (2013), Konkle and Caramazza (2013) and Konkle and Oliva (2012)), yet such sensitivity was argued to be mediated by categorical identity and/or stimulus affordance rather than by conceptual size *per se* (i.e., knowledge that an object is big or small). In order to examine whether a more abstract representation of size may be encoded in high-level visual cortex, we used meaningless shapes of identical retinal sizes but of different acquired conceptual sizes. When conducting a size-comparison task among the shapes, a ‘distance effect’ was obtained, suggesting that processing of the shapes’ conceptual sizes reached an automatic level. As mentioned above, and in accord with some of the findings of retinal- and perceived-size preferences in occipitotemporal cortex, the PPA and OPA regions showed an enhanced BOLD activation for shapes conceived as big relative to shapes conceived as small. In addition, stronger responses were obtained for the former type of shapes in early visual cortex (EVC), mirroring previous findings obtained when using stimuli perceived as big versus small via perspective cue manipulations (i.e., Ponzo illusion, see e.g., Murray et al. (2006)). In line with the latter findings, we propose that activity in early visual areas may be modulated not only by information about perceived size but also by higher level information about conceptual size. A possible support for our proposal is the fact that PPA and EVC were significantly intercorrelated with each other.

The parahippocampal cortex (PHC) has been typically associated with scene and place processing (Epstein et al., 1999; Epstein and Kanwisher, 1998), yet this region appears to be involved in a range of other cognitive functions, such as spatial navigation and episodic memory (Aguirre et al., 1996; Davachi et al., 2003). In fact, over the last decade, the precise role of the PHC has been the focus of a continuing debate. Some researchers have argued that the fundamental function of the PHC is to process contextual associations (Aminoff et al., 2007; Bar and Aminoff, 2003). Others have emphasized its role in spatial processing and navigation, demonstrating greater PHC activation for ‘space-defining’ than for ‘space-ambiguous’ objects (Mullally and Maguire (2011), Park et al. (2014), Troiani et al. (2012), see also Bohbot et al. (2015)), or for spaces through which people typically interact with objects (Bainbridge and Oliva, 2015). According to the latter approaches, the PHC is primarily concerned with visual representations that depict a local space or a place, whether these are defined by whole scenes or by single objects. Interestingly, the extent to which an object is considered and perceived to be ‘space defining’ was found to be strongly correlated with its real-world size. Namely, the larger an object is, the more it evokes a sense of the surrounding space (Mullally and Maguire (2011), Troiani et al. (2012), but see Bainbridge and Oliva (2015) for space-related findings which are orthogonal to the objects’ real-world size). Note that when controlling for retinal size factors, both perceptual as well as conceptual (real-world) size representations are confounded with stimulus distance (i.e., large stimuli are typically perceived, or conceived, as distant while small stimuli are typically perceived/conceived as proximal). Consequently, several researchers have argued that distance, rather than size, underlies the activation pattern in the PHC (Amit et al., 2012).

Here we show that meaningless geometrical shapes, arbitrarily associated with real-world sizes and presented in isolation—thus presumably conveying minimal contextual, spatial, or distance information—influence PHC activation. Furthermore, digits conveying small or large magnitudes were additionally found to modulate PHC activation (yet only in the right hemisphere). Clearly, numeral stimuli are abstracted from real-world places or spaces, or from categorical identity which characterizes objects and scenes. The fact that greater activity was seen for big than for small numerical value in the right PPA strongly suggests that this

region is not only responsive to physical and perceptual visual size (e.g., Cate et al. (2011) and Levy et al. (2001)), or to the functional properties of every-day objects (e.g., Konkle and Oliva (2012)). Rather, this visual associative region may also be sensitive to a more abstract conceptual size representation. In line with this suggestion, previous research conducted with congenitally blind participants has revealed that even in the absence of any visual experience, PHC is activated through haptic experience with “scene-like” layouts (Wolbers et al., 2011) or through verbal stimuli depicting large objects (He et al., 2013), suggesting that this region may encompass a multimodal, or a relatively abstract space and/or size representation.

One potential limitation of the present study is that, in contrast to Konkle and Oliva (2012), who demonstrated a preference for big as well as for small objects in various areas within the ventral visual cortex, our study revealed size-preference activations only for conceptually big stimuli. While a small-preference region (in the OTS) was found when contrasting small versus big real-world stimuli, no regions demonstrating enhanced activation for ‘small’ relative to ‘big’ shapes (or numbers) were found. A possible account for this lack of small-preference regions is that the “small” sizes forming the conceptual scale in the shape-comparison task were not sufficiently small in order to activate previously demonstrated small-preference regions (e.g., within LO or occipitotemporal sulcus). Thus, for example, Konkle and Oliva (2012) used real world objects typically smaller than, or similar to the size of a fist (e.g., a ring, a mushroom, a clip, an orange, etc). Other studies showing activation in hand-selective areas within LO have utilized relative small objects that could be used as effectors (e.g., a pen, a plier, a comb, a hammer, see Bracci and Peelen (2013)). In contrast, the animals used as reference anchors for learning the small conceptual sizes in the present study were markedly larger (e.g. cats and dogs). In fact, some of these animals (e.g., dogs) could be considered as “big” with respect to the size categories used by Konkle and Oliva (2012). The conceptually “small” shapes in the present study, therefore, were presumably too large in order to activate regions which are potentially sensitive to very small stimuli. While the latter account is mere speculation, future research will undoubtedly need to test the effects of conceptual size representation, using a wider range of object sizes than the one used in the current research.

Another possible caveat of the present research refers to the manner in which scene-selective (or building selective) ROIs were defined, by contrasting images of buildings versus faces (e.g., Levy et al. (2001) and Malach et al. (2002)). Since buildings are larger than faces, these ROIs may be potentially biased toward obtaining enhanced activation for big stimuli. Indeed, most studies investigating place/scene/building selective regions typically use ROIs which contrast large with small real-world stimuli (e.g., scenes versus faces or objects). By definition, then, these areas may be sensitive to various size and space parameters of visual stimuli (e.g., Bainbridge and Oliva (2015), Mullally and Maguire (2011), Park et al. (2014) and Troiani et al. (2012)). As mentioned earlier, however, the fact that arbitrary shapes which are associated with large conceptual size values via mere experimental training additionally activate such regions, serves as an important evidence for their sensitivity to a more abstract representation than typically observed. Our finding becomes even more dramatic when concerning the ROI analysis effects of numeral digits on the two scene/size-selective areas (i.e., right PPA and OPA).

Finally, in an attempt to minimize categorical and/or functional differences that may be associated with small and big shapes, during training all shapes were compared to real-world stimuli belonging to the same superordinate category (i.e., mammals). One could nevertheless argue that although real-world objects never appeared in the fMRI size comparison task, and despite the

fact that the latter were all chosen from the same category, participants nevertheless associated the shapes with small or large mammals presented during the training phase (e.g., via mental imagery). Thus, the size effects observed in the ventral visual cortex may reflect differences in the associated semantic properties of animals of different sizes, rather than differences in conceptual size *per se*. While we cannot strictly rule out this account, we believe that it is unlikely to explain our results. First, as mentioned earlier, previous research has failed to find differences in cortical activation when manipulating animal size. That is, in contrast to inanimate stimuli, presentation of small and big animal images did not modulate ventral stream activation (Konkle and Caramazza, 2013). It seems unlikely, therefore, that any association with the animals could account for the differences observed between the conceptually 'small' and 'big' geometrical shapes. Second, recall that in the last session of the training phase (before entering the MRI scanner), participants conducted a size-comparison task, in which only geometrical shape exemplars were presented (i.e., animal images were excluded altogether). This test yielded a 'distance effect' typically obtained with numbers, both at the group level and at the individual level, strongly suggesting that size representation of the shapes has reached an automatic level similar to the processing of numerical value. We believe that such a high proficiency of processing of the shapes most likely reflects the abstraction of their size representation from the animals used as reference points during the training phase. Finally, the fact that numbers, which represent size (or magnitude) in a purely symbolic fashion, also modulated cortical activation in the right PPA and OPA strongly implies that these regions are indeed sensitive to a more abstract size representation.

In accord with the latter finding, previous behavioral research has documented a possible relation between numerical perception and size perception, whether the latter is measured by retinal size (e.g., Besner and Coltheart (1979), Dehaene (1992) and Henik and Tzelgov (1982)), perceived size (e.g., Goldfarb and Tzelgov (2005)) or conceptual size (e.g., Gabay et al. (2013)) manipulations. Note that in contrast to numbers, which denote precise values, the representations of physical and/or conceptual sizes have no exact values. The observed interactions between an exact number representation and an approximate size representation may therefore support recent suggestions regarding a core cognitive system that was originally designed to compute continuous magnitudes which, with evolutionary development, has been exploited in the development of the numerical system (Cantlon et al., 2009; Henik et al., 2011). Furthermore, we recently suggested that the shift from evaluation and perception of continuous, non-countable properties of objects (e.g., physical size) to the fully developed numerical system may have been mediated by the use of conceptual sizes (Gabay et al., 2013). Conceptual sizes convey long-term semantic knowledge of an object's size, regardless of the object's actual retinal size; similar to numerals that denote (symbolically) long-term knowledge of specific quantities and/or magnitudes. From an evolutionary perspective, therefore, conceptual size may have served as a possible bridge between continuous and numerical magnitude representations. The finding that the right PPA and OPA are sensitive to both conceptual size and numerical value suggests that these cortical regions may serve as remnants to a common cognitive system originally underlying different magnitude representations.

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References

- Aguirre, G.K., Detre, J.A., Alsop, D.C., D'Esposito, M., 1996. The parahippocampus subserves topographical learning in man. *Cereb. Cortex* 6 (6), 823–829.
- Aminoff, E., Gronau, N., Bar, M., 2007. The parahippocampal cortex mediates spatial and nonspatial associations. *Cereb. Cortex* 17 (7), 1493–1503.
- Amit, E., Mehoudar, E., Trope, Y., Yovel, G., 2012. Do object-category selective regions in the ventral visual stream represent perceived distance information? *Brain Cogn.* 80 (2), 201–213.
- Bainbridge, W.A., Oliva, A., 2015. Interaction envelope: Local spatial representations of objects at all scales in scene-selective regions. *NeuroImage* 122, 408–416.
- Bar, M., Aminoff, E., 2003. Cortical analysis of visual context. *Neuron* 38 (2), 347–358.
- Besner, D., Coltheart, M., 1979. Ideographic and alphabetic processing in skilled reading of English. *Neuropsychologia* 17 (5), 467–472.
- Bohbot, V.D., Allen, J.J.B., Dagher, A., Dumoulin, S.O., Evans, A.C., Petrides, M., Kalina, M., Stepankova, K., Nadel, L., 2015. Role of the parahippocampal cortex in memory for the configuration but not the identity of objects: converging evidence from patients with selective thermal lesions and fMRI. *Front. Hum. Neurosci.* 9 (431). <http://dx.doi.org/10.3389/fnhum.2015.00431>.
- Bracci, S., Peelen, M.V., 2013. Body and object effectors: the organization of object representations in high-level visual cortex reflects body-object interactions. *J. Neurosci.* 33 (46), 18247–18258.
- Cantlon, J.F., Platt, M.L., Brannon, E.M., 2009. Beyond the number domain. *Trends Cognit. Sci.* 13 (2), 83–91.
- Cappelletti, M., Lee, H.L., Freeman, E.D., Price, C.J., 2010. The role of right and left parietal lobes in the conceptual processing of numbers. *J. Cognit. Neurosci.* 22 (2), 331–346.
- Cate, A.D., Goodale, M.A., Köhler, S., 2011. The role of apparent size in building- and object-specific regions of ventral visual cortex. *Brain Res.* 1388, 109–122.
- Davachi, L., Mitchell, J.P., Wagner, A.D., 2003. Multiple routes to memory: distinct medial temporal lobe processes build item and source memories. *Proc. Natl. Acad. Sci.* 100 (4), 2157–2162.
- Dehaene, S., 1992. Varieties of numerical abilities. *Cognition* 44 (1), 1–42.
- Dilks, D.D., Julian, J.B., Paunov, A.M., Kanwisher, N., 2013. The occipital place area is causally and selectively involved in scene perception. *J. Neurosci.* 33 (4), 1331–1336.
- Epstein, R., Harris, A., Stanley, D., Kanwisher, N., 1999. The parahippocampal place area: recognition, navigation, or encoding? *Neuron* 23 (1), 115–125.
- Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. *Nature* 392 (6676), 598–601.
- Fang, F., Boyaci, H., Kersten, D., Murray, S.O., 2008. Attention-dependent representation of a size illusion in human V1. *Curr. Biol.* 18 (21), 1707–1712.
- Feigenson, L., Dehaene, S., Spelke, E., 2004. Core systems of number. *Trends Cognit. Sci.* 8 (7), 307–314.
- Gabay, S., Leibovich, T., Henik, A., Gronau, N., 2013. Size before numbers: conceptual size primes numerical value. *Cognition* 129 (1), 18–23.
- Goldfarb, L., Tzelgov, J., 2005. Is size perception based on monocular distance cues computed automatically? *Psychon. Bull. Rev.* 12 (4), 751–754.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., Malach, R., 1999. Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* 24 (1), 187–203.
- He, C., Peelen, M.V., Han, Z., Lin, N., Caramazza, A., Bi, Y., 2013. Selectivity for large nonmanipulable objects in scene-selective visual cortex does not require visual experience. *NeuroImage* 79, 1–9.
- Henik, A., Leibovich, T., Naparstek, S., Diesendruck, L., Rubinsten, O., 2011. Quantities, amounts, and the numerical core system. *Front. Hum. Neurosci.* 5.
- Henik, A., Tzelgov, J., 1982. Is three greater than five: the relation between physical and semantic size in comparison tasks. *Mem. Cogn.* 10 (4), 389–395.
- Hyde, D.C., Boas, D.A., Blair, C., Carey, S., 2010. Near-infrared spectroscopy shows right parietal specialization for number in pre-verbal infants. *NeuroImage* 53 (2), 647–652.
- Konkle, T., Caramazza, A., 2013. Tripartite organization of the ventral stream by animacy and object size. *J. Neurosci.* 33 (25), 10235–10242.
- Konkle, T., Oliva, A., 2011. Canonical visual size for real-world objects. *J. Exp. Psychol.: Hum. Percept. Perform.* 37 (1), 23.
- Konkle, T., Oliva, A., 2012. A real-world size organization of object responses in occipitotemporal cortex. *Neuron* 74 (6), 1114–1124.
- Levy, I., Hasson, U., Avidan, G., Hendler, T., Malach, R., 2001. Center-periphery organization of human object areas. *Nat. Neurosci.* 4 (5), 533–539.
- Malach, R., Levy, I., Hasson, U., 2002. The topography of high-order human object areas. *Trends Cognit. Sci.* 6 (4), 176–184.
- Moyer, R.S., Landauer, T.K., 1967. Time required for judgements of numerical inequality.
- Mullally, S.L., Maguire, E.A., 2011. A new role for the parahippocampal cortex in representing space. *J. Neurosci.* 31 (20), 7441–7449.

- Murray, S.O., Boyaci, H., Kersten, D., 2006. The representation of perceived angular size in human primary visual cortex. *Nat. Neurosci.* 9 (3), 429–434.
- Park, S., Konkle, T., Oliva, A., 2014. Parametric coding of the size and clutter of natural scenes in the human brain. *Cereb. Cortex*, bht418.
- Sperandio, I., Chouinard, P.A., Goodale, M.A., 2012. Retinotopic activity in V1 reflects the perceived and not the retinal size of an afterimage. *Nat. Neurosci.* 15 (4), 540–542.
- Troiani, V., Stigliani, A., Smith, M.E., Epstein, R.A., 2012. Multiple object properties drive scene-selective regions. *Cereb. Cortex*, bhs364.
- Wolbers, T., Klatzky, R.L., Loomis, J.M., Wutte, M.G., Giudice, N.A., 2011. Modality-independent coding of spatial layout in the human brain. *Curr. Biol.* 21, 984–989.