Decoding the neural representation of size using multivariate pattern analyses and high density electroencephalography

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Abstract

The perception of object size is not a simple process. The retinal size of an object scales with distance to the observer, and human beings lack a dedicated system for accurately measuring object distance outside a limited range. Here, we seek to answer three general questions about size perception: Which regions of visual cortex represent the perceived size of an object? What are the feedforward and feedback interactions that underlie the neural representation of object size? What are the domain specific and domain general characteristics of the neural representation of object size? Previous research, using principally fMRI techniques, has indicated primary visual cortex (V1) as playing a primary role in representing perceived object size. Here we examine the neural representation of perceived size using High Definition Electroencephalography (HD EEG) and Multivariate Pattern Analysis (MVPA) techniques in an attempt to characterize the time course and localization of perceived size processing within the brain. We find that perceived size is represented throughout the visual system in a largely domain specific fashion, and that processing perceived size does not take place in a simple feedforward fashion originating in early visual areas.

Keywords: Size Perception, HD EEG, MVPA, Ebbinghaus, Depth Illusion.
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1. Introduction

We are constantly judging the sizes of objects in our environment, both for convenience and for our survival. E.g. “Is that doorway large enough that I can walk through it, or is that a doggy door? Is that person hitting on my significant-other larger than I am?” Clearly, the majority of these judgments are made with at least a reasonable degree of accuracy, as we do not often observe sober adults attempting to squeeze through unreasonably tight openings. How exactly are these size judgments executed? The answer to this question is not trivial. Objects possess not only a physical size (the veridical size of the object), but also a retinal size (the size of the image projected onto the eye’s retina), and a perceived size (the size that we perceive the object to be based on the available information). The challenge in representing the size of an object originates at the earliest stages of visual processing. Specifically, the size of an object’s image on our retina scales with our distance to the object (Emmert, 1881; Irwin, 1969) and thus the retinal image does not provide direct access to the object’s size (Figure 1). Moreover, except for a narrow depth-range (Fleet, Wagner, and Heeger, 1996; Hochberg, 1971; Hofsten, 1976; Wallach and Floor, 1971), we do not possess a sensory system dedicated to direct measurement of viewing distance. Ocular cues such as accommodation, vergence and binocular disparity have been shown to give effective cues to distance, but only at ranges of a few meters or less (Fleet et al., 1996; Hochberg, 1971; Hofsten, 1976; Wallach and Floor, 1971). Dynamic information in our environment can also provide cues to relative object depth. Phenomena such as motion parallax, optic flow, and texture
accretion/deletion give clues to the relative depths of various objects in the environment based on the motion of objects across the retina in response to observer motion (Gibson, 1966; Gibson et al., 1969; Longuet-Higgins and Prazdny, 1980; Prazdny, 1980; Rogers and Graham, 1979). Monocular depth cues such as perspective projection, familiar size, texture gradients, and object shadows provide additional information that may be used by the visual system to determine the distance of objects (Gibson, 1950; Ittleson, 1951; Kersten et al., 1996; Pirenne, 1970; Stevens, 1979). Therefore, in order to construct the size of an object, the visual system must also construct the object’s distance. Recently, we discovered that ambiguity also exists in the representation of the retinal image size, and such ambiguity can greatly influence the perceived size of an object (Mruczek, Blair, & Caplovitz, 2014; Mruczek, Blair, Strother, and Caplovitz, 2015). Thus the representation of object size is not solely based on the integration of perceived distance and size of the retinal image but also includes other visual cues related to the representation of size. These include prior knowledge about the expected size of familiar objects and the relative size of different objects simultaneously present within the visual scene or viewed across time.
Figure 1: Emmert’s Law. 
Illustration of how retinal size scales with object distance highlighting the inherent ambiguity in size perception.

The contributions various cues make towards the representation of size can be demonstrated through a number of size illusions in which objects of the same physical size appear to be different sizes. For example, two same-sized objects viewed in the context of a corridor, or some other scene implying depth through the use of linear perspective or other depth cues, appear to be different sizes if placed in such a way as to appear at different ends of the corridor (Fang et al., 2008; Murray et al. 2006; Ni et al., 2014) (Figure 2C) (Shepard, 1990). Contextual elements may also lead to size contrast and size assimilation effects. In the classic Ebbinghaus illusion, a circle surrounded closely by smaller circles appears larger than a circle of the same size surrounded by larger circles at a greater eccentricity (Burton, 2001; Mruczek et al., 2015; Thiéry, 1896) (Figure 2A). Through the use of adaptation, objects may be made to appear of a different size in the absence of any immediate contextual elements. Specifically, if an object of slightly larger size is viewed at the same position as a following object,
the following object is perceived smaller than its actual size (Köhler & Wallach, 1944; Pooresmaeili et al., 2013). These few examples highlight the fact that the behavioral principles by which various visual cues influence object size perception are well studied and documented (Burton, 2001; Fleet, Wagner, & Heeger, 1996; Gibson, 1950; Gibson, 1966; Gibson et al., 1969; Hochberg, 1971; Hofsten, 1976; Kersten et al., 1996; Kersten, Mamassian, & Knill, 1997; Mruczek et al., 2014; Mruczek et al., 2015; Longuet-Higgins & Prazdny, 1980; Ittelson, 1951; Pirene, 1970; Prazdny, 1980; Rogers and Graham, 1979; Stevens, 1979; Thiéry, 1896; Wallach & Floor, 1971). In contrast, the neural mechanisms by which the perceived size of an object is represented in the brain have only recently begun to be revealed and much remains unknown.

Figure 2: Classic Size Illusions
(A) Ebbinghaus Illusion
(B) Ponzo Illusion
(C) Perceived Depth Illusion
1.1 Neural Correlates of Perceived Size

In recent years, a number of studies have applied Functional Magnetic Resonance Imaging (fMRI) techniques to identify neural correlates of perceived size. These studies focus on the ‘spread of activity’ within given areas of visual cortex corresponding to the representation of a given object. The studies have found that stimulus manipulations that increase the perceived size of an object can increase the spread of activity within regions of retinotopic cortex, specifically within V1 (Fang et al., 2008; Murray et al., 2006; Ni et al., 2014; Pooresmaeili et al., 2013; Sperandio et al., 2012; Sterzer and Reese, 2006). Intriguingly, these studies have demonstrated such effects in V1 using different manipulations of perceived size including adaptation (Pooresmaeili et al., 2013), 2D depth cues (Fang et al., 2008; Murray et al., 2006), and afterimages viewed on surfaces at different distances (Sperandio et al., 2012). In addition, a very recent study using single unit recording in monkeys again identified neural correlates of perceived size in V1 as modulated by 2D depth cues (Ni et al., 2014). Furthermore, in experiments done using adaptation to alter the perceived size of objects, Pooresmaeili et al. (2013) showed that the size of adaptation effects, as measured in extent of activity, was greater in V1 than in V4, consistent with the hypothesis that these illusory size effects are originating in V1 and propagating in a feedforward fashion to higher visual areas in the cortex (Pooresmaeili et al., 2013). In studies examining a correlation between the size of visual areas and the relative strengths of the Ebbinghaus and Ponzo Illusions (Figure 2B), it was found that there was a significant relationship between functionally defined V1
size in an individual and the strength of these illusions (Schwarzkopf and Rees, 2013; Schwarzkopf, Song, and Rees, 2011). However, this significant relationship did not hold for V2 and V3. Furthermore, in experiments examining perceived size using afterimages, V1 activity was correlated with perceived size, while no such pattern was observed in V2 or V3 (Sperandio et al., 2012). While V1 has shown the strongest and most consistent perceived size dependent Blood Oxygen Level Dependent (BOLD) activity modulations, there are indications that areas such as V2, V3, V4 and LO also exhibit BOLD changes as a result of viewing stimuli of different perceived sizes (Pooresmaeili et al., 2013). Thus there is direct evidence, at least in some contexts, for a distributed representation of perceived size that extends beyond V1.

There is also a fascinating path through the literature examining the hypothesis for multiple and distinct neural representations of object size: one for conscious perception and one for action (Haffenden, Schiff, and Goodale, 2001). In experiments that required participants to both judge target size and grasp targets in Ebbinghaus displays (i.e. Figure 2A), it appeared that the inducing circles had a greater effect on perception than on grasp aperture (Danckert et al., 2002; Haffenden et al., 2001). This would imply that one representation of an object’s size (that more accurately reflects its physical size) can co-occur with a separate independent representation of size (that is less accurate and modulated by context). It is reasonable to conclude that these representations are instantiated in different areas of visual cortex (i.e. ventral-stream: illusory, dorsal-stream: accurate; Haffenden et al., 2001). However, further studies have
challenged this initial finding, showing no evidence for a differential effect of the Ebbinghaus illusion on perception and grasping (Dankert et al., 2002; Franz and Gegenfurtner, 2008; Handlovsky et al., 2004). Another study indicates that the mere presence of the flankers, independent of any effect they have on perceived size, causes an alteration in grasp aperture, and thus confuses any conclusions that may be drawn from results using this paradigm (Gilster et al., 2006). When the paradigm is changed so that participants are pointing, instead of grasping, the effect of the illusion on action appears robust, further supporting the view that there may be no separation between perception and action for size judgment (Handlovsky et al., 2004).

While experiments with the Ebbinghaus illusion may not indicate any perception and action differences for perceived size, patient data from a woman with damage to lateral occipital and parasagittal occipitoparietal regions indicated that she could not make object discriminations based on size, but nonetheless showed appropriate grasping aperture for objects of various sizes (Goodale et al., 1991; Logothetis and Sheinberg, 1996). Further patient work has identified individuals with damage to areas beyond V1 that also have issues with size discrimination, implicating the involvement of later visual areas (Berryhill, Fendrich, and Olson, 2009) and a distributed representation of perceived size.

1.2 The challenge of representing perceived size in V1

What remains unclear is how perceived size (as opposed to retinal size) is being represented this early in the visual system. While it is possible that effects
of context, adaptation, depth, etc. originate in area V1 and are then propagated across the cortex in a feedforward manner (Pooresmaeili et al., 2013), this seems problematic. Given our inability to directly measure depth outside the range of ocular cues such as accommodation, vergence and disparity, one might expect that visual areas as early as V1 may not have access to depth information in representing object size, at least initially. Furthermore, given the retinotopic organization of V1 (Hubel and Wiesel, 1959; Tootell et al., 1988), one might question how contextual information from across relatively larger portions of the visual field might be combined to produce perceived size changes this early in the visual system. It has recently been hypothesized that modulations in the representation of size within V1 may be mediated by positional shifts in the receptive fields of form-detecting neurons (Ni et al., 2014). However, it remains unknown what mechanism underlies the occurrence of these shifts. It seems likely that contextual elements influencing perceived size may first be integrated in higher visual areas with larger receptive fields able to integrate multiple sources of information, before affecting V1 activity through feedback mechanisms (Fang et al., 2008; Hupe et al., 1998; Murray et al., 2006; Sterzer and Reese, 2006). In the case of depth, this supposition is supported by the fact that anodal stimulation to early visual areas using Transcranial Direct Current Stimulation (tDCS) interferes with size, but not distance perception (Costa et al., 2014). It is also possible that the mechanisms for instantiating perceived size in the brain are different depending on whether perceived size is being altered by contextual/depth cues, or by adaptation (Pooresmaeili et al., 2013). Evidence for
the effects of feedback from higher visual areas on earlier visual processes is well established in other perceptual domains. For example, Hupe et al. (1998) showed that cooling of monkey area V5/MT led to a 39% decrease in spikes per second in V1, a 91% decrease in V2, and 40% decrease in V3. Furthermore, this inhibition of activity affected behavioral performance in figure from ground differentiation tasks. Specific evidence for the possible role of feedback in size perception comes from studies showing that drawing attention away from objects in the scene whose apparent sizes are altered by surrounding depth cues (Fang et al., 2008) or Ebbinghaus context (Yan et al., 2011) reduces the effects of perceived size on V1 activity.

1.3 Domain Specific or Domain General

As previously noted, imaging work has implicated V1 in the representation of perceived size in contexts defined by depth, adaptation, and afterimages (Fang et al., 2008; Murray et al., 2006; Ni et al., 2014; Pooresmaeili et al., 2013; Sperandio et al., 2012; Sterzer and Reese, 2006). However, due to temporal resolution constraints of fMRI, it is not clear if the processes involved in instantiating this activity in V1 are the same for each context type. There is some evidence that certain representations of illusory object size may be represented directly in V1 without feedback, while others are not. For example, certain size illusions, such as the Ponzo Illusion, show strong interocular transfer, indicating the involvement of higher visual areas (Song, Schwarzkopf, and Rees, 2011). On the other hand, other illusions, such as the Ebbinghaus Illusion, show weak
interocular transfer, which would be consistent with an earlier V1 representation (Song et al., 2011). Furthermore, patient work done by Goodale et al. implicates the involvement of the ventral stream in making judgments (1991). Interestingly, a patient with ventral damage in lateral occipital and parasagittal occipitoparietal regions was unable to make discriminations between objects based on size, but was still capable of performing appropriate grasping motions based on object size (Goodale, 1991). Further work done by Berryhill et al. implicates the involvement of dorsal areas in judging size and distance (2009). Specifically, a patient with parietal damage showed difficulties in judging both the size of objects as well as their distance from them (Berryhill et al., 2009). These observations imply the existence of multiple mechanisms coding for different aspects of perceived object size in the brain.

1.4 Unanswered Questions about the representation of perceived size

Although great progress has been made in elucidating the neural basis of size perception, there are a number of fundamental questions that remain unanswered: Which regions of visual cortex represent the perceived size of an object? What are the feedforward and feedback interactions that underlie the neural representation of object size? What are the domain specific and domain general characteristics of the neural representation of object size? By addressing these questions, we can move closer to a complete understanding of how object size is represented in the brain.
We approach answering these questions in the following ways: In order to more completely examine areas that might represent the perceived size of an object, we have used anatomical and functional MRI to map out a comprehensive collection of regions of interest (ROIs) within the visual system beyond what has already been examined in the previously described studies. We then are able to source localize neural activity associated with perceived size differences to these various ROIs. To address the potential feedback and feedforward mechanisms responsible for processing perceived object size, we record participant's neural data using High Density Electroencephalography (HD EEG), while they view stimuli whose perceived size has been altered. Given the higher temporal resolution of EEG recording techniques, we can see when activity differences are occurring. We are also able to preserve locational information by source localizing EEG activity associated with perceived size differences to individual ROIs.

In order to address the domain general and domain specific characteristics of perceived size processing in the brain, we recorded our data while participants viewed targets in the context of two different perceived size altering illusions, a depth illusion and the Ebbinghaus illusion. We are thus able to identify areas that represent perceived size in one condition or the other (domain specific), as well as those that appear to represent perceived size in both conditions (domain general). These domain general areas are candidates for areas representing the size of the object, while those which are domain specific may represent integrative processes particular to the context being
integrated with the target object (e.g. depth cues, size contrast cues etc.). In analyzing our data, we make use of both univariate analyses examining magnitude differences in the signals associated with different perceived sizes, paralleling work that has been done in fMRI research (Fang et al., 2008; Murray et al., 2006; Ni et al., 2014; Pooresmaeili et al., 2013; Sperandio et al., 2012; Sterzer and Reese, 2006), as well as Multivariate Pattern Analyses (MVPA) to examine differences in the pattern of activity that may be associated with size percepts (Norman et al., 2006).

Our results show that we can effectively classify physical and perceived size differences in the context of depth and Ebbinghaus illusions at both the electrode and source localized levels. Furthermore, classification is possible throughout multiple visual areas, and displays a pattern of activity across ROIs consistent with both feedforward and feedback processing of perceived size.

2. Methods

2.1 Stimuli

2.1.1 Depth Illusion

Stimuli consisted of white and black checkered spheres presented on an apparent corridor background. Spheres could appear near the apparent front or back of the corridor as shown in Figure 3. Spheres could be one of two sizes (1.5°, 3° radius).
2.1.2 Ebbinghaus Illusion

Stimuli consisted of white and black checkered spheres. Spheres could be one of two sizes (1°, 2° radius). Different radii were used for Ebbinghaus targets to accommodate the size of the large targets and largest surrounding stimuli (Figure 3).

![Figure 3: Experimental Stimuli](image)

Targets and surrounding context used in each trial condition in both experiments.

2.2 Conditions

2.2.1 Depth Illusion

The experiment consisted of four unique conditions: small smaller, small larger, large larger, and large smaller. Smaller conditions were designed to make the targets appear smaller. Larger conditions were designed to do the opposite. In the small smaller condition, participants viewed the smaller sphere at the lower
left portion of the screen where it appeared to be at the front of the corridor. In the small larger condition, participants viewed the smaller sphere at the upper right portion of the screen where it appeared to be at the back of the corridor. In the large larger condition, participants viewed the larger sphere at the upper right portion of the screen where it appeared to be at the back of the corridor. In the large smaller condition, participants viewed the larger sphere at the lower left portion of the screen where it appeared to be at the front of the corridor (Figure 3).

2.2.2 Ebbinghaus Illusion

The experiment consisted of four unique conditions: small smaller, small larger, large larger, and large smaller. Conditions were designed to serve the same function as in the Depth Illusion experiment. In all conditions, participants viewed targets at the center of the screen surrounded by a ring of evenly spaced checkered spheres. In the small smaller condition, the smaller sphere was surrounded by a ring of six spheres. The ring had a radius of 6° and each sphere in the ring had a radius of 3°. In the small larger condition, the smaller sphere was surrounded by a ring of eight spheres. The ring had a radius of 1.7° and each sphere in the ring had a radius of .55°. In the large larger condition, the larger sphere was surrounded by a ring of eight spheres. The ring had a radius of 3.4° and each sphere in the ring had a radius of 1.1°. In the large smaller condition, the larger sphere was surrounded by a ring of six spheres. The ring had a radius of 12° and each sphere in the ring had a radius of 6° (Figure 3).
2.3 Trial Progression

2.3.1 Depth Illusion

At the beginning of each trial, participants fixated a fixation point on an otherwise neutral gray screen for 500-700ms as the point moved from center screen to either the bottom left, or upper right portion of the screen. At this point, a picture of a corridor filled the screen, while the fixation point maintained its position. After a period of 800-1000ms, a checkered sphere appeared centered on the fixation point. The black and white checkers on the sphere proceeded to exchange locations at a rate of 2 Hz for a total of four exchanges after the initial appearance of the sphere. Five hundred milliseconds after the final exchange, participants then viewed the fixation point in isolation for 50ms before receiving a prompt to advance to the next trial (Figure 4). It must be noted that the checker exchanges used to drive a visually evoked potential constitute contrast reversals and the neural activity we suppose to be related to differences in perceived size is being driven by these changes in contrast.

2.3.2 Ebbinghaus

At the beginning of each trial, participants fixated a fixation point, on an otherwise neutral gray screen, for 500-700ms at the center of the screen. At this point, a ring of checkered spheres (but not the target) appeared on the screen, while the fixation point maintained its position. After a period of 800-1000ms, a checkered sphere appeared centered on the fixation point. The black and white checkers
on the sphere proceeded to exchange locations at a rate of 2 Hz for a total of four exchanges after the initial appearance of the sphere. Five hundred milliseconds after the final exchange, participants then viewed the fixation point in isolation for 50ms before receiving a prompt to advance to the next trial.

Figure 4: Trial Progression
In the Depth experiments, participants first viewed a fixation point in isolation as it moved to its appropriate position for 500-700ms. The context was then presented for 800-1000ms before the stimulus appeared.
2.4 General Methods

2.4.1 Participants

Participants consisted of ten instructors and graduate students at the University of Nevada, Reno (two female, ages 25-46). Eight of these participants had their data source localized (one female, ages 25-46). All participants reported normal, or corrected to normal vision and were right handed. Participants were instructed to maintain fixation at all times during the experiment, except when taking breaks, and to minimize all movements during stimulus presentations.

2.4.2 Apparatus and Display

All stimuli were generated and presented using the Psychophysics Toolbox (Brainard, 1997) for MATLAB (Mathworks Inc., Natick, MA). Stimuli were displayed on a Mitsubishi Diamond Pro270 (20in, 1024 x 768) with a refresh rate of 85Hz. The stimulus computer was a 2.6GHz Intel Core i7 (4GB 1600 MHz DDR3 RAM) Mac Mini with an Intel HD 4000 graphics processor (768MB of DDR3 SDRAM). Behavioral responses were recorded via keyboard button presses.

2.4.3 EEG Data Acquisition

EEG data were continuously recorded during the experiments using a 256 channel HydroCel Geodesic Sensor Net via a Net Amps 300 amplifier (Electrical Geodesics Inc., Eugene, OR) at a sampling rate of 1000 Hz. Individual trial
markers were time locked to each of the checker exchanges, but not the initial appearance of spheres. In this way, 800 checker exchanges, or individual trials, were marked (200 for each unique condition). Data were collected and processed using Netstation 5.0(1) software.

2.4.4 Data Analysis

2.4.4.1 Data Processing

The first stage of processing was performed using NetStation Tools (Electrical Geodesics Inc., Eugene, OR). Raw EEG data were first high-pass filtered at .5 Hz and low-pass filtered at 50 Hz using a finite impulse response (FIR) filter. The continuous EEG data were then segmented such that each segment contained 100 seconds of pre-stimulus baseline and 500 ms of post-stimulus activity. Artifact rejection routines were applied to the segmented EEG data to identify segments including common artifacts. Channels were identified as containing artifacts if the segment contained amplitude values exceeding 200 µV (microvolts). Additionally, segments containing eye blinks with amplitude values greater than 140 µV were rejected prior to further analysis. Finally, segments containing eye movements with amplitude values greater than 55 µV were also discarded. Bad channel replacement was then performed (Electrical Geodesics, Inc, 2003). Finally, the data were rereferenced to the average before being exported to a MATLAB format for further processing (Electrical Geodesics, Inc, 2003). Further processing was all performed using MATLAB (Mathworks Inc.,
At this point, trials were sorted by condition and underwent baseline correction using the 100 milliseconds prior to stimulus onset as the defined baseline period.

2.4.4.2 VEP/MVPA

Averaged waveforms were observed at the electrode corresponding to Oz to confirm that a clear visually evoked potential (VEP) was present in response to stimulus presentation, and make initial comparisons between conditions. Comparisons of VEP waveforms at Oz were also made between large and small target trials for the enhanced condition (large targets made to look larger compared to small targets made to look smaller), diminished condition (large targets made to look smaller compared to small targets made to look larger), and collapsed across enhanced and diminished trials condition. Comparisons were made using a two-tailed t-test. For each participant, multivariate pattern analysis (MVPA) was performed on their EEG data across all 256 electrodes to determine classification accuracy for large vs. small stimuli overall, for large vs. small stimuli in the enhanced condition and diminished condition, and classification accuracy for made to appear larger vs. made to appear smaller stimuli in the large and small conditions. To determine classification accuracy at each time point (with particular attention to 0-500ms after stimulus onset), EEG activity across all 256 electrodes for a sliding window of 51ms centered on the time point of interest (for smoothing purposes) was examined using two separate classification methods. MVPA was used in an attempt to detect differences present in the pattern of
activity across electrodes that might not be evident in amplitude differences in a univariate analysis (Norman et al., 2006). As there are multiple pattern classification techniques, we wanted to determine which would give the clearest representation of the neural activity underlying the representation of object size. After an initial analysis of the differentiability of neural activity underlying the representation of physical size differences in the depth condition using both methods, we determined that Method 1 produced cleaner and more interpretable data.

In Method 1, data were correlated between training and test sets for all conditions at each time point. Training sets were made by taking the average of half of the trials in a condition, and a test set was constructed by taking an average of the remaining half. The absolute value of the difference in EEG waveform amplitude at each time point between the training and test sets was also taken for each electrode, and an average distance was calculated across electrodes. Using this method, each millisecond of the 51ms window of interest was treated as a separate feature for the purposes of the analysis. For each iteration, time points at which the correlations between training and test sets from the same trial type were higher than those for training and test sets from different trial types and at which the absolute value of the difference between the test and training sets was lower for sets of the same trial type were marked as correct. For those trials where only one of these conditions was met, these time points were marked as 50% correct. Averages were taken across trial types and 1000
iterations to build a plot of classification accuracy over time for each classification of interest.

In Method 2, data were classified according to a support vector machine (SVM) analysis. Using this method, individual timepoints in the 51ms sliding windows of interest were averaged together and did not serve as individual features for the purposes of this analysis. Data were analyzed using ten folds, in which the data were divided into ten roughly equal segments. On each fold, nine of the ten segments would serve as the training set, and the remaining set would serve as the test set. To account for the relatively noisy nature of EEG data, data were subaveraged within each segment. In this way, the training set was made of nine observations from each category to be differentiated. The training set thus included one observation for each category to be differentiated. The number of features in the analysis was limited using a principal components analysis (PCA) function that limited the features on each fold, at each time point, to those that accounted for 90% of the observed variability. Accuracy was then averaged over the ten separate folds for each time point. Method 2 was only used to analyze physical size difference data for the Depth Illusion experiment.

2.4.4.3 MRI Apparatus/Scanning Procedure
Anatomical data were acquired for eight of our ten participants. As described previously by Killebrew, Mruczek, and Berryhill (2015), all functional ROI and anatomical data were acquired at the University of California, Davis Imaging Research Center. These data were acquired using a 3T Skyra MRI System
(Siemens Healthcare, Erlangen, Germany) using a 64 channel phased-array head coil. Functional images were obtained using T2* fast field echo, echo planar functional images (EPIs) sensitive to BOLD contrast (TR = 2.5s, TE = 25ms, 32 axial slices, 3.0 mm², matrix size = 80 x 80, 3.5 mm thickness, interleaved slice acquisition, 0.5 mm gap, FOV = 240 x 240, flip angle = 71º). High-resolution structural scans (MPRAGE: 208 sagittal slices, 0.9 mm² in-plane voxel resolution, matrix size = 256 x 256, slice-thickness = 0.95 mm, FOV = 243 x 243 x 187 mm, TE = 4.33ms, TR =10ms, flip angle = 7º) were collected to support reconstruction of the cortical hemisphere surfaces using FreeSurfer (http://surfer.nmr.mgh.harvard.edu, Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999).

2.4.4.4 Retinotopic Mapping

As described previously by Killebrew, Mruczek, and Berryhill (2015), for eight participants, a series of topographic regions of interest (ROIs) on each participant’s cortical surfaces were defined using AFNI (http://afni.nimh.nih.gov/afni/Cox, 1996), SUMA (http://afni.nimh.nih.gov/afni/suma, Saad, Reynolds, Cox, Argall, & Japee, 2004). Standard retinotopic mapping was performed for each participant using a color and luminance varying flickering (4 Hz) checkerboard stimulus (Arcaro, McMains, Singer, & Kastner, 2009; Swisher et al., 2007). Participants performed 8 runs of polar angle mapping and 2 runs of eccentricity mapping.
For half of the polar angle mapping runs, the moving wedge covered a 45° angle and spanned from 0.5° to 13.5° eccentricity; for the other half, the wedge spanned from 8° to 13.5° eccentricity. The later trials were included to limit stimulation of the central portion of visual space, since voxels in higher-order topographic regions may be stimulated by all wedge positions, decreasing the spatial specificity of the signal during polar angle mapping (Dumoulin & Wandell, 2008). Polar angle mapping runs were comprised of eight 40 s stimulus cycles (speed of 9°/s) with a 20 s blank period at the beginning of each run. Consecutive runs alternated between clockwise and counterclockwise wedge rotation.

For the eccentricity mapping runs, the stimulus was a moving ring with a 1.7° width along its eccentricity. Over a single cycle, the ring traversed the space between 0° and 13.5° eccentricity from fixation. All eccentricity mapping runs were comprised of eight 40 s stimulus cycles (speed of 9°/s) with a 10 s blank period interleaved between cycles and a 20 s blank period at the beginning of each run. The addition of a blank period between cycles avoids the potential ambiguity in discerning central fovea and far periphery representations when the ring stimulus immediately wraps around upon reaching the near or far extreme of the stimulus extent. Consecutive runs alternated between expanding and contracting ring movements.

For both polar angle and eccentricity mapping, participants were instructed to maintain fixation on a central spot while covertly attending to the wedge or ring stimulus and to report via a button press the onset of a uniform
gray patch in the stimulus that served as the target. Targets appeared, on average, every 4.5 s.

As described in Erlikman, Gurariy, Mruczek, and Caplovitz (submitted) polar angle and eccentricity representations were extracted from separate runs using standard phase encoding techniques (Bandettini, Jesmanowicz, Wong, & Hyde, 1993; Engel, Glover and Wandell, 1997; Sereno et al., 1995). For each participant, we defined a series of topographic ROIs on each cortical hemisphere surface using AFNI/SUMA (Figure 5). Borders between adjacent topographic areas of the intraparietal sulcus were defined by reversals in polar angle representations at the vertical or horizontal meridians as described in Wang et al. (2015) using standard definitions (Amano et al., 2009; Arcaro, McMains, Singer, & Kastner, 2009; Brewer, Liu, Wade, & Wandell, 2005; DeYoe et al. 1996; Engel et al. 1997; Press et al., 2001; Kastner et al., 2007; Konen and Kastner, 2008; Larsson and Heeger, 2006; Sereno et al. 1995; for review, see Silver and Kastner, 2009; Wade, Brewer, Rieger, & Wandell, 2002; Wandell and Winawer, 2011). Topographic areas mapped for the purpose of these experiments were done for each hemisphere and were as follows: V1 (Primary Visual Cortex), LO1 (Lateral Occipital), LO2, TO1 (Temporal Occipital), TO2, V3a, V3b, IPS0 (i.e., V7), IPS1 (Intraparietal Sulcus), IPS2, IPS3, IPS4, IPS5, V2v (Secondary Visual Cortex, ventral), V2d (dorsal), V3v (ventral), V3d (dorsal), hV4 (Human Area V4), VO1 (Ventral Occipital), VO2, PHC1 (Parahippocampal Cortex), PHC2.
2.4.4.5 Source Localization

Source localization was performed for the eight participants with anatomical and ROI information available. This was accomplished using a noise-normalized estimate (sLORETA, standardized Low Resolution brain Electromagnetic TomogrAphy) (Pascual-Marqui, Esslen, Kochi, & Lehmann, 2002; Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011). Using each participant’s individual anatomy file, and a BEM headmodel generated in Brainstorm (Gramfort et al., 2010; Kybic et al., 2005; Tadel et al., 2011), sources were computed based on the averaged EEG data for each condition.

2.4.4.6 Source Localized Difference Magnitudes

A difference wave for the average perceived size difference (across small and large targets) was calculated for each electrode before the resulting difference waves were source localized in Brainstorm (Tadel et al., 2011). Mean Dipole waveforms were then exported for each ROI. As part of the averaging process within ROIs, the orientation of certain dipoles may be flipped in order to minimize effects of the topography of the underlying cortical surface (Tadel et al., 2011). Waveforms were averaged across hemispheres and particular ROIs as follows: V1, V2d, and V2v to form V12, LO1 and LO2 to form LO, TO1 and TO2 to form TO, V3a and V3b to form V3ab, IPS0, IPS1 and IPS2 to form IPp (posterior), IPS3, IPS4, and IPS5 to form IPa (anterior), V3v and V3d to form V3, VO1 and VO2 to form VO, and PHC1 and PHC2 to form PHC (Figure 5A). Average difference waves for each ROI were then baseline corrected.
2.4.4.7 Source Localized MVPA

MVPA for source localized participant data was run in the same way as previously described in method one, with the following differences: classification accuracies were calculated for each ROI separately (collapsed across hemispheres, such that a single MVPA was performed for each ROI: V12, V3, LO, V3ab, IPp, IPa, TO, hV4, VO, and PHC), and dipole amplitudes were used as features in place of electrodes. Furthermore, given the results of the VEP MVPA, classification accuracy was only calculated for perceived size differences (targets of the same physical size made to look larger vs. made to look smaller).

Figure 5: Regions of Interest and Visual Area Classifications
(A) ROIs analyzed after collapsing across particular ROIs (also collapsed across hemispheres) (note that the hFEF was also localized, but not used in our analyses).
(B) Areas of the visual system defined as early, mid-level, dorsal, and ventral.
2.4.4.8 No Target Control

Each experiment was run a second time, but with the alteration that while the context, timing, and participant actions remained exactly the same, a target was never presented. This control was performed to establish the potential contributions, if any, of the context separate from the target to any observed differences in neural activity across our various conditions.

2.4.5 Statistical Analysis

For MVPA analyses, times at which classification accuracy was greater than the average classification during baseline (or chance, whichever was higher) were calculated using a one-tailed t-test. Comparisons were made to the average of baseline activity to account for any effects that might be due to anticipation as stimuli were presented in a temporally predictable manner. A two-tailed t-test was used to determine if there were significant differences between the classification accuracies for two conditions. For source localized difference magnitudes, a one-sample t-test was run comparing the difference scores for each time point (averaged over a 51ms window 25ms before and 25ms after the time point) to the average difference magnitudes of the baseline period for each ROI. All resulting p values were compared to an alpha of 0.05.
3. Results

3.1 Physical Size Differences

As a first step in our analyses, we sought to establish that neural activity associated with the perception of physical size differences was significantly differentiable before any attempt was made to differentiate neural activity for perceived size differences.

3.1.1 Depth Illusion

3.1.1.1 VEP at Oz

As an initial univariate analysis, we examined the VEPs associated with each trial condition at Oz. Results for physical size differences are displayed in Figure 6. For all comparisons, a period of significant difference was found between 100 and 200ms post stimulus onset. When the comparison is made between large and small trials collapsed across larger and smaller conditions, we find significance between 126 and 146ms (Figure 6, B). In the enhanced conditions, we see significance between 121 and 145ms (Figure 6, C). In the diminished conditions, we see significance between 148 and 178ms (Figure 6, D). In all no target conditions, there was no clear VEP, and waveform amplitudes were relatively small (Figure 7).
Figure 6: VEP Results for Physical Size Differences: Depth
(A) Average VEP for all conditions at Oz.
(B) Significant amplitude difference at ~100-200ms between large and small targets.
(C) Earlier significant amplitude difference between enhanced conditions
(D) Later significant amplitude difference between diminished conditions
Figure 7: VEP Results for No Target Conditions: Depth
Lower overall waveform amplitude and no definite VEP in no target conditions.
3.1.1.2 MVPA/Method 1

To establish whether there were significant differences in the pattern of neural activity across all 256 electrodes, we performed an MVPA analysis taking the 256 electrodes as features.

Results for classifying large vs. small stimuli are displayed in Figure 8. In all conditions, large and small trials could be classified with accuracy significantly greater than chance around 80-100ms post-stimulus onset. Contrary to previous predictions, classification in the enhanced condition was never significantly greater than that for the diminished condition (Figure 8, D). One might expect that classification accuracy would be greater when differentiating a large stimulus made to look larger from a small stimulus made to look smaller, as opposed to when differentiating a large stimulus made to look smaller from a small stimulus made to look larger. In fact, there was a brief period where classification accuracy was higher for the diminished condition. In all no target conditions, classification accuracy was never greater than chance during the post-baseline period (Figure 9).
MVPA: Depth
Method 1: Correlation/Absolute Distance

Figure 8: MVPA Results for Physical Size Differences: Depth
(A-C) Significant classification possible for overall, enhanced, and diminished physical size difference conditions around 100-200ms.
(D) Classification of diminished differences is significantly greater than that for enhanced differences at ~50ms.
3.1.1.3 MVPA/Method 2

Results for Method 2 are displayed in Figure 10. Once again, areas of significant classification could be found in all conditions. When comparing diminished and enhanced conditions, it was once again found that, perhaps counter intuitively, there were periods where diminished classification performance was significantly greater than enhanced classification performance (Figure 10, D). Given the relative noisiness of SVM results as compared to those using Method 1, and the

Figure 9: MVPA Results for Physical Size Differences: Depth No Target
No periods of significant classification accuracy for no target conditions.
successful classification achieved with Method 1, Method 2 was not used for any further analyses.

Figure 10: SVM Results for Physical Size Differences: Depth
(A-C) As with Method 1, significant classification is possible between ~100-200ms. However, these periods are briefer for enhanced conditions.
(D) Diminished classification accuracy is again significantly higher than enhanced classification accuracy.
3.1.2 Ebbinghaus Illusion

3.1.2.1 VEP at Oz

VEP results are displayed in Figure 11 for comparisons made between large and small conditions. Short time periods of significance can be found throughout the timecourse for all comparisons between 100 and 200ms post stimulus onset. In all no target conditions, there was no clear VEP, and waveform amplitudes were relatively small (Figure 12).

3.1.2.2 MVPA/Method 1

Results for classifying large vs. small stimuli are displayed in Figure 13. In all conditions, large and small trials could be classified with accuracy significantly greater than chance around 100 to 200ms post-stimulus onset. Contrary to previous predictions, classification in the enhanced condition was never significantly greater than that for the diminished condition (Figure 13, D). In the no target conditions, classification accuracy was never greater than chance (Figure 14).
Figure 11: VEP Results for Physical Size Differences: Ebbinghaus
(A) Average VEP for all conditions at Oz.
(B) Significant amplitude difference at ~100-200ms between large and small targets.
(C) Earlier significant amplitude difference between enhanced conditions
(D) Later significant amplitude difference between diminished conditions
Figure 12: VEP Results for No Target Conditions: Ebbinghaus
Lower overall waveform amplitude and no definite VEP in no target conditions.
Figure 13: MVPA Results for Physical Size Differences: Ebbinghaus

(A-C) Significant classification possible for overall, enhanced, and diminished physical size difference conditions around 100-200ms.

(D) No significant difference in classification accuracy for diminished and enhanced conditions.
Perceived Size Differences

Given that we can classify the neural activity associated with physical size differences with significant accuracy, we next sought to examine whether significant neural activity differences could be observed for perceived size differences. As our three main questions address questions related to perceived size, further analyses addressing the neural activity associated with physical size differences were not performed.

Figure 14: MVPA Results for Physical Size Differences: Ebbinghaus No Target
No periods of significant classification accuracy for no target conditions.

3.2 Perceived Size Differences
3.2.1 Electrode Level Analyses

3.2.1.1 Depth Illusion

3.2.1.1.1 VEP at Oz

Data for perceived size conditions are depicted in Figure 15. In this case, significance is found at Oz for distinguishing larger and smaller large targets, and only briefly for distinguishing small targets made to look smaller from those made to look larger. In all no target conditions, there was no clear VEP, and waveform amplitudes were relatively small (Figure 7).

**Figure 15: VEP Results for Perceived Size Differences: Depth**

(A) Significant amplitude difference for large targets made to look larger vs. large targets made to look smaller at ~100-200ms.

(B) Brief significant amplitude difference for small targets made to look larger vs. small targets made to look smaller at ~100-200ms.
3.2.1.1.2 MVPA/Method 1

Classification accuracy for same sized targets made to appear differently sized is shown in Figure 16. Classifying perceived size differences was possible with significant accuracy overall and for large stimuli (at around 90-100ms), but not for small stimuli (Figure 16, A-C). Across all conditions, it appeared that physical size differences could be classified with significantly greater accuracy than perceived size differences (Figure 16, D-F). In all no target conditions, classification accuracy was never greater than chance during the post-baseline period (Figure 17).
Figure 16: MVPA Results for Perceived Size Differences: Depth

(A-C) Significant classification accuracy possible for overall perceived size and large larger vs. large smaller stimuli, but not small smaller vs. small larger stimuli, at ~100-150ms.

(D-F) Classification accuracy for physical size differences is significantly greater than that for perceived size differences.
Figure 17: MVPA Results for Perceived Size Differences: Depth No Target
Significant classification accuracy only found during baseline period.
3.2.1.2 Ebbinghaus Illusion

3.2.1.2.1 VEP at Oz

When comparisons are made between larger and smaller conditions (as shown in Figure 18), significance is no longer found around the P100. Once again, in all no target conditions, there was no clear VEP, and waveform amplitudes were relatively small (Figure 12).

![VEP Data (Oz): Ebbinghaus](image)

Figure 18: VEP Results for Perceived Size Differences: Ebbinghaus
No significant amplitude differences near the peak of the VEP in original or random label conditions.

3.2.1.2.2 MVPA/Method 1

Classification accuracy for same sized targets made to appear differently sized is shown in Figure 19. Classification accuracy for differentiating perceived size differences was only significant in the small stimulus condition and this period of
significant classification was very early and brief. (Figure 19, A-C). Once again, it appeared that physical size differences could be classified with significantly greater accuracy than perceived size differences across all conditions (Figure 19, D-F). However, this difference was only significant in comparison to the large stimulus condition. In the no target conditions, classification accuracy was only ever greater than chance in the small larger vs. small smaller condition (Figure 20).
Figure 19: MVPA Results for Perceived Size Differences: Ebbinghaus

(A-C) Classification accuracy is only significant in the small vs. small larger condition and only briefly and fairly early.

(D-F) Classification accuracy was significantly greater for physical size differences as compared to perceived differences for large targets, but not in other conditions.
Figure 20: MVPA Results for Perceived Size Differences: Ebbinghaus No Target
Significant classification accuracy found early in small smaller vs. small larger condition.
3.2.2 Source Localized Analyses

Having established that it is possible to identify neural correlates of perceived size differences at the electrode level, in order to answer our questions about where, and when in the brain these correlates are represented, we performed similar analyses at a source localized level.

3.2.2.1 Depth Illusion

3.2.2.1.1 Source Localized Difference Magnitude

The magnitude of the dipole activity for perceived size differences was significantly different than the average level during baseline at various time points in areas V3, V3ab, and hV4 (Figure 21). The earliest time, post stimulus onset, at which a significant difference magnitude was observed in each ROI, is shown in Figure 22. Significant classification was possible in V12 at 15ms, hV4 at 29ms, V3 at 159ms, and V3ab at 181ms. Significance was also found in the no target condition in V3, LO, IPp, IPa, TO, hV4 and VO (Figure 23).
Source Localized Difference Magnitudes: Depth/Perceived Differences

Figure 21: Univariate Analysis of Source Localized Difference Magnitudes: Depth

Periods of significant magnitude differences can be found in V12, V3, V3ab, and hV4 in the post baseline period.
Figure 22: Point of Earliest Significant Difference Magnitude for Univariate Analysis: Depth
Areas in which significant classification accuracy was never present are marked in gray.
Source Localized Difference Magnitudes: Depth/Perceived Differences No Target

Significant magnitude differences can be found in V3, LO, IPp, IPa, TO, hV4 and VO in the post baseline period in the no target condition.

Figure 23: Univariate Analysis of Source Localized Difference Magnitudes: Depth No Target
3.2.2.1.2 Source Localized MVPA

Periods of significant classification accuracy for perceived size differences in each ROI are shown in Figure 24. Significant classification accuracy was possible in areas V12, V3, IPp, IPa, and TO. The earliest time, post stimulus onset, at which significant classification was possible in each ROI, is shown in Figure 25. Significant classification was possible in IPp at 67ms, TO at 102ms, IPa at 108ms, V3 at 120ms, and V12 at 138ms. By comparison, no target conditions showed fewer areas where significant classification took place, overall lower classification accuracy, and shorter periods of significant classification (Figure 26).
Figure 24: MVPA Results for Source Localized Perceived Size Difference Conditions: Depth
Periods of significant classification accuracy can be found in V12, V3, IPp, IPa, and TO in the post baseline period.
Figure 25: Point of Earliest Significant Classification Accuracy for MVPA Analysis: Depth
Areas in which significant classification accuracy was never present are marked in gray.
Figure 26: MVPA Results for Source Localized Perceived Size Difference Conditions: Depth No Target

Significant classification accuracy was possible in IPp in the no target condition.
3.2.2.2 Ebbinghaus Illusion

3.2.2.2.1 Source Localized Difference Magnitude

The magnitude of the dipole activity for perceived size differences was significantly different than the level during baseline at various time points in areas V12, V3, IPa, and PHC in the post baseline period (Figure 27). The earliest time, post stimulus onset, at which a significant difference magnitude was observed in each ROI, is shown in Figure 28. Significant classification was possible in V12 at 7ms, V3 at 27ms, IPa at 167ms, and PHC at 415ms. Significance was also found in the no target condition in LO and PHC (Figure 29).
Figure 27: Univariate Analysis of Source Localized Difference Magnitudes: Ebbinghaus

Periods of significant magnitude differences can be found in V12, V3, IPa, and PHC in the post baseline period.
Figure 28: Point of Earliest Significant Difference Magnitude for Univariate Analysis: Ebbinghaus

Areas in which significant classification accuracy was never present are marked in gray.
Figure 29: Univariate Analysis of Source Localized Difference Magnitudes: Ebbinghaus No Target

Periods of significant magnitude differences can be found in LO, and PHC in the post baseline period.
3.2.2.2 Source Localized MVPA

Periods of significant classification accuracy for perceived size differences in each ROI are shown in Figure 30. Significant classification accuracy was possible in areas V3, LO, V3ab, IPp, IPa, hV4, VO, and PHC. The earliest time, post stimulus onset, at which significant classification was possible in each ROI, is shown in Figure 31. Significant classification was possible in PHC at 7ms, V3Ab at 58ms, IPp at 91ms, VO at 92ms, LO at 112ms, hV4 at 182ms, IPa at 196ms, and V3 at 321ms. Once again, while areas were found where classification accuracy was significant for no target conditions, fewer of areas showed significance in these conditions (Figure 32).
Figure 30: MVPA Results for Source Localized Perceived Size Difference Conditions: Ebbinghaus
Periods of significant classification accuracy can be found in V3, LO, V3ab, IPp, IPa, hV4, VO and PHC in the post baseline period.
Figure 31: Point of Earliest Significant Classification Accuracy for MVPA Analysis: Ebbinghaus
Areas in which significant classification accuracy was never present are marked in gray.
Source Localized MVPA: 
Ebbinghaus/Perceived Differences No Target

Figure 32: MVPA Results for Source Localized Perceived Size Difference Conditions: Ebbinghaus No Target
Significant classification accuracy was possible in V3, LO, IPp, IPa, and TO in the no target condition.
4. Discussion

The preceding results allow us to address aspects of all three questions originally posed in our introduction: Which regions of visual cortex represent the perceived size of an object? What are the feedforward and feedback interactions that underlie the neural representation of object size? What are the domain specific and domain general characteristics of the neural representation of object size?

4.1 Which regions of visual cortex represent the perceived size of an object?

As suggested by our source localized analyses, early, mid-level, dorsal, and ventral visual areas (Figure 5B) may play a role in processing the perceived size of objects. Between our Ebbinghaus and depth illusion conditions, we are able to classify perceived size differences with significant accuracy, and/or identify significant difference magnitudes at some point in all ROIs of interest. It must be noted that periods of significance found for certain ROIs were in the pre-50ms post stimulus onset range. Given the impossibility of neural representations being processed with this speed, the contributions of these areas to perceived size are questionable, at least at these particular points in time. When a more conservative analysis is performed identifying only ROIs in which significant differences are found at least 50ms after stimulus onset, the order of areas showing significant classification accuracy or difference magnitude changes slightly (Figure 33). However, all ten areas show significance at some point between our two experiments whether the analysis is more or less conservative.
and it seems clear from our results that processing of perceived size is at least distributed throughout the visual system.

While the effects of perceived size differences have been principally observed in V1 for many studies using brain imaging techniques, our results indicate that even when significant classification accuracy was possible in early visual areas, these were not the sites where the classification accuracy is the highest, or the difference magnitude is greatest (Fang et al., 2008; Murray et al., 2006; Ni et al., 2014; Pooresmaeili et al., 2013; Sperandio et al., 2012; Sterzer and Reese, 2006). While these differences may not be significant, this is still somewhat surprising, given that even when correlates of perceived size were found outside of V1 in previous MRI studies (Pooresmaeili et al., 2013), they were generally of lesser magnitude.

How do these results relate to the debate concerning multiple representations for perceived and physical size? Previous studies had posited that illusory object size is represented in the ventral-stream, while physical, or veridical, size is represented in the dorsal-stream (Haffenden et al., 2001). Given that we see significant classification accuracy throughout all levels of the visual system, and thus in both streams, our results do not support this supposition. If anything, the processing of perceived size due to contextual depth cues may be confined largely to the dorsal-stream and early visual areas. While not definitive support for the existence of a unified perception and action system regarding object size, our results suggest that there is no clear/clean dichotomy to be found.
Figure 33: Point of Earliest Significant Classification Accuracy/Difference Magnitude: Conservative Estimate. Areas not showing significant classification accuracy/difference magnitudes after 50ms have been omitted.
4.2 What are the feedforward and feedback interactions that underlie the neural representation of object size?

When we examine the apparent temporal ordering of processing associated with perceived size differences, we see differences based on the nature of the analysis. In our less conservative analyses, univariate analyses show significant difference magnitudes in earlier visual areas in both the depth and Ebbinghaus conditions before significance in later visual areas, suggesting potential feedforward mechanisms (Figures 22 & 28). However, when MVPA analyses are performed on the same data, significant classification accuracy is instead possible first in later visual areas, suggesting the activity of potential feedback processes (Figures 25 & 31). When the data are examined under more conservative constraints (as described above), the ordering of first significance occurrence seems to indicate the presence of feedback processes in the case of the Ebbinghaus univariate analysis for representing perceived size (Figure 33).

Given the diversity of our results as indicated by our various analyses, it seems likely that both feedback and feedforward mechanisms are at play in representing perceived size differences. Furthermore, as indicated in Table 1, significant classification accuracy/difference magnitudes could be found in the same ROI at different times. This might be indicative of feedforward and feedback mechanisms working through the same ROIs at different points. It is also somewhat instructive that one can identify different areas displaying significance when measuring magnitude (univariate), or pattern (MVPA) related differences.
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<td>V3ab</td>
<td>58-169</td>
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Table 1: Periods of Significant Classification Accuracy/Difference Magnitude: Conservative Estimate
Time periods where perceived size could be significantly differentiated in the various ROIs. Multiple areas had multiple times at which there was a period of significance.
4.3 What are the domain specific and domain general characteristics of the neural representation of object size?

In differentiating domain general and domain specific characteristics, we are referring to characteristics of the processes that represent object size that may be shared regardless of how an object’s perceived size is changed (general), and those that may only make a contribution when an object’s perceived size is altered by a particular type of context (specific). It is possible that any similarities in areas implicated in processing perceived size in multiple contexts may represent areas concerned with representing an object’s size, while those that are only implicated in specific contexts may be involved in constructing the object’s perceived size. Our results seem to indicate that perceived size is processed differently depending on the context that led to the perceived size change, specifically in regards to context elements altering perceived depth as opposed to those leading to size contrast and size assimilation (as found in the Ebbinghaus illusion). First, the highest significant classification accuracy (as compared to average baseline classification accuracy) can be found in different areas of the visual system (Depth: IPp; Ebbinghaus: V3ab). Second, significant classification accuracy/difference magnitudes were found in a greater number of areas in the context of the Ebbinghaus illusion (9), as compared to the Depth illusion context (7). Thus, it appears that the processing of perceived size differences is more widely distributed in the case of the Ebbinghaus illusion.

It must be noted that there were various systematic differences between our Depth and Ebbinghaus conditions. For one, participants maintained central
fixation throughout the Ebbinghaus experiments, while they fixated the upper right, or lower left of the screen in Depth experiments. Furthermore, size differences for the large and small targets were different between the Depth and Ebbinghaus conditions in order to accommodate the largest targets and inducers in the Ebbinghaus experiments. While these may be contributing factors to differences present in our data, it must be noted that in our no target conditions, where these factors, but not the targets, are still present, we do not observe the same differences in these apparent domain specific ROIs (Figures 23, 26, 29 and 32). This lends credence to the supposition that differences observed here are indeed due to processing unique to integrating targets with their particular context.

Areas V12, V3, V3ab, IPp, IPa, and hV4 were implicated in processing perceived size differences induced by both depth illusion and Ebbinghaus contexts. All this points to at least some domain general characteristics of the neural representation of perceived size. However, it must be noted that significant classification accuracy/difference magnitude measures are not necessarily present at the same time points in the same areas across conditions. Thus, there appear to be many domain specific characteristics of the neural representation of perceived object size.

The involvement of early visual areas such as V1 and V2 in processing perceived size was replicated in both illusions (Fang et al., 2008; Murray et al., 2006; Pooresmaeili et al., 2013; Sperandio et al., 2012; Sterzer and Reese, 2006). Further, in MRI research examining the role of V1 in representing
perceived size in the context of Ebbinghaus and size adaptation illusions, it was suggested that V1 plays a role not simply in encoding the results of other perceived size rescaling processes, but in the generation of such rescaling (Kreutzer, Weidner, & Fink, 2015). This may explain why we find the involvement of V12 in processing perceived size in both contexts. Furthermore, it may explain why we would see evidence of feedforward processing in constructing perceived size representations.

The significant classification accuracy found in V3ab in both conditions may be indicative of the necessity of processing global form in order to produce perceived size changes. This would fall in line with a study indicating that the processing of the global structure of glass patterns produced significant power changes in V3a as measured by magnetoencephalography (MEG) (Swettenham, Anderson, & Thai, 2010). Similarly, MRI research correlating brain activity with size perception in the context of the moon illusion has indicated that area V3v may be involved in integrating retinal size with contextual information (Weidner et al., 2014), as would be necessary in the context of both Ebbinghaus and depth illusions. Such integration taking place in later visual areas such as V3, and V3ab may be necessary before feeding back into earlier visual areas such as V1 for encoding.

It should also be noted that areas V1, V2, and V4 have been implicated in processing perceived size based on disparity differences (Kreutzer et al., 2015, Thomas, Cumming, & Parker, 2002; Umeda, Tanabe, & Fujita, 2007). While there were no disparity differences between our various targets in any condition,
this does highlight the potential role of these areas in constructing perceived size from depth cues. In particular, given the demonstrated role of V4 in integrating contextual features to construct percepts related to color constancy, it would not be unreasonable to suppose that it may perform a similar function in constructing size constancy (Kreutzer et al., 2015; Roe et al. 2012).

4.4 What do we know?

We set out to characterize the neural representation of perceived size both in regards to where and when it is represented in the human visual system. At this point, a few facts are clear: Perceived size is represented throughout the visual system, not strictly, or even principally in early visual areas such as V1, or in the ventral-stream. Perceived size is not processed in a strict feedforward fashion originating in early visual areas and then propagating to later visual areas. And finally, perceived size effects produced by different contexts appear to have both domain specific and domain general characteristics.

4.5 What does this tell us?

While our results clarify many outstanding questions regarding the processing of perceived object size, we feel it is reasonable to make some suppositions on the nature of visual processing in general based on our findings. First, our results fall in line with previous research showing distributed processing of visual stimuli (Berryhill et al., 2009; Hupe et al., 1998; Pooresmaeili et al., 2013). Our results once again highlight the importance of interactions between
multiple visual areas in constructing our representation of the visual world. Our results also indicate that such a distribution is not necessarily propagated strictly from earlier to later visual areas. And finally, even when the perceived result is the same (e.g. a target is made to appear a different size) the processing mechanisms within our visual system may still be quite different if the contextual stimuli leading to that result are not the same (e.g. depth cues vs. size contrast/size assimilation). As indicated, these may be general truths about our visual system, and not just in regards to processing perceived size.

How might these conclusions apply to general brain function? One might suppose that assuming these same principles hold true in all areas of brain processing is a logical step. However, given differences that have been demonstrated between the processing capabilities of our different sensory systems alone, this may be a dangerous supposition to make out of hand. For example, research has shown that while our visual system dominates when processing spatial information, visual perceptions can be altered by conflicting auditory inputs (Botvinick & Cohen, 1998; McGurk & MacDonald, 1976; Shams, Kamitani, & Shimojo, 2000). The rubber hand illusion demonstrates the dominance of visual processing for spatial information over our proprioceptive and touch senses, as participants perceive the touches they feel as coming from a fake hand on the table when the fake hand and their own hidden hand are touched simultaneously (Botvinick & Cohen, 1998). On the other hand, when visual information is presented quickly and paired with auditory information, the available auditory information may alter the visual percept. For example, when a
brief flash of light is paired with two quick tones, participants perceive two flashes instead of one (Shams, Kamitani, & Shimojo, 2000). Given such existing demonstrations of differences between various sensory processing modalities, we may just as well not presume to draw conclusions about other processing modalities within the brain based on the apparent functioning of the visual system. In any case, further testing of similar questions in other brain functioning modalities would be appropriate before drawing any strong conclusions.

4.6 The representation of physical size differences

As a necessary first step in conducting our study, we wanted to determine that we could decode the neural activity associated with physical object size differences before attempting to decode those associated with perceived size differences. As demonstrated by our VEP data and MVPA performed at the electrode level, we were able to do so with relatively high accuracy. A prediction was made early on that physical size differences should be classified with greater accuracy should they be enhanced (larger targets are made to look larger and then compared to small targets made to look smaller). However, somewhat surprisingly, our results have indicated that classification accuracy for differentiating neural activity associated with large vs. small targets was not any greater when the perceived differences between targets were enhanced. However, in spite of our failure to meet this secondary prediction, we were nonetheless able to classify perceived size differences alone with significant accuracy.
4.7 Limitations

While the results of these experiments are informative, they are not without limitations. Just as we have employed EEG techniques to circumvent the temporal resolution issues of fMRI, we must now deal with spatial resolution issues inherent in EEG, even when HD EEG source localization techniques are used. Various studies examining the spatial resolution of EEG source localization indicate that resolution is within the 10mm to 1.1cm range (Cohen & Cuffin, 1991; Cuffin et al., 1991; Cuffin, Schomer, Ives, & Blume, 2001). This somewhat limits the strength of the conclusions we can draw about the particular location of activity associated with processing perceived size in the brain. However, we have been largely conservative in defining our ROIs (collapsing multiple ROIs), and feel that conclusions based on our defined areas of early, mid-level, ventral, and dorsal (Figure 5B) fall reasonably within the spatial resolution capabilities of the source localization of HD EEG.

In making comparisons between targets of different sizes, we have the potential confound of spatial frequency. Namely, the smaller targets have smaller checkers, and thus a higher spatial frequency. Thus, it is possible that results obtained for differentiating targets of different sizes may be due, at least in part, to spatial frequency differences. In making perceived size comparisons, the physical spatial frequencies of the targets are the same, though the perceived spatial frequency of the target may be changed along with its perceived size. Thus, our neural differences observed in our experiments may be representative
of perceived spatial frequency, perceived contrast, and/or perceived size differences.

It must be noted that significant classification found in our no target conditions may be indicative of processing differences based on the physical differences in the surrounding contexts, and not just their interactions with the target stimuli. Thus, the observed neural effects of perceived size difference may be due in part to differences in processing the context and not just the stimulus itself, despite our attempts to eliminate such contaminations by holding all but the stimulus constant during EEG recording. In spite of this potential confound, it is worth noting that when there are overlapping areas between target and no target conditions where significant classification is possible, significant classification is often not seen at the same time points within these areas, suggesting that these effects are not driven purely by physical differences in the surrounding context.

This control also addresses other issues inherent in our different conditions. Different eye positions (Liu et al., 2009) in the depth condition, differences in perceived depth plane, as well as different local features when fixating the top right or bottom left of the corridor may influence the resulting neural signal. However, as previously noted, if such differences were responsible for the observed difference magnitudes and differences in classification accuracy observed in the target present conditions, we would expect to see significance in the same ROIs at similar time points in the no target conditions, which does not seem to be the case (Figures 23, 26, 29 and 32). Furthermore, while the effects of eye position (Liu et al., 2009) may only be apparent when a target change
related VEP is present (and thus not be apparent in the no target condition), when perceived size differences are made, collapsed over large and small targets, eye position is balanced for perceived larger and perceived smaller targets. It is worth noting that eye position may, at least in part, be driving the VEP at Oz for our perceived size differences in the Depth condition. This might also explain the greater amplitude difference and longer period of significance at P1 in the Large Larger vs. Large Smaller Depth condition as compared to the same Ebbinghaus condition.

4.8 Univariate and MVPA analyses

MVPA appears well suited for analyzing HD EEG data at both the electrode and source localized level. In addition to the pattern information gained by using MVPA, at the electrode level, MVPA allows for a compact representation of the differences in brain activity between conditions, while still using all of the available information. In the case of source localized data, MVPA performs this same function, while simultaneously circumventing the issue of dipole orientation (Tadel et al., 2011). Specifically, the orientation of dipoles created via source localizing HD EEG data determines the direction of the resulting activity wave for that dipole. Thus, dipoles with an opposite orientation, but similar activity will tend to cancel one another if an average is taken between the two. A univariate analysis of differences between dipoles in source localized ROIs requires that averages be taken at some point, and questions regarding how to handle dipole orientation inevitably arise (e.g. flipping signs, taking
absolute values). By comparing the patterns across individual dipoles, MVPA does not suffer from the need to make any such decisions.

4.9 Future Directions

Given potential confounds and limitations present within our experimental design (eye position, are we measuring contrast/spatial frequency), there are various ways in which we might conduct this study differently in the future. For one, these experiments could be repeated with isoluminant stimuli to avoid contrast issues. However, it may be difficult to produce a convincing three dimensional depth illusion using only isoluminant stimuli. The potential effects of physical and apparent spatial frequency may also be somewhat mitigated if stimuli were of a solid color, rather than checkered. In regards to eye position, this potential confound could be addressed in a few ways. In one, eye position could be further balanced in the depth condition by making a condition where the apparent front of the corridor is in the upper right of the screen and the apparent back of the corridor is in the lower left of the screen. It would also be possible to alter the context such that the target was always presented at the center of the screen, though the size of the context would have to be made smaller in order to fit these constraints.

A wealth of circumstances and illusions that change the perceived size of an object are present in the visual perception literature (Burton, 2001; Fang et al., 2008; Köhler and Wallach, 1944; Murray et al. 2006; Mruczek et al., 2015; Ni et al., 2014; Pooresmaeili et al., 2013; Thiéry, 1896). Using techniques similar to
those described here, one might test the degree to which each of these may use the same, or different neural processes and architecture to produce perceived size differences. This may further elucidate if the majority of neural processes that produce perceived size differences are indeed domain specific, or if the Ebbinghaus illusion, or depth illusion represent a special case, while other representations of perceived size are handled by a more domain general process.

It may also be worthwhile to more confidently disentangle the effects of interactions between the target and context and the effects of the context itself on the perceived differences in neural activity. While some timecourse information may be lost, use of Steady State Visual Evoked Potential (SSVEP) techniques may be appropriate for assessing the different contributions of target and context to observed neural differences throughout the brain (Müller, Teder-Sälejärvi, & Hillyard, 1998). SSVEPs allow for simultaneous recording of separate signals associated with simultaneously presented stimuli flickering at different frequencies. By measuring the amplitude differences of those particular frequencies between different trial types, one can see changes in activity specific to particular stimuli, even when they are presented at the same time as other stimuli (Müller, Teder-Sälejärvi, & Hillyard, 1998). Furthermore, these differences may also be source localized if recorded using HD EEG.

While the neural correlates of perceived size still remain largely unexplored, a few facts are now apparent. Despite the clear involvement of V1 in representing perceived size, as previously demonstrated (Fang et al., 2008;
Murray et al., 2006; Ni et al., 2014; Pooresmaeili et al., 2013; Sperandio et al., 2012; Sterzer and Reese, 2006), its true role in this representation is unclear. For one, the representation of perceived size is distributed throughout the visual system, and does not appear to result from a feedforward mechanism originating in early visual areas. Furthermore, there does not appear to be one domain general process in the brain for representing perceived size differences resulting from different contextual elements.

In my years as a graduate student at the university of Nevada, Reno, I have developed skills in programming, research, experimental design, data analysis, and teaching under the watch care of my advisor and the various instructors in the UNR department of Psychology. My studies have covered topics including synesthesia, attention, motion perception, size perception, and form/motion interactions. This, combined with my studies in various seminars, has given me a solid grounding in visual perception research, and prepared me to expand my skillset into other realms of psychological research. I feel confident that I am prepared to continue to conduct impactful research, while instructing the next generation of psychologists.
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